



Shipboard microcosm simulations of eddy-driven water mass mixing reveal distinct strategies of prokaryotic and eukaryotic microbiomes

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Abstract. Mesoscale eddies strongly influence marine microbiomes, but their effects on microbiome association and stability remain unclear. We conducted 16-day shipboard microcosm experiments using surface water, DCM water, and 1:1 mixed seawater from eddy-influenced and non-eddy-influenced sites in the Kuroshio Extension. We hypothesized that eddy enhanced nutrients and light would alleviate resource competition, promoting diversity and deterministic assembly by shifting taxa from stress tolerant to growth adapted strategies. Prokaryotes and microeukaryotes responded divergently. Eddy associated conditions increased prokaryotic richness and evenness but reduced microeukaryotic richness. Microeukaryotes showed narrower niche breadth in surface and mixed treatments and stronger heterogeneous selection, especially in the DCM. Assembly was strongly depth dependent. Surface communities were restructured more than DCM communities. In surface and mixed layers, prokaryotes showed increased dispersal limitation and decreased homogeneous selection under eddy associated conditions, whereas the DCM showed the opposite. Microeukaryotes generally exhibited opposite depth dependent patterns. Co occurrence networks were more complex and robust under eddy associated conditions, mainly driven by prokaryotes. DCM networks had higher robustness and lower vulnerability. Weakened correlations between prokaryotic composition and environmental variables suggest a shift from top down environmental filtering to bottom up biotic control. These results reveal distinct adaptive strategies of prokaryotic and eukaryotic microbiomes and highlight the role of eddies in sustaining microbial resilience and ecosystem functioning in the open ocean.

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1 Introduction

Mesoscale eddies are pervasive features of ocean circulation that strongly influence marine ecosystems by redistributing heat, nutrients, plankton, and particulate organic matter (Mcgillicuddy et al., 2007; Baldocchi, 2003; Abernathy and Haller, 2018; Zhang et al., 2014). Through vertical transport and mixing, eddies can modify nutrient availability and light exposure,

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thereby affecting primary production and microbial biogeochemical processes (Shulenberger and Reid, 1981; Gula et al., 2016; Lee et al., 1991; Glenn and Ebbesmeyer, 1994; McGillicuddy Jr, 2016). In particular, vertical displacement can expose deep-water microbiomes to elevated irradiance and induce photoacclimation (Richardson et al., 1983; Cullen and Macintyre, 1998), while phototrophic and heterotrophic microbiomes can adjust photosynthetic and metabolic activities in response to changing light conditions (Chen et al., 2010; He et al., 2002; Malzahn et al., 2010). Eddy-associated effects have been documented across oceanic regions including the North Pacific (Brzezinski et al., 1998), Hawaii (Vaillancourt et al., 2003) and Bermuda (Krause et al., 2009), highlighting the importance of mesoscale physical processes in structuring marine microbiomes.

However, microbial responses to eddy-associated environmental forcing are different across major microbial groups (Blooms, 2012). Eddies can alter bacterial activity, microeukaryotic biomass, phytoplankton metabolism, and heterotrophic bacterial processes, with consequences extending across marine food webs and biogeochemical pathways (Belkin et al., 2022; Wear et al., 2020; Dufois et al., 2016; McGillicuddy et al., 2007; Mikaelyan et al., 2023; Allen et al., 2005). Prokaryotes and microeukaryotes also differ in physiological traits, ecological niches, and responses to environmental stress, potentially leading to divergent strategies of community organization and persistence (Li et al., 2025). Beyond changes in taxonomic composition, environmental forcing can modify how microbiomes are assembled and associated with one another. Microbial co-occurrence networks provide a complementary framework for characterizing emergent organizational properties and potential community stability (Mengting Maggie Yuan and Shi, 2021; Kajihara and Hynson, 2024). Network robustness, vulnerability, and compositional stability can further reflect the capacity of microbial communities to resist or recover from environmental perturbations (Zelikova et al., 2014b; Landi et al., 2018a; Wu et al., 2021). Yet, most existing evidence is derived from field observations in which multiple environmental gradients covary, making it difficult to disentangle how eddy-associated physical forcing reorganizes microbial assembly and network properties. In particular, whether prokaryotic and eukaryotic microbiomes exhibit distinct organizational and stability responses remains poorly understood.

The Kuroshio Extension (KE) is an especially dynamic region characterized by frequent mesoscale eddies and strong gradients in temperature, light, and nutrient availability (Hu et al., 2018). These physical processes provide an appropriate natural setting for examining how transient changes in water-column conditions are reflected in microbial community organization. However, field observations alone cannot readily separate effects associated with water-mass origin from those arising during subsequent mixing and community succession. Controlled shipboard microcosm experiments therefore provide a useful complementary approach by reducing environmental heterogeneity while retaining naturally occurring microbial assemblages. In this study, seawater was collected from an eddy-influenced and a non-eddy-influenced region of the KE and incubated using surface water, deep chlorophyll maximum (DCM) water, and controlled surface–DCM mixtures. Importantly, these manipulations were designed to examine microbial responses to contrasting source-water conditions and vertical mixing, rather than to reproduce the full hydrodynamic dynamics of mesoscale eddies. The 16-day incubation enabled temporal tracking of changes in microbial composition, assembly processes, and network organization under controlled conditions.



The goals here are to explore: (1) how do contrasting eddy-associated source-water conditions and surface-DCM mixing alter microbial community assembly and succession; (2) do these environmental conditions differentially reorganize the co-occurrence structure and stability of prokaryotic and eukaryotic microbiomes; and (3) which ecological processes and environmental factors are associated with the divergent responses of these two microbial domains? We hypothesized that changes in light and nutrient availability associated with contrasting water-column conditions would shift the relative importance of deterministic selection, dispersal, and stochastic processes, while reorganizing microbial associations and network stability. Given their different ecological strategies and life-history traits, we further expected prokaryotes and microeukaryotes to exhibit distinct trajectories of community assembly and network organization. By integrating temporal community profiling, ecological assembly analyses, and network-based approaches, this study aims to clarify how short-term physical and resource perturbations associated with mesoscale oceanographic variability can reorganize marine microbiomes and reveal domain-specific strategies of community persistence.

2. Materials and methods

2.1 Study sites and shipboard microcosm experiment

Seawater samples were collected during cruises aboard R/V Dongfanghong 3 in the Kuroshio Extension region from an eddy-uninfluenced site (D2; 32.34°N, 145.83°E; June 22, 2022) and the edge of a warm eddy-influenced site (P31; 31.01°N, 150.01°E; July 12, 2022) (Fig. S1). Seawater was collected with a SeaBird CTD–Niskin rosette from the surface (2 m) and deep chlorophyll maximum (DCM) layers and passed through a 200-μm acid-washed nylon mesh to remove large zooplankton.

For each source-water region, three water-column conditions were established: surface water (Surface), DCM water (DCM), and a 1:1 mixture of surface and DCM water (Mix), with three replicate bottles for each condition. This distinction allows the culturing experiment to evaluate microbial responses associated with contrasting source-water environments. The surface-DCM mixture was used as a controlled vertical-mixing treatment and was not intended to reproduce the hydrodynamic dynamics of natural eddies.

Each 20 L transparent polycarbonate bottles (Nalgene 2251-0050) was maintained as an independent experimental unit throughout the incubation, and the total incubation volume was 360 L. Bottles were shaken and homogenized three times daily to minimize particle settling and spatial heterogeneity, and subsampling was conducted after homogenization. No additional seawater, nutrients, or other external materials were added during the incubation. The incubation lasted 16 days, and samples were collected on days 0, 2, 4, 6, 8, 10, 12, 14, and 16.

For microbial analyses, 500 mL of seawater was filtered sequentially through 3-μm and 0.22-μm filters using a gentle vacuum (<25 cm Hg). Filters were placed in 2 mL lysis buffer (50 mM Tris-HCl, 1 mM EDTA, 150 mM NaCl, and 0.1% SDS), immediately frozen in liquid nitrogen, and stored at –80°C. The filtered seawater samples were applied for nutrient concentration analysis of PO_4^{3-} , $\text{NO}_3^-/\text{NO}_2^-$, and SiO_3^{2-} , and it was measured using a continuous-flow autoanalyzer (AA3,



Seal Analytical) following established colorimetric methods (Whitledge et al., 1981; Coverly et al., 2009). During the shipboard microcosm experiments, the temperature of the culture water, which was influenced by using surface seawater as the circulating water, and natural light intensity were continuously monitored using DEFI-T and DEFI-F sensors (JFE Advantech). The recorded temperature ranged from 23.5 to 30.9 °C, with a mean of 26.1 °C, and light intensity ranged from 3.3 to 532.8 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. At the end of incubation, 0.6–1 L of seawater was filtered onto GF/F filters (Whatman, Maidstone, UK) for chlorophyll a analysis. Pigments were extracted in 90% acetone at –20°C in darkness for 18–22 h and quantified using a Turner Trilogy fluorometer (Zhang et al., 2018).

2.2 DNA extraction, sequencing, and sequence processing

DNA was extracted using a phenol-chloroform-isoamyl alcohol extraction and precipitation protocol (Stoeck and Epstein, 2003; Boström et al., 2004). DNA concentration and purity were assessed using a NanoDrop spectrophotometer. The V4 region of prokaryotic 16S rRNA genes was amplified using primers 515F/806R (Caporaso et al., 2012), while the V4 region of microeukaryotic 18S rRNA genes was amplified using primers 528F/706R (Cheung et al., 2010). PCR amplification and purification followed the published protocols (Lian et al., 2023). Briefly, PCR reaction conditions were 94 °C for 5 min, followed by 30 cycles of 94 °C for 30 s, 52 °C for 30 s, 72 °C for 30 s, and a final extension at 72 °C for 10 min. Amplicons were sequenced using the Illumina MiSeq PE300 platform (MajorBio, China).

The raw sequences were processed using QIIME 2 (2021.4) (Bolyen, 2019). Within the QIIME 2 workflow, paired reads were merged and primer sequences were removed, low-quality reads with a quality score <25 were discarded, and amplicon sequence variants (ASVs) were inferred using DADA2 (Callahan et al., 2016). ASVs detected in fewer than two samples or represented by fewer than 22 reads across the dataset were removed. Representative ASV sequences were taxonomically classified against the SILVA database (v138) using the SILVA 138-99-515-806 classifier (Quast et al., 2013). After quality filtering, 4,496 prokaryotic and 6,265 microeukaryotic ASVs were retained. For analyses requiring equal sequencing depth, ASV tables were rarefied to 40,000 reads per sample. Sequence data are available under the SRA BioProject number PRJCA048229.

2.3 Community organization and assembly

Microbial community composition was visualized using non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities with the “vegan” package. Levins’ niche breadth and niche overlap were calculated using the “spaa” package (Zhang and Zhang, 2013). Niche breadth was calculated from the distribution of each ASV across the defined environmental groups, with larger values indicating broader habitat/resource utilization. The same calculation framework was applied separately to prokaryotic and microeukaryotic ASVs. Phylogenetic structure was evaluated using mean nearest taxon distance (MNTD) (Kembel et al., 2010).

Microbial community assembly processes were quantified using iCAMP, which partitions assembly into heterogeneous selection, homogeneous selection, homogenizing dispersal, dispersal limitation, and drift (Stegen et al., 2013; Vellend et al.,



2014). iCAMP analyses were performed using non-rarefied ASV data. The neutral community model (NCM) was additionally used to evaluate the potential contribution of neutral processes and immigration to community assembly, and was calculated by the “Hmisc”, “minpack.lm” and “stats4” packages (Sloan et al., 2006).

2.4 Microbial co-occurrence networks

Multi-domain co-occurrence networks were constructed from prokaryotic and microeukaryotic ASVs using Pearson correlations of log-transformed abundance data (Table S1 and S2). ASVs detected in at least 25% of samples were retained, and network thresholds were determined using a random matrix theory (RMT)-based approach (Luo et al., 2006; Zhou et al., 2010). Networks were visualized and characterized in Gephi (version 0.9.2).

The topological characteristics of microbial co-occurrence networks were assessed using multiple indexes, including components, degree, clustering coefficient, modularity, diameter, clusters, graph density, and average path length (Watts and Strogatz, 1998; Guidi et al., 2016; Mori et al., 2017; Zhou et al., 2010). Nodes with high degree or betweenness centrality were considered key taxa maintaining network structure and stability (Gibson et al., 2015; Freeman, 1977; Freeman, 1980; Saavedra et al., 2011). Network analysis was also performed at the species level to identify general interaction patterns among microbes.

Microbial network complexity and stability, reflected by parameters including network size, connectivity, average clustering coefficient, modularity, robustness, and vulnerability, were assessed using topological and statistical analyses. Robustness of network is defined as the proportion of the remaining species in this network after random or targeted node removal (Montesinos-Navarro et al., 2017; Dunne et al., 2002). For simulations of random species removal, a certain proportion of nodes was randomly removed. For simulations of targeted removal, certain numbers of module hubs were removed. The vulnerability of each node measures the relative contribution of the node to the global efficiency. The node persistence is defined as the proportion of coexisting species (over the total number of species) at an ecological regime (Landi et al., 2018b). The compositional stability evaluates the change in community structure over time (Zelikova et al., 2014a).

2.5 Statistical analysis

All statistical analyses were conducted in R version 4.1.0. Differences in microbial diversity and community composition were evaluated using permutation-based approaches implemented in the “vegan” package, including ANOSIM and Mantel tests where appropriate. Piecewise structural equation model (SEM) was used to evaluate the direct and indirect effects of environmental factors on prokaryotic and eukaryotic microbiomes using the “piecewiseSEM” package (Grace, 2006). The models were specified separately for prokaryotic and microeukaryotic communities, and model adequacy was evaluated using the reported goodness-of-fit statistics.

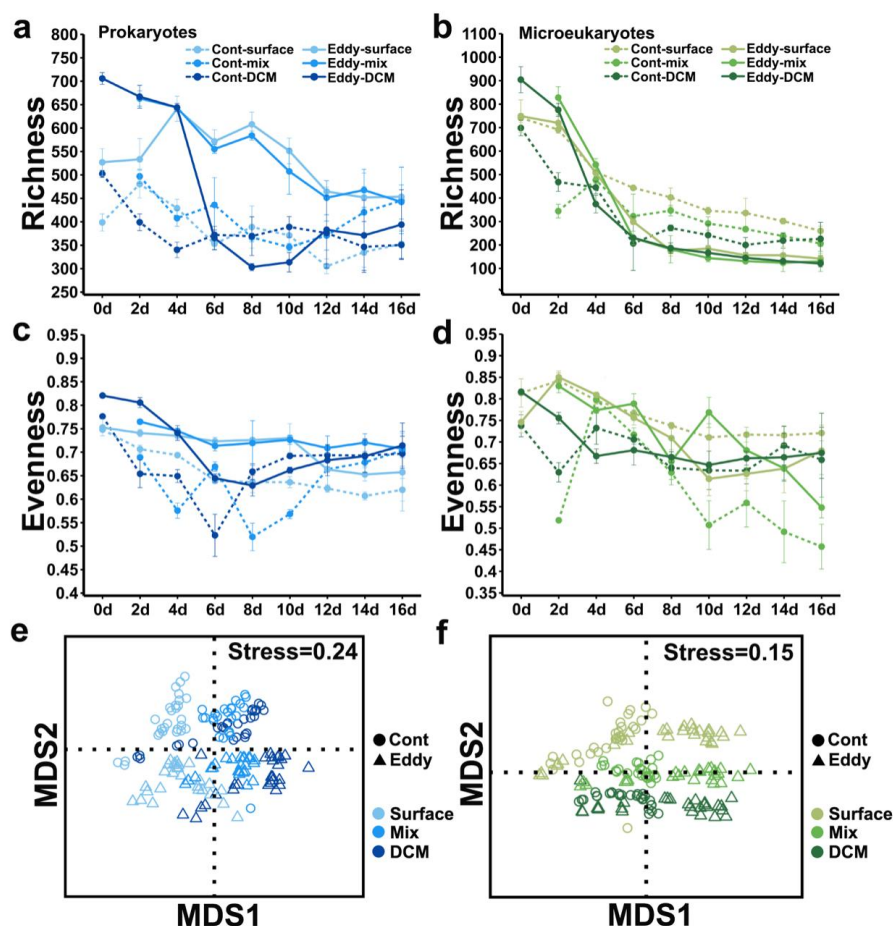


3. Results

160 3.1 Contrasting source-water conditions reshaped microbial diversity and compositions

The shipboard microcosm experiment revealed clear physicochemical contrasts between the eddy-influenced and non-eddy-influenced source waters. At the DCM layer, the eddy-influenced region exhibited lower concentrations of phosphate (0.054 vs 0.075 μM), nitrate/nitrite (0.139 vs 0.877 μM), and silicate (2.540 vs 3.230 μM) compared to the eddy-uninfluenced (control) region (Table S3). In contrast, surface water from the eddy-influenced region contained slightly higher phosphate
 165 (0.021 vs 0.019 μM) and silicate (1.631 vs 1.262 μM)(Table S3). In the non-eddy-influenced region, nitrate/nitrite concentrations in the Mix treatment were higher than those in the Surface treatment (0.534 vs. 0.109 μM) and declined to 0.105 μM by day 6. Thus, surface–DCM mixing generated a transient increase in nutrient availability that was followed by rapid nutrient depletion during incubation.

Prokaryotic and microeukaryotic communities showed distinct diversity responses across different source-water conditions
 170 (Fig. 1a-d). At day 0, prokaryotic richness and evenness were generally higher in eddy-influenced than in non-eddy-influenced communities, whereas microeukaryotic richness showed the opposite pattern. During incubation, prokaryotic richness remained higher under eddy-influenced conditions in most treatments, although DCM communities became lower than their non-eddy-influenced counterparts on days 8–10. Prokaryotic richness also generally declined from Surface to Mix and DCM treatments under eddy-influenced conditions. Microeukaryotic richness showed a similar depth-related decline in
 175 the non-eddy-influenced region, whereas other treatment contrasts were comparatively weak. Prokaryotic evenness was generally higher in eddy-influenced communities, while microeukaryotic evenness showed no consistent difference among treatments. Notably, prokaryotic diversity in the non-eddy-influenced Mix treatment increased after day 10 and approached that of the eddy-influenced Mix treatment by day 16 (Fig. 1a,c).



180 **Figure 1. Alpha and beta diversity of prokaryotic and microeukaryotic communities. Panels (a, c) and (b, d) show the alpha**
 185 **diversity of prokaryotic and microeukaryotic communities, respectively, while panels (e) and (f) depict their beta diversity. Non**
eddy-influenced conditions, abbreviated as “Cont” (Control).

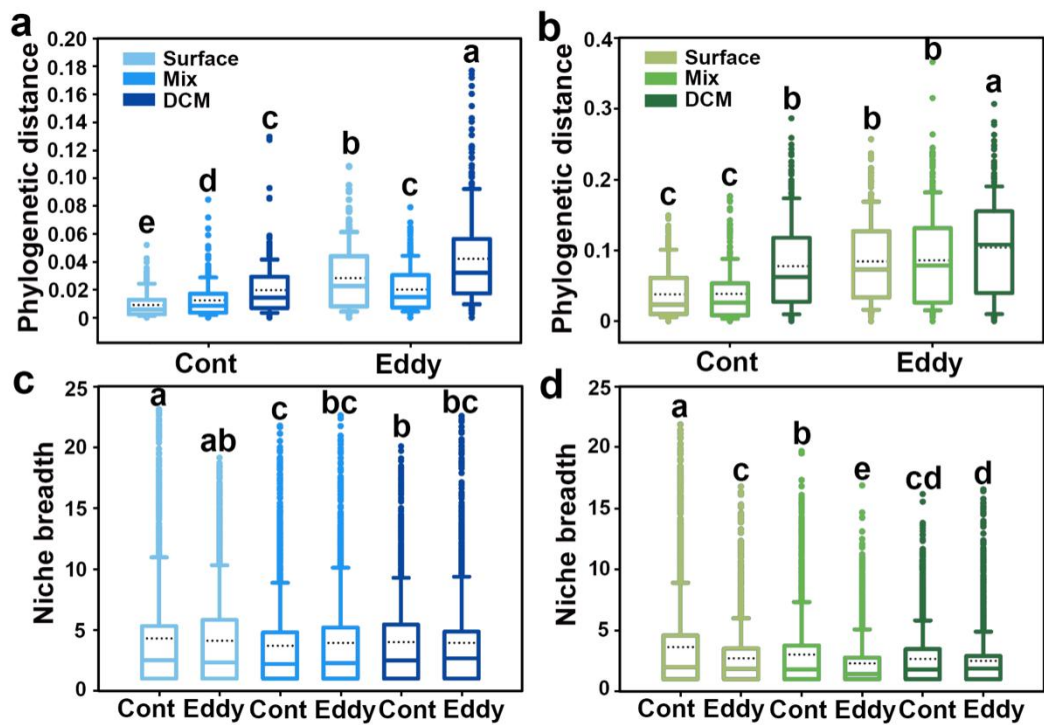
Community composition also differed between the two source-water environments (Fig. 1e,f; Table S4). Eddy-influenced conditions were associated with shifts in both prokaryotic and microeukaryotic taxonomic composition. Among
 185 microeukaryotes, the relative abundance of Dinoflagellata and Arthropoda decreased, whereas Diatom and Chlorophyta increased under eddy-influenced conditions. Similarly, Actinobacteria and Bacteroidota were relatively enriched, whereas Cyanobacteria and Gammaproteobacteria were reduced. These compositional shifts were accompanied by clear separation of community structures among Surface, Mix, and DCM samples (Fig. 1e,f).

Prokaryotic community composition differed more markedly between eddy influenced and uninfluenced regions, whereas
 190 microeukaryotic communities were strongly structured by the vertical stratification from the Surface to DCM groups (Fig. 1e, f). Microeukaryotic community structure was particularly more sensitive to the variation of light intensity within the culture and depth, with diversity decreasing as light availability declined. These trends were supported by ANOSIM and Mantel

tests, which revealed that depth (groups), cultivation time, temperature and light intensity within the culture significantly shaped microbiome compositions, especially for microeukaryotes (Table S5).

195 **3.2 Eddy-associated conditions altered niche breadth and shifted community assembly processes**

Phylogenetic structure and niche breadth further revealed contrasting responses between prokaryotic and microeukaryotic communities (Fig. 2). During the incubation period, the prokaryotic and microeukaryotic communities originating from the eddy-influenced region exhibited significantly greater phylogenetic distances across three culturing groups (Surface, Mix, and DCM) (Fig. 2a, b), indicating the stronger potential for ecological diversification of microbiomes. Prokaryotic niche
200 breadth did not differ significantly between eddy-influenced and non-eddy-influenced communities (Fig. 2c), whereas microeukaryotic niche breadth was significantly narrower in the eddy-influenced Surface and Mix treatments (Fig. 2d). No significant difference in microeukaryotic niche breadth was detected between DCM communities. These results indicate that prokaryotes and microeukaryotes differed in their resource utilization under contrasting source-water conditions.



205 **Figure 2. Phylogenetic distance and niche breadth of prokaryotic (a, c) and microeukaryotic (b, d) communities in (non)eddy-influenced regions. Values with different superscript letters (a, b) indicate significant differences among columns ($P < 0.05$). Non eddy-influenced conditions, abbreviated as “Cont” (Control).**

The contribution of stochastic processes to community assembly was lower in eddy-influenced Surface and DCM communities than in their non-eddy-influenced counterparts (Fig. 3a,b). A similar reduction in stochastic contributions was



210 observed in the non-eddy-influenced Mix treatment, indicating that surface – DCM mixing altered the balance between stochastic and deterministic assembly.

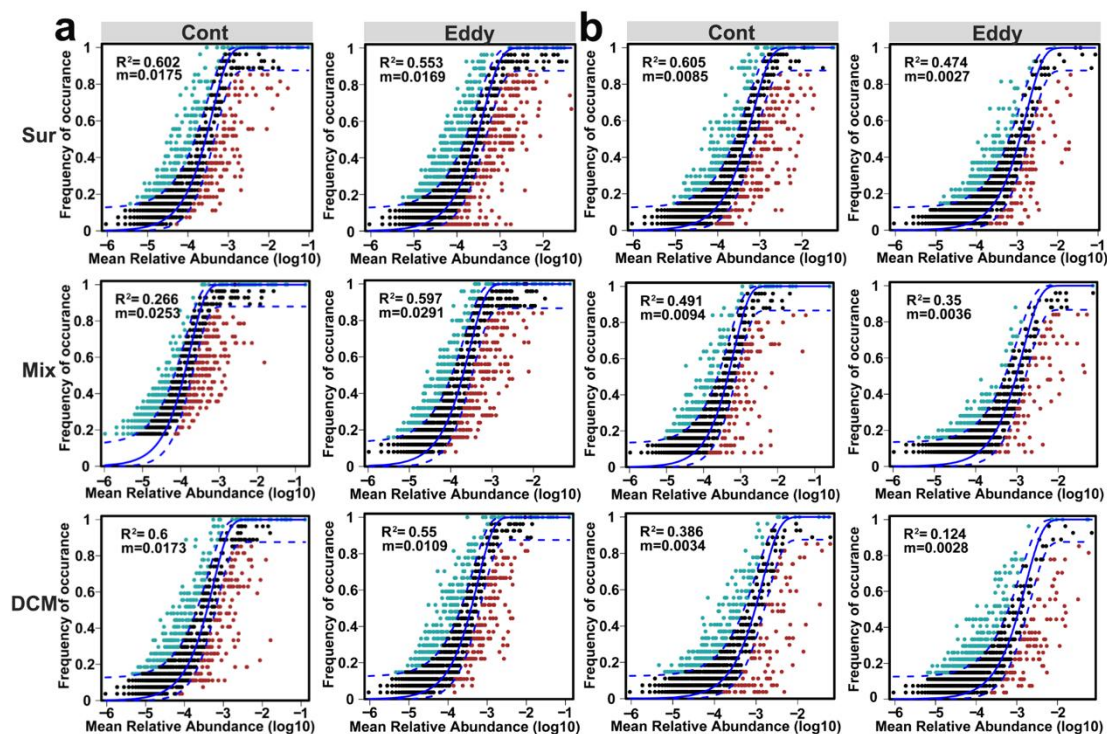


Figure 3. Fit of Sloan's neutral model to prokaryotic (a) and microeukaryotic (b) communities across different water layers and regions. Non eddy-influenced conditions, abbreviated as “Cont” (Control).

215 Homogeneous selection and dispersal limitation were the dominant assembly processes across treatments, with homogeneous selection contributing more strongly to prokaryotic than to microeukaryotic communities, whereas dispersal limitation contributed relatively more to microeukaryotes (Fig. 4a,b). In prokaryotic communities, eddy-associated conditions increased the contribution of dispersal limitation and decreased homogeneous selection in the Surface and Mix treatments, whereas the DCM showed the opposite tendency. In microeukaryotic communities, eddy-associated conditions increased heterogeneous selection, particularly in the DCM treatment.

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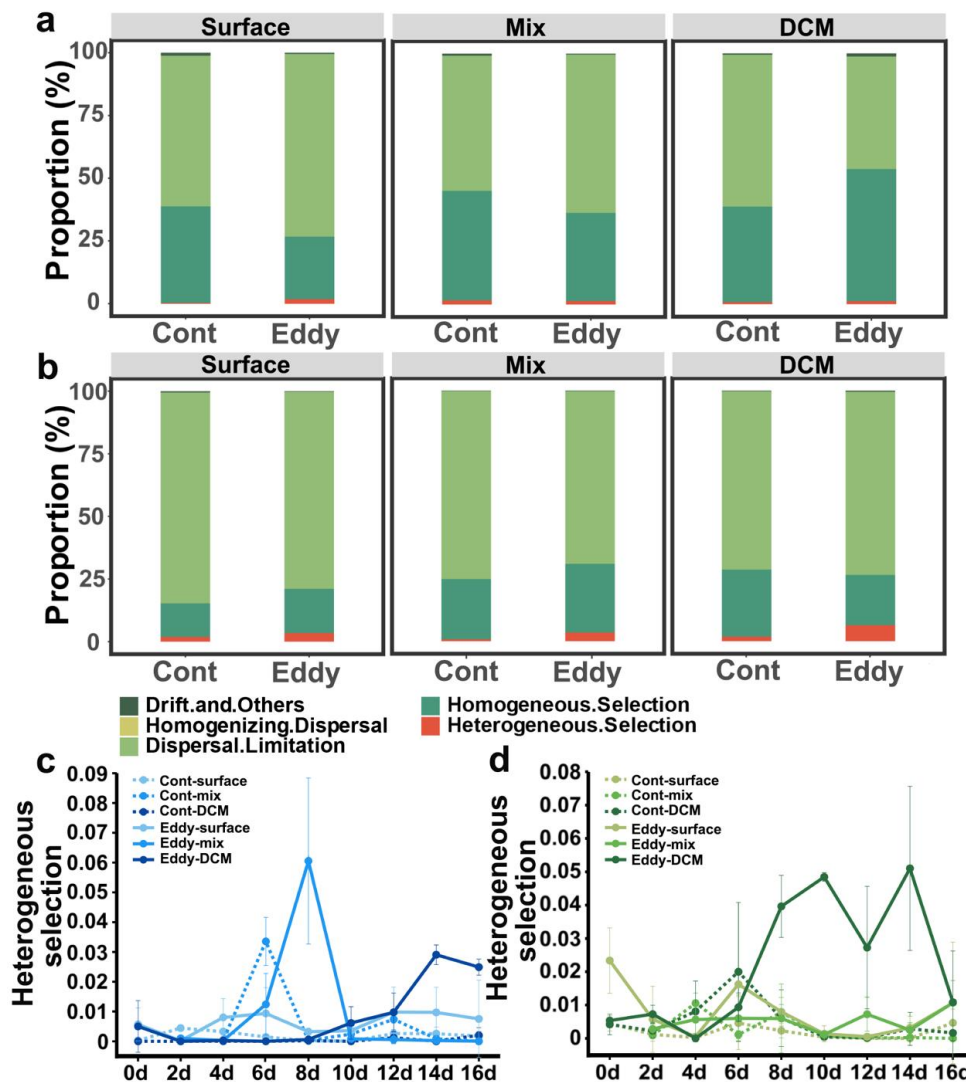


Figure 4. Contributions of different ecological processes to the assembly of prokaryotic (a) and microeukaryotic (b) communities. Variations in the contribution of heterogeneous selection to prokaryotic (c) and microeukaryotic (d) communities over the culture period. Non eddy-influenced conditions, abbreviated as “Cont” (Control).

The temporal dynamics of heterogeneous selection also differed among treatments (Fig. 4c,d). For prokaryotes, its contribution in the Mix treatment peaked on day 6 under non-eddy-influenced conditions and on day 8 under eddy-influenced conditions, while Surface and DCM communities showed less temporal variation. Microeukaryotic heterogeneous selection remained relatively high in the eddy-influenced DCM treatment, and mixing further increased its contribution. These results suggest that seawater mixing enhances deterministic assembly in prokaryotes, while light-related factors may



play a dominant role in structuring microeukaryotic communities. Together, these results demonstrate that source-water conditions and vertical mixing altered the relative importance of deterministic and stochastic assembly processes, with distinct responses between prokaryotes and microeukaryotes.

235 3.3 Eddy-associated communities exhibited reorganized network structure and stability

Microbial co-occurrence networks showed distinct organizational patterns of the eddy influenced/uninfluenced communities across the Surface, Mix and DCM groups (Fig. 5a; Table S1). The eddy-influenced Surface and DCM networks contained more nodes and edges than the corresponding non-eddy-influenced networks, suggesting their more complexes networks (Fig. 5a). For instance, the Surface and DCM microbial co-occurrence network had more nodes (345 vs 236; 286 vs 187) and
 240 edges (820 vs 784; 1166 vs 238) at eddy-influenced treatment than those in the control. Network complexity was also strongly depth-dependent, with the Mix treatment generally containing more nodes than the Surface and DCM treatments. For example, the non-eddy-influenced networks had more nodes (392 vs 236, 187) in the Mix group compared to those in the Surface and DCM groups, suggests the control microbial communities in the Mix groups were more complex and prone to the eddy effected microbiomes. Eddy-associated conditions increased modularity, the number of components, and cluster
 245 number in the Surface network, whereas DCM networks exhibited stronger “small-world” properties (Table S1).

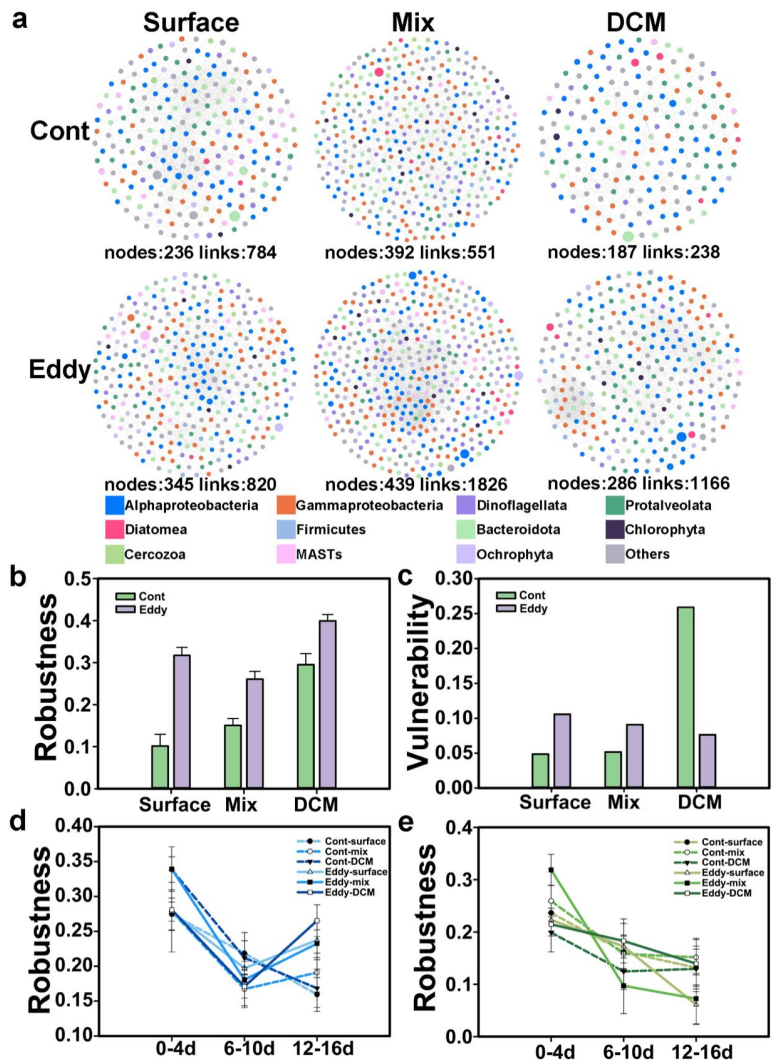


Figure 5. Co-occurrence networks (a) and stability (b–e) of microbial communities in the Surface, Mix, and DCM layers of non-eddy-influenced (abbreviated as “Cont”) and eddy-influenced regions.

250 Network stability showed contrasting patterns between (non)eddy-influenced conditions (Fig. 5b–e). Network robustness was greater under eddy-influenced conditions across the Surface, Mix, and DCM treatments (Fig. 5b). However, vulnerability was also higher in the eddy-influenced Surface and Mix networks than in the corresponding non-eddy-influenced networks (Fig. 5b,c). In contrast, the eddy-influenced DCM network combined higher robustness with lower vulnerability, resulting in a distinct stability profile. The increased robustness of eddy-influenced Surface, Mix, and DCM

255 networks was primarily associated with prokaryotic rather than microeukaryotic components (Fig. S2; Table S2). The robustness of eddy-uninfluenced prokaryotic networks of Mix group was increased after 12-16 days cultivation, and



eventually approaching to the robustness levels in the eddy-influenced treatments (Fig. 5d and e). These results suggest that prokaryotic communities had the ability to more quickly adapted to eddy currents, and this convergence was accompanied by changes in community composition and assembly processes, particularly in the Mix treatment.

260 3.4 Factors differentially associated with prokaryotic and microeukaryotic community dynamics

Mantel test analysis results showed significant associations between microbial community variation and environmental variables, including nitrate/nitrite, phosphate, silicate, light intensity, temperature, and culturing time (Table 1). The strength and combination of these associations differed among water layers, source-water conditions, and microbial domains. Prokaryotic communities generally showed weaker associations with environmental variables under eddy-influenced conditions than under non-eddy-influenced conditions, whereas microeukaryotic communities retained stronger environmental associations in eddy-influenced treatments (Table 1). The Mix treatment also showed relatively strong associations with nutrient concentrations and other environmental variables.

270 **Table 1. Factors structuring the eddy-affected microbial community dynamics based on ANOSIM and Mantel tests. Only statistically significant values are shown in the table.**

Microbial groups	Factors	Control			Eddy effected		
		Surface	Mix	DCM	Surface	Mix	DCM
Prokaryotic community	Nitrate/nitrite	0.67*	0.80*	0.70*			
	Phosphate		0.75*	0.71*			
	Silicate	0.66*	0.76*	0.61*			0.74*
	PAR	0.78*	0.45*	0.62*			
	Temperature	0.39*	0.69*	0.30*		0.75*	0.75*
	Time	0.98*	0.98*	0.79*			
Microeukaryotic community	Nitrate/nitrite	0.59*	0.79*	0.76*			
	Phosphate		0.78*	0.85*		0.76*	
	Silicate	0.69*	0.67*	0.50*		0.40*	
	PAR	0.69*	0.52*	0.66*			
	Temperature	0.47*	0.64*				0.88*
	Time	0.82*	0.88*	0.61*			

*, $P < 0.01$.

Piecewise SEM further identified direct and indirect relationships between environmental variables and major microbial groups (Figs. S3,S4). The variation of environmental factors was less correlated to the dynamic of major prokaryotic groups



in the eddy-influenced group compared to those in the control (Fig. S3), suggesting eddy caused seawater mixing facilitated the efficient use of light and nutrients. For prokaryotes, temperature and light intensity were critical predictors of community variation, particularly in the non-eddy-influenced Mix treatment, and it also influenced other environmental factors, such as the variation of silicate. Increasing temperature was positively associated with SAR406_clade and Bacteroidota and negatively associated with Planctomycetota, Cyanobacteria, and Gammaproteobacteria. Increasing light intensity was positively associated with Bacteroidota and negatively associated with SAR406_clade. Silicate, temperature, and light availability were also linked to changes in Myxococcota, Verrucomicrobiota, Bdellovibrionota, Betaproteobacteria, and Gammaproteobacteria through direct or indirect pathways (Fig. S3).

Microeukaryotic communities were less sensitive to the environmental variation in the eddy-influenced conditions (Fig. S4). Temperature was positively associated with Ochrophyta and Chrysophyceae but negatively associated with Centrohelida, Prymnesiophyceae, and Diatom. Light availability was positively associated with Chrysophyceae, Haptophyta, and Picozoa and negatively associated with Retaria. Through correlations with silicate, temperature and light availability also influenced other microeukaryotic groups, such as Cerozoa. Overall, the environmental associations indicated domain-specific responses to temperature, light, and nutrient variability across the culturing conditions.

4. Discussion

4.1 Eddies reshaped the community assembly of microbiomes

Our shipboard microcosm experiment, using seawater collected from eddy-influenced and eddy-uninfluenced regions, revealed that contrasting source-water conditions were associated with distinct microbial assembly and association patterns, with divergent responses between prokaryotic and microeukaryotic communities.

The surge in nutrients and light availability within eddies likely acts as an ecological switch, shifting the predominant microbial life-history strategy from stress tolerance to rapid growth. The strong shear forces at the edges of the eddy create a physical barrier, partially isolating the eddy-influenced region from the surrounding water (Sweeney et al., 2003; Baltar et al., 2010). Previous study also found that the eddy caused changes in biogeochemical dynamics (Sweeney et al., 2003; Baltar et al., 2010) and microbial populations (Villar et al., 2015) compared to those in the adjacent areas. This alleviation of resource competition may contribute to the increased prokaryotic diversity and the shift toward more deterministic assembly processes. The decline in microeukaryotic diversity and increased heterogeneous selection suggest stronger environmental filtering or trophic constraints on these communities (Fig. 1a-d). Larger size and slower replication rates may render microeukaryotes more vulnerable to top-down control. For example, the larger size limits their passive diffusion capacity (Farjalla et al., 2012; Wu et al., 2018). The nutrient conditions may stimulate a rapid response from prokaryotic prey, which could in turn alter trophic interactions and grazing pressure on microeukaryotes.

The pronounced depth-dependent characteristics further illuminate the contrasting ecological responses of prokaryotic and eukaryotic microbiomes to source-water conditions. Eddy-associated conditions altered the relative contributions of niche-



based selection and dispersal-related processes across the Surface-DCM gradient (Fig. 4). The significant restructuring in Surface communities aligns with the fact that the surface ocean microbiome is inherently more dynamic and variable, and is frequently exposed to rapid changes in light, temperature, and nutrient availability. The enhanced dispersal limitation observed in Surface and Mixed-layer prokaryotes suggests that in a resource-rich and physically heterogeneous environment, the relative contribution of immigration and local community sorting may change as new ecological niches become available. These depth-dependent patterns indicate that the effects associated with eddy-influenced source waters are not uniform across the water column, but depend strongly on the environmental characteristics and resource availability of microbiomes.

4.2 Prokaryotes outpace microeukaryotes under eddy-associated conditions

Prokaryotes exhibited greater flexibility under eddy-associated conditions than microeukaryotes. Prokaryotes possess broader niches, partly because horizontal gene transfer is more prevalent in them than in microeukaryotes, potentially facilitating rapid adjustment to changing environmental conditions (Arnold et al., 2022). In contrast, microeukaryotes may have narrower niches because of their stronger dependence on specific environmental resources, such as light availability (Carscadden et al., 2020). These differences may contribute to the contrasting responses of the two major microbiome groups to eddy-associated environmental changes.

The eddy-influenced microbiomes were more affected by dispersal limitation. Reduced migration among populations can restrict gene flow and promote genetic differentiation (Gavrilets, 2014; Burrige and Waters, 2020; Ortego et al., 2021). The contrasting responses of prokaryotes and microeukaryotes across depths instead suggest different ecological strategies and short-term community reorganization under eddy-associated conditions. In the DCM, the stronger contribution of homogeneous selection may reflect the relatively stable environmental conditions of this specialized depth layer, consistent with previous findings that selection and drift can contribute differently to prokaryotic and microeukaryotic community assembly (Osburn et al., 2021).

4.3 Eddy-associated conditions fosters more complex and stable microbiome networks

The eddy environment fosters more complex and robust microbiome co-occurrence networks, with prokaryotes contributing substantially to this pattern. Increased connectivity and robustness may indicate greater potential for niche partitioning, more efficient resource utilization and energy flow, and more extensive interspecies interactions, such as cross-feeding and mutualism, within the stabilized eddy environments (Sulheim and Mitri, 2023; Habedank et al., 2025). The coexistence of high robustness and vulnerability suggests that eddy-associated microbiomes may maintain both network stability and the capacity for reorganization under environmental perturbation.

The weaker correlation between community composition and environmental variables further suggests that the measured abiotic variables explained a smaller proportion of community variation under eddy-associated conditions. This decoupling may indicates a transition from a system primarily governed by top-down environmental filtering to one where bottom-up



biotic interactions become the dominant organizers of community structure. This shift from abiotic to biotic control could be a hallmark of mature and stable ecosystems (Jiao et al., 2024; Zengler and Zaramela, 2018).

Our microcosm results revealed a convergent trajectory in which mixing and incubation shifted marine microbiomes toward an eddy-associated state, providing experimental support for field observations that eddies are hotspots of distinct microbial activity (Baltar et al., 2010). Given the limitations of the microcosm experiment and the use of single-variable region sequencing of 16S/18S rRNA genes (Gloor et al., 2017), further investigations involving in situ sampling and metagenomic sequencing of (non)eddy-influenced waters are warranted, and it could provide deeper insights into microbial composition and functional dynamics.

Ocean eddies regulate the transport and redistribution of salt, heat, oxygen, carbon, and nutrients, thereby influencing marine ecosystems and biogeochemical cycling (Zhang et al., 2014; Dong et al., 2014; Omand et al., 2015; Conway et al., 2018; Zhai et al., 2010; Hewitt et al., 2022; Wang et al., 2023). Eddy activity has increased by 2-5% per decade in eddy-rich regions over recent decades (Martínez-Moreno et al., 2021), and future warming may further intensify surface eddy kinetic energy in many regions, including the Kuroshio Current system (Yun et al., 2024; Beech et al., 2022; Li et al., 2024). Such changes could alter the frequency and magnitude of resource redistribution and environmental heterogeneity experienced by marine microbiomes. By demonstrating contrasting short-term responses of prokaryotic and microeukaryotic communities and associated changes in network organization, our study highlights the importance of considering different prokaryotic and microeukaryotic communities assembly and association patterns when evaluating how mesoscale physical processes may influence ocean biogeochemical cycling under a changing climate.

5. Conclusions

Shipboard microcosm experiments in the Kuroshio Extension region revealed that eddy-associated conditions reshaped the assembly and network stability of prokaryotic and eukaryotic microbiomes, with greater flexibility in prokaryotes and stronger compositional and assembly responses in microeukaryotes. The emergence of more complex and stable co-occurrence networks, primarily driven by prokaryotes, suggests increased community organization under eddy-associated conditions, although these associations do not directly demonstrate biological interactions. The convergent changes observed during mixing and incubation further indicate that eddy-associated conditions can reorganize microbial community assembly and association patterns. This shift was further evidenced by the weakened correlation between microbiome composition and environmental variables, indicating a potential transition from top-down environmental filtering to bottom-up biotic control. Overall, this study highlights contrasting responses of prokaryotic and eukaryotic microbiomes and the importance of microbial community organization in understanding how mesoscale oceanographic processes may influence marine biogeochemical cycling.



Code and data availability

The raw sequence data presented in this paper have been submitted to the Genome Sequence Archive (Chen et al., 2021) in National Genomics Data Center (Members and Partners, 2021), China National Center for Bioinformation / Beijing Institute of Genomics, Chinese Academy of Sciences (GSA: CRA032179 and CRA032180) that are publicly accessible at <https://ngdc.cncb.ac.cn/gsa>.

Author contributions

CZ and HW designed the study. CZ conducted the onboard incubation experiments. YL analyzed and interpreted the data, YL, MW, HG and ZC discussed the results. YL, CZ and HW contributed to refining the manuscript. All authors read and approved the final manuscript. The final draft was meticulously reviewed and approved by all contributing authors.

Competing interests

The authors claim that they have no personal interests or associations that could be perceived as affecting the objectivity of this paper.

Acknowledgements

We thank the support of the high-performance servers of the Center for High Performance Computing and System Simulation, Pilot National Laboratory for Marine Science and Technology (Qingdao), the Marine Big Data Center of the Institute for Advanced Ocean Study of the Ocean University of China, the IEMB-1, a high-performance computing cluster operated by the Institute of Evolution and Marine Biodiversity, and Marine Big Data Center of Institute for Advanced Ocean Study of Ocean University of China.

Financial support

This research was supported by the National Key Research and Development Program of China (2024YFC2815800 and 2022YFC2807500), Natural Science Foundation of Shandong Province (ZR2024MD106), National Natural Science Foundation of China (32672076, 42120104006, and 42176111). Data and samples were collected onboard of R/V “Dongfanghong 3”, supported by the Fundamental Research Funds for the Central Universities (grant number: 202072001).



390 References

- Abernathy, R. and Haller, G.: Transport by Lagrangian vortices in the eastern Pacific, *Journal of Physical Oceanography*, 48, 667-685, 2018.
- Allen, J. T., Brown, L., Sanders, R., Mark Moore, C., Mustard, A., Fielding, S., Lucas, M., Rixen, M., Savidge, G., and Henson, S.: Diatom carbon export enhanced by silicate upwelling in the northeast Atlantic, *Nature*, 437, 728-732, 2005.
- 395 Arnold, B. J., Huang, I. T., and Hanage, W. P.: Horizontal gene transfer and adaptive evolution in bacteria, *Nature Reviews Microbiology*, 20, 206-218, 10.1038/s41579-021-00650-4, 2022.
- Baldocchi, D. D.: Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future, *Global change biology*, 9, 479-492, 2003.
- Baltar, F., Aristegui, J., Gasol, J. M., Lekunberri, I., and Herndl, G. J.: Mesoscale eddies: hotspots of prokaryotic activity and differential community structure in the ocean, *The ISME journal*, 4, 975-988, 2010.
- 400 Beech, N., Rackow, T., Semmler, T., Danilov, S., Wang, Q., and Jung, T.: Long-term evolution of ocean eddy activity in a warming world, *Nature Climate Change*, 12, 910-917, 10.1038/s41558-022-01478-3, 2022.
- Belkin, N., Guy-Haim, T., Rubin-Blum, M., Lazar, A., Sisma-Ventura, G., Kiko, R., Morov, A. R., Ozer, T., Gertman, I., and Herut, B.: Influence of cyclonic and anticyclonic eddies on plankton in the southeastern Mediterranean Sea during late summertime, *Ocean Science*, 18, 693-715, 2022.
- 405 Blooms, P.: Eddy-Driven Stratification Initiates North Atlantic Spring, *science*, 1218740, 337, 2012.
- Bolyen, E.: Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2, *Nat Biotechnol*, 37, 852-857, 10.1038/s41587-019-0209-9, 2019.
- Boström, K. H., Simu, K., Hagström, Å., and Riemann, L.: Optimization of DNA extraction for quantitative marine bacterioplankton community analysis, *Limnology and Oceanography: Methods*, 2, 365-373, <https://doi.org/10.4319/lom.2004.2.365>, 2004.
- 410 Brzezinski, M. A., Villareal, T. A., and Lipschultz, F.: Silica production and the contribution of diatoms to new and primary production in the central North Pacific, *Marine Ecology Progress Series*, 167, 89-104, 1998.
- Burridge, C. P. and Waters, J. M.: Does migration promote or inhibit diversification? A case study involving the dominant radiation of temperate Southern Hemisphere freshwater fishes, *Evolution*, 74, 1954-1965, <https://doi.org/10.1111/evo.14066>, 2020.
- 415 Callahan, B. J., McMurdie, P. J., Rosen, M. J., Han, A. W., Johnson, A. J., and Holmes, S. P.: DADA2: High-resolution sample inference from Illumina amplicon data, *Nat Methods*, 13, 581-583, 10.1038/nmeth.3869, 2016.
- Caporaso, J. G., Lauber, C. L., Walters, W. A., Berg-Lyons, D., Huntley, J., Fierer, N., Owens, S. M., Betley, J., Fraser, L., 420 Bauer, M., Gormley, N., Gilbert, J. A., Smith, G., and Knight, R.: Ultra-high-throughput microbial community analysis on the Illumina HiSeq and MiSeq platforms, *The ISME Journal*, 6, 1621-1624, 10.1038/ismej.2012.8, 2012.



- Carscadden, K. A., Emery, N. C., Arnillas, C. A., Cadotte, M. W., Afkhami, M. E., Gravel, D., Livingstone, S. W., and Wiens, J. J.: Niche Breadth: Causes and Consequences for Ecology, Evolution, and Conservation, *The Quarterly Review of Biology*, 95, 179-214, 10.1086/710388, 2020.
- 425 Chen, C.-H., DeMay, B. S., Gladfelter, A. S., Dunlap, J. C., and Loros, J. J.: Physical interaction between VIVID and white collar complex regulates photoadaptation in *Neurospora*, *Proceedings of the National Academy of Sciences*, 107, 16715-16720, 2010.
- Chen, T., Chen, X., Zhang, S., Zhu, J., Tang, B., Wang, A., Dong, L., Zhang, Z., Yu, C., Sun, Y., Chi, L., Chen, H., Zhai, S., Sun, Y., Lan, L., Zhang, X., Xiao, J., Bao, Y., Wang, Y., Zhang, Z., and Zhao, W.: The Genome Sequence Archive Family:
 430 Toward Explosive Data Growth and Diverse Data Types, *Genomics, Proteomics & Bioinformatics*, 19, 578-583, <https://doi.org/10.1016/j.gpb.2021.08.001>, 2021.
- Cheung, M. K., Au, C. H., Chu, K. H., Kwan, H. S., and Wong, C. K.: Composition and genetic diversity of picoeukaryotes in subtropical coastal waters as revealed by 454 pyrosequencing, *Isme j*, 4, 1053-1059, 10.1038/ismej.2010.26, 2010.
- Conway, T. M., Palter, J. B., and de Souza, G. F.: Gulf Stream rings as a source of iron to the North Atlantic subtropical gyre,
 435 *Nature Geoscience*, 11, 594-598, 10.1038/s41561-018-0162-0, 2018.
- Coverly, S., Aminot, A., and K  rouel, R.: Nutrients in seawater using segmented flow analysis, *Practical Guidelines for the Analysis of Seawater*, 143-178, 2009.
- Cullen, J. J. and MacIntyre, J. G.: Behavior, physiology and the niche of depth-regulating phytoplankton, *Nato Asi Series G Ecological Sciences*, 41, 559-580, 1998.
- 440 Dong, C., McWilliams, J. C., Liu, Y., and Chen, D.: Global heat and salt transports by eddy movement, *Nature Communications*, 5, 3294, 10.1038/ncomms4294, 2014.
- Dufois, F., Hardman-Mountford, N. J., Greenwood, J., Richardson, A. J., Feng, M., and Matear, R. J.: Anticyclonic eddies are more productive than cyclonic eddies in subtropical gyres because of winter mixing, *Science Advances*, 2, e1600282, doi:10.1126/sciadv.1600282, 2016.
- 445 Dunne, J. A., Williams, R. J., and Martinez, N. D.: Food-web structure and network theory: The role of connectance and size, *Proc Natl Acad Sci U S A*, 99, 12917-12922, 10.1073/pnas.192407699, 2002.
- Farjalla, V. F., Srivastava, D. S., Marino, N. A., Azevedo, F. D., Dib, V., Lopes, P. M., Rosado, A. S., Bozelli, R. L., and Esteves, F. A.: Ecological determinism increases with organism size, *Ecology*, 93, 1752-1759, 10.1890/11-1144.1, 2012.
- Freeman, L. C.: A Set of Measures of Centrality Based on Betweenness, *Sociometry*, 40, 35-41, 1977.
- 450 Freeman, L. C.: The gatekeeper, pair-dependency and structural centrality, *Quality and Quantity*, 14, 585-592, 1980.
- Gavrilets, S.: Models of Speciation: Where Are We Now?, *Journal of Heredity*, 105, 743-755, 10.1093/jhered/esu045, 2014.
- Gibson, T. E., Amir, B., Hong-Tai, C., Weiss, S. T., Yang-Yu, L., and Jeff, G.: On the Origins and Control of Community Types in the Human Microbiome, *PLoS Computational Biology*, 12, 2015.
- Glenn, S. M. and Ebbesmeyer, C. C.: Observations of Gulf Stream frontal eddies in the vicinity of Cape Hatteras, *Journal of*
 455 *Geophysical Research: Oceans*, 99, 5047-5055, 1994.



- Gloor, G. B., Macklaim, J. M., Pawlowsky-Glahn, V., and Egozcue, J. J.: Microbiome Datasets Are Compositional: And This Is Not Optional, *Frontiers in Microbiology*, Volume 8 - 2017, 10.3389/fmicb.2017.02224, 2017.
- Grace, J. B.: *Structural Equation Modeling Natural Systems*, fish & fisheries, 2006.
- Guidi, L., Chaffron, S., Bittner, L., Eveillard, D., Larhlami, A., Roux, S., Darzi, Y., Audic, S., Berline, L., Brum, J., Coelho, L.,
 460 P., Espinoza, J. C. I., Malviya, S., Sunagawa, S., Dimier, C., Kandels-Lewis, S., Picheral, M., Poulain, J., Searson, S.,
 Stemmann, L., Not, F., Hingamp, P., Speich, S., Follows, M., Karp-Boss, L., Boss, E., Ogata, H., Pesant, S., Weissenbach, J.,
 Wincker, P., Acinas, S. G., Bork, P., de Vargas, C., Iudicone, D., Sullivan, M. B., Raes, J., Karsenti, E., Bowler, C., and
 Gorsky, G.: Plankton networks driving carbon export in the oligotrophic ocean, *Nature*, 532, 465-470, 10.1038/nature16942,
 2016.
- 465 Gula, J., Molemaker, M. J., and McWilliams, J. C.: Submesoscale dynamics of a Gulf Stream frontal eddy in the South
 Atlantic Bight, *Journal of Physical Oceanography*, 46, 305-325, 2016.
- Habedank, J., Horn, S., Lemke, P., Sidorenko, V., and Wiltshire, K. H.: A new perspective for revealing ‘hidden’ interactions
 in ecological networks, *Methods in Ecology and Evolution*, 16, 1314-1321, <https://doi.org/10.1111/2041-210X.70077>, 2025.
- He, Q., Cheng, P., Yang, Y., Wang, L., Gardner, K. H., and Liu, Y.: White collar-1, a DNA binding transcription factor and a
 470 light sensor, *Science*, 297, 840-843, 10.1126/science.1072795, 2002.
- Hewitt, H., Fox-Kemper, B., Pearson, B., Roberts, M., and Klocke, D.: The small scales of the ocean may hold the key to
 surprises, *Nature Climate Change*, 12, <https://doi.org/10.1038/s41558-022-01386-6>, 2022.
- Hu, D., Chen, X., Mao, K. F., Teng, J., and Peng, X. D.: Statistical Characteristics of Mesoscale Eddies near the Kuroshio
 Extension Region, *Oceanologia et Limnologia Sinica*, 2018.
- 475 Jiao, N. Z., Luo, T. W., Chen, Q. R., Zhao, Z., Xiao, X. L., Liu, J. H., Jian, Z. M., Xie, S. C., Thomas, H., Herndl, G. J.,
 Benner, R., Gonsior, M., Chen, F., Cai, W. J., and Robinson, C.: The microbial carbon pump and climate change, *Nature
 Reviews Microbiology*, 10.1038/s41579-024-01018-0, 2024.
- Kajihara, K. T. and Hynson, N. A.: Networks as tools for defining emergent properties of microbiomes and their stability,
Microbiome, 12, 184, 10.1186/s40168-024-01868-z, 2024.
- 480 Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P., and Webb, C. O.:
 Picante: R tools for integrating phylogenies and ecology, *Bioinformatics*, 26, 1463-1464, 10.1093/bioinformatics/btq166,
 2010.
- Krause, J. W., Lomas, M. W., and Nelson, D. M.: Biogenic silica at the Bermuda Atlantic Time-series Study site in the
 Sargasso Sea: Temporal changes and their inferred controls based on a 15-year record, *Global Biogeochemical Cycles*, 23,
 485 2009.
- Landi, P., Minoarivelo, H. O., Brännström, Å., Hui, C., and Dieckmann, U.: Complexity and stability of ecological networks:
 a review of the theory, *Popul. Ecol.*, 60, 319-345, 10.1007/s10144-018-0628-3, 2018a.
- Landi, P., Minoarivelo, H. O., Brännström, Å., Hui, C., and Dieckmann, U.: Complexity and stability of ecological networks:
 a review of the theory, *Population Ecology*, 60, 319-345, 2018b.



- 490 Lee, T. N., Yoder, J. A., and Atkinson, L. P.: Gulf Stream frontal eddy influence on productivity of the southeast US
 continental shelf, *Journal of Geophysical Research: Oceans*, 96, 22191-22205, 1991.
- Li, X., Wang, Q., Danilov, S., Koldunov, N., Liu, C., Müller, V., Sidorenko, D., and Jung, T.: Eddy activity in the Arctic
 Ocean projected to surge in a warming world, *Nature Climate Change*, 14, 156-162, 10.1038/s41558-023-01908-w, 2024.
- Li, Y., Li, Y., Wang, H., Zhang, C., Lian, K., Liu, F., Liang, Y., Chen, Z., Zhang, Y., Shao, H., McMinn, A., and Wang, M.:
 495 Community organization and network stability of co-occurring microbiota under the influence of Kuroshio Current, *Marine
 Pollution Bulletin*, 213, 117637, <https://doi.org/10.1016/j.marpolbul.2025.117637>, 2025.
- Lian, K., Liu, F., Li, Y., Wang, C., Zhang, C., McMinn, A., Wang, M., and Wang, H.: Environmental gradients shape
 microbiome assembly and stability in the East China sea, *Environmental Research*, 238, 117197, 2023.
- Luo, F., Zhong, J., Yang, Y., Scheuermann, R. H., and Zhou, J.: Application of random matrix theory to biological networks,
 500 *Physics Letters A*, 357, 420-423, <https://doi.org/10.1016/j.physleta.2006.04.076>, 2006.
- Malzahn, E., Ciprianidis, S., Káldi, K., Schafmeier, T., and Brunner, M.: Photoadaptation in *Neurospora* by Competitive
 Interaction of Activating and Inhibitory LOV Domains, *Cell*, 142, 762-772, <https://doi.org/10.1016/j.cell.2010.08.010>, 2010.
- Martínez-Moreno, J., Hogg, A. M., England, M. H., Constantinou, N. C., Kiss, A. E., and Morrison, A. K.: Global changes in
 oceanic mesoscale currents over the satellite altimetry record, *Nature Climate Change*, 11, 397-403, 10.1038/s41558-021-
 505 01006-9, 2021.
- McGillicuddy, D. J., Anderson, L. A., Bates, N. R., Bibby, T., Buesseler, K. O., Carlson, C. A., Davis, C. S., Ewart, C.,
 Falkowski, P. G., Goldthwait, S. A., Hansell, D. A., Jenkins, W. J., Johnson, R., Kosnyrev, V. K., Ledwell, J. R., Li, Q. P.,
 Siegel, D. A., and Steinberg, D. K.: Eddy/Wind Interactions Stimulate Extraordinary Mid-Ocean Plankton Blooms, *Science*,
 316, 1021-1026, doi:10.1126/science.1136256, 2007.
- 510 McGillicuddy Jr, D. J.: Mechanisms of physical-biological-biogeochemical interaction at the oceanic mesoscale, *Annual
 Review of Marine Science*, 8, 125-159, 2016.
- Members, C.-N. and Partners: Database Resources of the National Genomics Data Center, China National Center for
 Bioinformatics in 2022, *Nucleic Acids Research*, 50, D27-D38, 10.1093/nar/gkab951, 2021.
- Mengting Maggie Yuan, X. G., Linwei Wu, Ya Zhang, Najia Xiao, Daliang Ning , and Shi, Z.: Climate warming enhances
 515 microbial network complexity and stability, *Nature climate change*, 11, 10.1038/s41558-021-00989-9, 2021.
- Mikaelyan, A. S., Zatsepin, A. G., Kubryakov, A. A., Podymov, O. I., Mosharov, S. A., Pautova, L. A., Fedorov, A. V., and
 Ocherednik, O. A.: Case where a mesoscale cyclonic eddy suppresses primary production: A Stratification-Lock hypothesis,
Progress in Oceanography, 212, 102984, <https://doi.org/10.1016/j.pocean.2023.102984>, 2023.
- Montesinos-Navarro, A., Hiraldo, F., Tella, J. L., and Blanco, G.: Network structure embracing mutualism–antagonism
 520 continuums increases community robustness, *Nature Ecology & Evolution*, 1, 1661-1669, 10.1038/s41559-017-0320-6, 2017.
- Mori, J. F., Ueberschaar, N., Lu, S., Cooper, R. E., Pohnert, G., and Küsel, K.: Sticking together: inter-species aggregation of
 bacteria isolated from iron snow is controlled by chemical signaling, *Isme j*, 11, 1075-1086, 10.1038/ismej.2016.186, 2017.



- Omand, M. M., D'Asaro, E. A., Lee, C. M., Perry, M. J., Briggs, N., Cetinić, I., and Mahadevan, A.: Eddy-driven subduction exports particulate organic carbon from the spring bloom, *Science*, 348, 222-225, 10.1126/science.1260062, 2015.
- 525 Ortego, J., Gutiérrez-Rodríguez, J., and Nogueras, V.: Demographic consequences of dispersal-related trait shift in two recently diverged taxa of montane grasshoppers, *Evolution*, 75, 1998-2013, 2021.
- Osburn, E. D., Aylward, F. O., and Barrett, J.: Historical land use has long-term effects on microbial community assembly processes in forest soils, *ISME Communications*, 1, 48, 2021.
- Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J., and Glöckner, F. O.: The SILVA ribosomal
 530 RNA gene database project: improved data processing and web-based tools, *Nucleic Acids Res*, 41, D590-596, 10.1093/nar/gks1219, 2013.
- Richardson, K., Beardall, J., and Raven, J.: Adaptation of unicellular algae to irradiance: an analysis of strategies, *New Phytologist*, 93, 157-191, 1983.
- Saavedra, S., Stouffer, D. B., Uzzi, B., and Bascompte, J.: Strong contributors to network persistence are the most vulnerable
 535 to extinction, *Nature*, 478, 233-235, 10.1038/nature10433, 2011.
- Shulenberger, E. and Reid, J. L.: The Pacific shallow oxygen maximum, deep chlorophyll maximum, and primary productivity, reconsidered, *Deep Sea Research Part A. Oceanographic Research Papers*, 28, 901-919, 1981.
- Sloan, W. T., Lunn, M., Woodcock, S., Head, I. M., Nee, S., and Curtis, T. P.: Quantifying the roles of immigration and chance in shaping prokaryote community structure, *Environ Microbiol*, 8, 732-740, 10.1111/j.1462-2920.2005.00956.x, 2006.
- 540 Stegen, J. C., Lin, X., Fredrickson, J. K., Chen, X., Kennedy, D. W., Murray, C. J., Rockhold, M. L., and Konopka, A.: Quantifying community assembly processes and identifying features that impose them, *The ISME journal*, 7, 2069-2079, 2013.
- Stoeck, T. and Epstein, S.: Novel eukaryotic lineages inferred from small-subunit rRNA analyses of oxygen-depleted marine environments, *Appl Environ Microbiol*, 69, 2657-2663, 10.1128/aem.69.5.2657-2663.2003, 2003.
- 545 Sulheim, S. and Mitri, S.: Breaking down microbial hierarchies, *Trends in Microbiology*, 31, 426-427, 10.1016/j.tim.2023.02.014, 2023.
- Sweeney, E. N., McGillicuddy, D. J., and Buesseler, K. O.: Biogeochemical impacts due to mesoscale eddy activity in the Sargasso Sea as measured at the Bermuda Atlantic Time-series Study (BATS), *Deep Sea Research Part II: Topical Studies in Oceanography*, 50, 3017-3039, <https://doi.org/10.1016/j.dsr2.2003.07.008>, 2003.
- 550 Vaillancourt, R. D., Marra, J., Seki, M. P., Parsons, M. L., and Bidigare, R. R.: Impact of a cyclonic eddy on phytoplankton community structure and photosynthetic competency in the subtropical North Pacific Ocean, *Deep Sea Research Part I: Oceanographic Research Papers*, 50, 829-847, 2003.
- Vellend, M., Srivastava, D. S., Anderson, K. M., Brown, C. D., Jankowski, J. E., Kleynhans, E. J., Kraft, N. J. B., Letaw, A. D., Macdonald, A. A. M., Maclean, J. E., Myers-Smith, I. H., Norris, A. R., and Xue, X.: Assessing the relative importance
 555 of neutral stochasticity in ecological communities, *Oikos*, 123, 1420-1430, <https://doi.org/10.1111/oik.01493>, 2014.



- Villar, E., Farrant, G. K., Follows, M., Garczarek, L., Speich, S., Audic, S., Bittner, L., Blanke, B., Brum, J. R., and Brunet, C.: Environmental characteristics of Agulhas rings affect interocean plankton transport, *Science*, 348, 1261447, 2015.
- Wang, H., Qiu, B., Liu, H., and Zhang, Z.: Doubling of surface oceanic meridional heat transport by non-symmetry of mesoscale eddies, *Nature Communications*, 14, 5460, 10.1038/s41467-023-41294-7, 2023.
- 560 Watts, D. J. and Strogatz, S. H.: Collective dynamics of ‘small-world’ networks, *Nature*, 393, 440-442, 10.1038/30918, 1998.
- Wear, E. K., Carlson, C. A., and Church, M. J.: Bacterioplankton metabolism of phytoplankton lysates across a cyclone-anticyclone eddy dipole impacts the cycling of semi-labile organic matter in the photic zone, *Limnology and Oceanography*, 65, 1608-1622, <https://doi.org/10.1002/lno.11409>, 2020.
- Whitledge, T. E., Malloy, S. C., Patton, C. J., and Wirick, C. D.: Automated nutrient analyses in seawater, United States, 10.2172/5433901, 1981.
- 565 Wu, M. H., Chen, S. Y., Chen, J. W., Xue, K., Chen, S. L., Wang, X. M., Chen, T., Kang, S. C., Rui, J. P., Thies, J. E., Bardgett, R. D., and Wang, Y. F.: Reduced microbial stability in the active layer is associated with carbon loss under alpine permafrost degradation, *Proc Natl Acad Sci U S A*, 118, 10.1073/pnas.2025321118, 2021.
- Wu, W., Lu, H. P., Sastri, A., Yeh, Y. C., Gong, G. C., Chou, W. C., and Hsieh, C. H.: Contrasting the relative importance of species sorting and dispersal limitation in shaping marine bacterial versus protist communities, *Isme j*, 12, 485-494, 10.1038/ismej.2017.183, 2018.
- Yun, J., Ha, K.-J., and Lee, S.-S.: Impact of greenhouse warming on mesoscale eddy characteristics in high-resolution climate simulations, *Environmental Research Letters*, 19, 014078, 10.1088/1748-9326/ad114b, 2024.
- Zelikova, T. J., Blumenthal, D. M., Williams, D. G., Souza, L., LeCain, D. R., Morgan, J., and Pendall, E.: Long-term exposure to elevated CO₂ enhances plant community stability by suppressing dominant plant species in a mixed-grass prairie, *Proceedings of the National Academy of Sciences*, 111, 15456-15461, 2014a.
- 575 Zelikova, T. J., Blumenthal, D. M., Williams, D. G., Souza, L., LeCain, D. R., Morgan, J., and Pendall, E.: Long-term exposure to elevated CO₂ enhances plant community stability by suppressing dominant plant species in a mixed-grass prairie, *Proc Natl Acad Sci USA*, 111, 15456-15461, 10.1073/pnas.1414659111, 2014b.
- 580 Zengler, K. and Zaramela, L. S.: The social network of microorganisms - how auxotrophies shape complex communities, *Nat Rev Microbiol*, 16, 383-390, 10.1038/s41579-018-0004-5, 2018.
- Zhai, X., Johnson, H. L., and Marshall, D. P.: Significant sink of ocean-eddy energy near western boundaries, *Nature Geoscience*, 3, 608-612, 10.1038/ngeo943, 2010.
- Zhang, C., Gao, H., Yao, X., Shi, Z., Shi, J., Yu, Y., Meng, L., and Guo, X.: Phytoplankton growth response to Asian dust addition in the northwest Pacific Ocean versus the Yellow Sea, *Biogeosciences*, 15, 749-765, 10.5194/bg-15-749-2018, 2018.
- 585 Zhang, J. and Zhang, M. J.: Package ‘spaa’, R package version, 1, 2013.
- Zhang, Z., Wang, W., and Qiu, B.: Oceanic mass transport by mesoscale eddies, *Science*, 345, 322-324, 2014.
- Zhou, J., Deng, Y., Luo, F., He, Z., Tu, Q., and Zhi, X.: Functional molecular ecological networks, *mBio*, 1, 10.1128/mBio.00169-10, 2010.