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Ocean acidification reduces diatom and photosynthetic gene abundance on plastic in an coastal bay mesocosm experiment

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ABSTRACT

Discarded plastics are accumulating in the global ocean and posing threats to marine life. The plastisphere - the community colonizing plastic surfaces - profoundly influences the environmental behavior of plastic, affecting its degradation and entry into marine food webs. Ocean acidification (OA) due to anthropogenic CO_2 emissions, is also threatening marine ecosystems, but the effect of OA on the structure and ecological functions of plastisphere communities remain poorly understood. Here, using a mesocosm experiment, we investigated the effects of OA on the plastisphere colonizing floating PET plastic bottles. The study was conducted using subtropical eutrophic coastal water from Southern China under two CO_2 conditions: increased CO_2 to 1000 μatm (HC) and ambient CO_2 410 μatm (LC). Metagenomic sequencing of the plastic samples, after exposure for 32 days, showed striking changes in relative abundance of eukaryotes and bacteria caused by HC. There was a 75.3 % decrease in eukaryote read abundances at high CO_2, most strikingly a 95.6% decrease in the relative abundance of diatoms. In addition, the relative abundance of genes involved in photosystem II light reactions and pigment synthesis decreased under high CO_2 conditions. This suggests that OA could reduce the photosynthetic potential of the plastisphere. Shifts in plastisphere community structure and potentially diminished photosynthesis under OA could influence food chains within plastisphere, plastic degradation, transportation, and carbon cycling involving plastics. Overall, our results suggest that OA can alter the functional ecology of the plastisphere, with potential implications for marine biogeochemical processes and food web dynamics in subtropical eutrophic coastal water.

1. Introduction

Among the various global environmental challenges occurring simultaneously, the accumulation of plastic debris has become a significant threat to marine ecosystems (Bergmann et al., 2017; Ryan and Moloney, 1993). Each year, about 236,000 metric tons of plastic enter the global ocean (Cressey, 2016; Van Sebille et al., 2015), causing countless deaths of marine animals (Thompson et al., 2009; Worm et al., 2017). Due to their physical and chemical durability, marine plastic items can last for decades, before being gradually broken down by a combination of UV light exposure and microbial activity (Du et al., 2022; Napper and Thompson, 2020; Worm et al., 2017), with a half-life ranging from weeks to years (Lott et al., 2021). Large pieces of plastic break down into smaller fragments, known as microplastics and nanoplastics (Franzellitti et al., 2019; Guzzetti et al., 2018; Sharma and Chatterjee, 2017; Wright et al., 2013), which pose significant environmental threats due to their small size and wide distribution.

Plastic objects in the ocean quickly acquire surface biofilms, known as the plastisphere (Amaral-Zettler et al., 2020; Qian et al., 2022). The formation of the plastisphere, driven by microbial succession, proceeds

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through sequential stages: organic conditioning (surface conditioning), microbial attachment, extracellular polymeric substances (EPS) production, and community maturation (De Carvalho, 2018; Qian et al., 2022; Remple et al., 2021). Plastic as an artificial physical substrate can also be bioavailable, in the sense that microorganisms within it can metabolize plastics and dissolved organic matter leached from the plastic (Vaksmaa et al., 2024), and thus plastic-derived carbon can alter the overall concentration and characteristics of stored organic carbon by changing the composition of bioavailable carbon, ultimately impacting the structure and function of ecosystems (Huang and Xia, 2024).

While plastics build up in the ocean, ocean acidification (OA) is simultaneously affecting marine ecosystems. This is caused by increasing CO_2 in the atmosphere dissolving in seawater to form carbonic acid, lowering seawater pH (Doney et al., 2020; Gattuso and Hansson, 2011). According to the IPCC, pH will decrease by a further ~0.15 and 0.4 units by 2100 under the medium and high CO_2 emissions scenario (RCP4.5, RCP8.5) (IPCC et al., 2023). Numerous experiments indicate that OA caused by future levels of atmospheric CO_2 will have profound effects on bacteria, phytoplankton, zooplankton, and animals in the ocean (Fabricius et al., 2011; Kroeker et al., 2012; Huang et al., 2024; Rodolfo-Metalpa et al., 2011). Laboratory studies show that phytoplankton responses range from positive and negative to neutral, varying by species (Gao et al., 2020). While a mesocosm experiment found that OA inhibited the succession of algal blooms from diatoms to dinoflagellates, suggesting diatoms benefit more (Huang et al., 2021). For marine bacteria, no significant OA impact has been generally observed (Joint et al., 2011). Similarly, zooplankton responses are species-specific, with OA potentially altering food web dynamics through changes in predator-prey interaction (Hammill et al., 2018). The plastisphere typically comprises primary producers (e.g., cyanobacteria and diatoms), predators (e.g., ciliates and hydroids), grazers (e.g., ciliates and bryozoans), organisms in symbiotic relationships, and heterotrophs (Amaral-Zettler et al., 2020). Understanding how OA affects the plastisphere is essential to evaluating the compounded ecological consequences of concurrent anthropogenic stressors. However, only a limited number of studies on the effects of OA on the plastisphere have been reported to date. Harvey et al. (2020) and Kerfahi et al. (2023) examined the effects of elevated CO_2 on the plastisphere using natural CO_2 seeps in Japan and revealed significant shifts in microbial community structure and functional gene abundance, notably a pronounced increase in diatom relative abundance under high-CO_2 conditions. Zhang et al. (2023) carried out a mesocosm experiment in eutrophic subtropical seawater in the East China Sea to investigate OA impacts on the plastisphere. The findings revealed that the high CO_2 marine environment significantly altered the prokaryotic community, with a relative increase in abundance of the phylum Planctomycetes of 49%, with no significant changes in eukaryotic communities based on 16S and 18S rDNA gene sequencing, which are widely methods used for profiling prokaryotic and eukaryotic microbial communities in environmental samples (Zhang et al., 2023). These findings diverge from earlier mesocosm-based investigations which reported limited effects of OA on both phytoplankton and bacterioplankton community composition (Huang et al., 2021; Lin et al., 2018). This highlights the need to move beyond taxonomic profiling to decipher the functional mechanisms underlying OA-driven changes.

Here, we employed metagenomic sequencing to investigate OA impacts on the plastisphere through mesocosm experiments. Global plastic production is currently dominated by a few key polymers, including polyethylene (PE), polypropylene (PP), polyvinyl chloride (PVC), and polyethylene terephthalate (PET), which are ubiquitous in daily life due to their durability and flexibility (P.G.C and P. and Amila Sandaruwan, 2024; Rhodes, 2018). Among these, PET is of particular environmental concern as it is the primary material used for single-use drinking bottles, making it a prevalent substrate in marine litter (De Vos et al., 2021). By utilizing PET as a representative model, we leveraged metagenomics primarily to discern shifts in functional profiles under OA conditions, while simultaneously characterizing taxonomic changes that might be overlooked by conventional amplicon sequencing. This study could advance a mechanistic understanding of OA's impact on the plastisphere and enable evaluation of the ecological consequences of the combination of OA and plastic pollution.

2. Materials and methods

2.1. Experimental setup

This study was carried out in Wuyuan Bay, Xiamen, China (24°31′48.00″N, 118°10′04.70″E) from October 9, 2019, over 32 days using The Mesocosm Facility for Ocean Acidification Impact Study of State Key Laboratory of Marine Environmental Science (MEL, Xiamen University) (FOANIC-XMU) platform (Supplementary Figure 1). We have successfully conducted six mesocosm experiments since 2013 utilizing this platform (Huang et al., 2021; Lin et al., 2018; Liu et al., 2017; Zhang et al., 2018, 2023). To simulate seawater conditions with a projected CO_2 concentration of 1000 μatm by the year 2100, approximately 11 L of CO_2-saturated seawater (referred to as HC) were added to polyurethane mesocosm bags (3 m deep, 1.5 m diameter) each filled with 3000 L *in situ* seawater that had been prefiltered (MU801-4T, Midea, China, pore size of 0.01 μm). These mesocosm bags with CO_2 saturated water were numbered 1, 3, 5, 7, and 9 served as high CO_2 controls (HC). Mesocosm bags 2, 4, 6, and 8 served as low CO_2 controls (LC) were not added with CO_2 saturated seawater. To maintain the CO_2 concentrations, both LC and HC bags were aerated with air containing 410 μatm CO_2 and premixed air-CO_2 with 1000 μatm CO_2 (5 L min^{-1}) in LC and HC treatment, respectively. After the carbonate system had been stabilized, and each mesocosm was inoculated with 80 L of *in situ* seawater filtered by a 180 μm mash to exclude large zooplankton, to initiate the coastal community (Supplementary Figure 1 a). Inside each mesocosm bag, three drinking plastic bottles were attached to the aeration tubes, as illustrated in Supplementary Figure 1 b. Seawater samples were collected by niskin bottle from 0.5 m depth every 1-3 days to measure pH_{total} and total alkalinity using an Environmental Water Analyzer (iSEA; Ma et al. (2018) and an Automated Spectrophotometric Analyzer (Li et al., 2013), respectively. The pH value of HC was 0.15-0.3 unit lower than that of LC from day 10 until day 32, as illustrated in Table 1. The pH was systematically lower in the HC treatment than in the LC treatment throughout the entire experiment. The phytoplankton community in the mesocosm was initially dominated by diatoms and then transitioned to nanoplankton in the late stage of the experiment (Rao et al., 2025). There were no significant differences in phytoplankton biomass and community between the HC and LC treatments throughout the experiment (Rao et al., 2025).

Table 1
The statistical significance of the pH difference between the High CO_2 (HC) and LowCO_2 (LC) groups as assessed by the Welch t-test at different time points.

Day	|ΔpH (LC − HC)|(Mean)	ΔpH(Sd)	p_Value
0	0.038	0.019	0.115
2	0.047	0.0095	0.003
4	0.043	0.012	0.017
6	0.034	0.033	0.349
8	0.080	0.040	0.096
10	0.200	0.089	0.059
12	0.262	0.16	0.150
14	0.230	0.16	0.201
16	0.219	0.12	0.152
20	0.183	0.071	0.070
22	0.150	0.033	0.004
24	0.129	0.023	0.002
26	0.111	0.035	0.032
29	0.137	0.037	0.016
32	0.107	0.035	0.022

2.2. Sampling, DNA extraction, shotgun metagenome sequencing, and data processing

After 32 days, the plastic bottles were taken out of the mesocosm. The plastisphere is considered to have entered a relatively mature stage following 32 days of incubation (Erni-Cassola et al., 2020; Wright et al., 2020). Two plastic bottles were randomly selected from a pool of three bottles for each bag (Zhang et al., 2023). The samples were washed with a lysis buffer (70 °C; composition: 100 mM Tris, 40 mM ethylenediaminetetraacetic acid, 100 mM NaCl, 1% sodium dodecyl sulfate) from plastic bottles. Subsequently, DNA extraction was performed using a preheated lysis buffer, followed by phenol-chloroform extraction and ethanol precipitation. The extracted DNA from the samples was then utilized for further analysis. DNA samples were sequenced for the whole metagenome using the Illumina MiSeq PE300 platform (Majorbio Bio-pharm Technology Co. Ltd.). Raw FASTQ sequences were pre-processed using fastp (v0.20.0) to remove adapter sequences, filter low-quality reads, and perform quality control. Clean reads were assembled into contigs using Megahit (v1.1.2). All sequencing data have been deposited in the NCBI Sequence Read Archive (SRA) under accession number PRJNA856479.

2.3. Gene prediction, taxonomy, and functional annotation

Open reading frames (ORFs) were predicted from assembled contigs using Prodigal (http://metagene.cb.k.u-tokyo.ac.jp/, v2.6.3), and genes with nucleotide lengths ≥100 bp were retained and translated into protein sequences using Emboss 6.6.0 (http://emboss.open-bio.org/, V6.6.0) and the NCBI translation table. (http://www.ncbi.nlm.nih.gov/Taxonomy/taxonomyhome.html/index.cgi?chapter=tgencodes#SG1). All predicted genes from each sample were clustered using CD-HIT (http://www.bioinformatics.org/cd-hit/, version 4.6.1) with 90% sequence identity and 90% coverage. High-quality reads were aligned to the non-redundant gene catalogs to calculate gene abundance with 95% identity using SOAPaligner (http://soap.genomics.org.cn/, version 2.21). The longest sequence in each cluster was selected as the representative to construct a non-redundant gene catalog. The non-redundant gene set was aligned against the NCBI NR database (nr_v20200604) using DIAMOND (BLASTP, e-value ≤ 1e-5). Functional annotation was further performed using the KEGG (v94.2) and GO (GO20200604) databases with DIAMOND (https://github.com/bbuchfink/diamond, version 0.8.35) under the same BLASTP parameters. KEGG is an integrated database resource that supports the biological interpretation and annotates the molecular functions of genes and proteins by associating them with ortholog groups (Kanehisa et al., 2016). Gene Ontology (GO) is a standardized framework that annotates genes and their products across species by hierarchically categorizing their functions into three ontologies: Biological Process, Molecular Function, and Cellular Component (Kanehisa et al., 2016).

2.4. Statistical analysis

Differences in pH values between HC and LC groups across different time points were assessed using one-way ANOVA in SPSS. Alpha diversity indices were calculated using mothur (v1.30.1), while beta diversity was determined based on Bray–Curtis dissimilarity using the vegan and stats packages in R (Version 3.3.1) (Dixon, 2003). Group differences in community structure were tested with the ANOSIM function.

Differences in functional profiles and gene abundance between treatment groups were evaluated using the Wilcoxon rank-sum test in R, with p-values <0.05 considered statistically significant. Venn diagrams, community bar plots, and heatmaps were generated using R, with heatmaps plotted via the pheatmap package. Principal Coordinates Analysis (PCoA) was performed using Bray–Curtis distances. Taxonomic biomarkers were identified using LEfSe analysis, with a default LDA score threshold of 2.0 and significance defined as $p < 0.05$ (Segata et al., 2011).

3. Results

3.1. The effects of high CO_2 on the plastisphere community structure at the broad taxonomic level

A total of 507 million raw reads were extracted from plastic samples, corresponding to 3.8 million non-redundant genes. Among all non-redundant genes, approximately 2.5 million were classified as bacteria-derived, 5150 as virus-derived, 277,220 as eukaryote-derived, and 8827 as fungal-derived. Proteobacteria, Bacteroidetes, Planctomycetes, and Actinobacteria were the four most dominant bacterial phyla, constituting 52.3%, 16.1%, 11.5%, and 5.3% of the total bacterial abundance, respectively (Fig. 1 a). In the total annotated eukaryotic community, Bacillariophyta, Chordata, Ciliophora, and Arthropoda were the four most dominant phyla, constituting 53.7%, 8.7%, 8.7%, and 3.9% of the total eukaryotic abundance, respectively (Fig. 1 b). Ascomycota, Basidiomycota, Mucoromycota, and Chytridiomycota were the four most dominant fungal phyla, constituting 37.7%, 22.1%, 18.5%, and 12.4% of the total fungal abundance, respectively (Fig. 1 c). Uroviricota and Nucleocytoviricota were the two most dominant virus phyla, constituting 40.8% and 11.5% of the total virus abundance, respectively (Fig. 1 d).

The Venn diagram indicated that the HC and LC groups collectively contain 20,297 bacterial taxa, 2550 eukaryotic taxa, 395 viral taxa, and 816 fungal taxa, accounting for 75.6%, 83.0%, 50.3%, and 85.8% of the total annotated organisms, respectively (Fig. 2 a, b, c, d). There were many more unique species under HC (5,754) compared to LC (945) for bacteria (Fig. 2 a). We observed an 75.3% reduction in overall eukaryotic sequence abundance under high CO_2 conditions (diatoms) (Supplementary Table 1). Notably, a total of 105 diatom taxa were annotated based on the NR database. The relative abundance of diatoms was markedly higher in the LC group (11.02%) than in the HC group (0.48%) and the relative abundance of diatoms decreased significantly by 95.6% under high CO_2 ($p < 0.05$; Fig. 2e). Among diatom-associated reads, Naviculales, Bacillariales, and Thalassiosirales were the dominant orders, collectively accounting for 97.1% of total diatom reads, and all three orders differed significantly in relative abundance between the HC and LC groups ($p < 0.05$). In addition, 36 diatom taxa showed significant differences in relative abundance between the two groups ($p < 0.05$; Supplementary Table 4). In contrast, the abundance of Actinobacteria increased markedly, with a 14.25 fold increase under high CO_2 ($p < 0.05$; Fig. 2 e).

The PCoA plot shows that viruses, fungi, bacteria, and eukaryotes all exhibit a similar response to high CO_2, with the HC samples being generally dispersed and the LC samples being relatively clustered (Supplementary Figure 2). However, no statistically significant difference in distribution patterns was detected between HC and LC based on ANOSIM analysis (Supplementary Fig. 2). LEfSe analysis (LDA >2) showed that only the genus *Mosigvirus* was enriched in the HC group, while all other significant taxa were associated with the LC group (Supplementary Figure 3).

3.2. The effects of ocean acidification on the gene functions based on KEGG database

Based on metagenomic data, the KEGG database enables the annotation of genes, assignment of their putative functions, mapping of potential functional pathways, and reconstruction of a community's functional profile, with strength in characterizing biogeochemical cycles and metabolic processes. In our study, using metagenomic data and KEGG analysis, we detected changes in microbial functions in plastisphere in response to OA. After aligning the genes of all samples to the

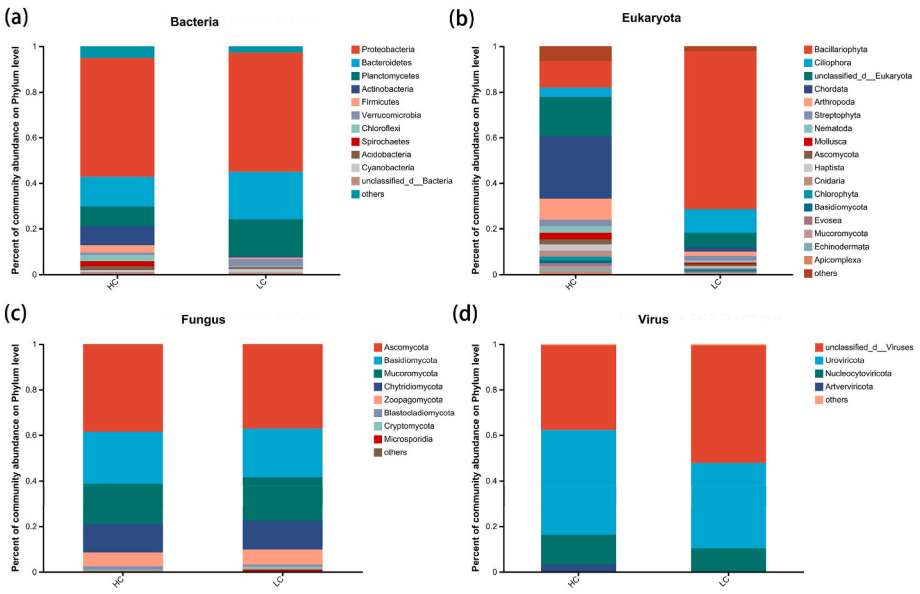

Fig. 1. The community composition of different samples at the phylum level from four different kingdoms (bacteria a, eukaryotes b, Fungus c, Virus d).

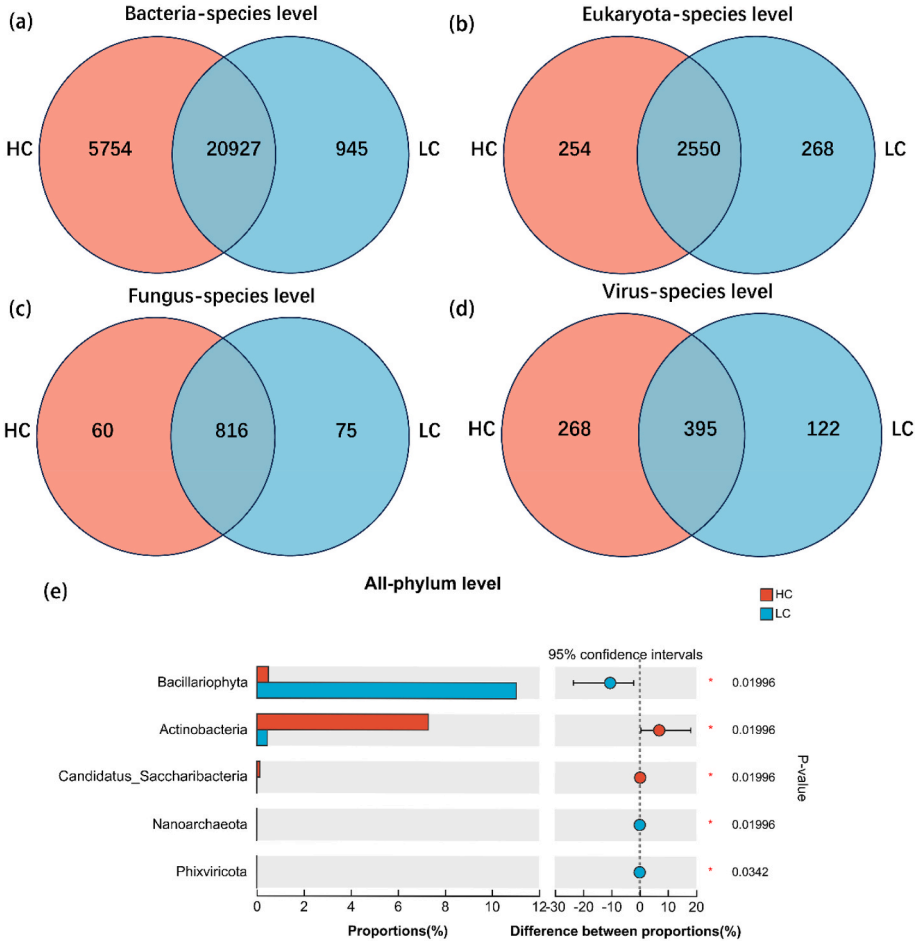

Fig. 2. The Venn diagram of unique species and shared species under HC and LC of the different kingdoms ((bacteria **a**, eukaryotes **b**, Fungus **c**, Virus **d**). Phyla with significant differences in relative abundance between HC and LC in the plastisphere **(e)**.

KEGG database, a total of 14,106 KEGG Orthology (KO) types were obtained. The distribution of genes in KEGG Pathway level 2 is shown in Fig. 3 a. Most KOs showed no significant differences between HC and LC groups, except for Glycan biosynthesis and metabolism, which was reduced in LC compared to HC (Supplementary Figure 4). PCoA at the KEGG Orthology level revealed less heterogeneous sample distribution

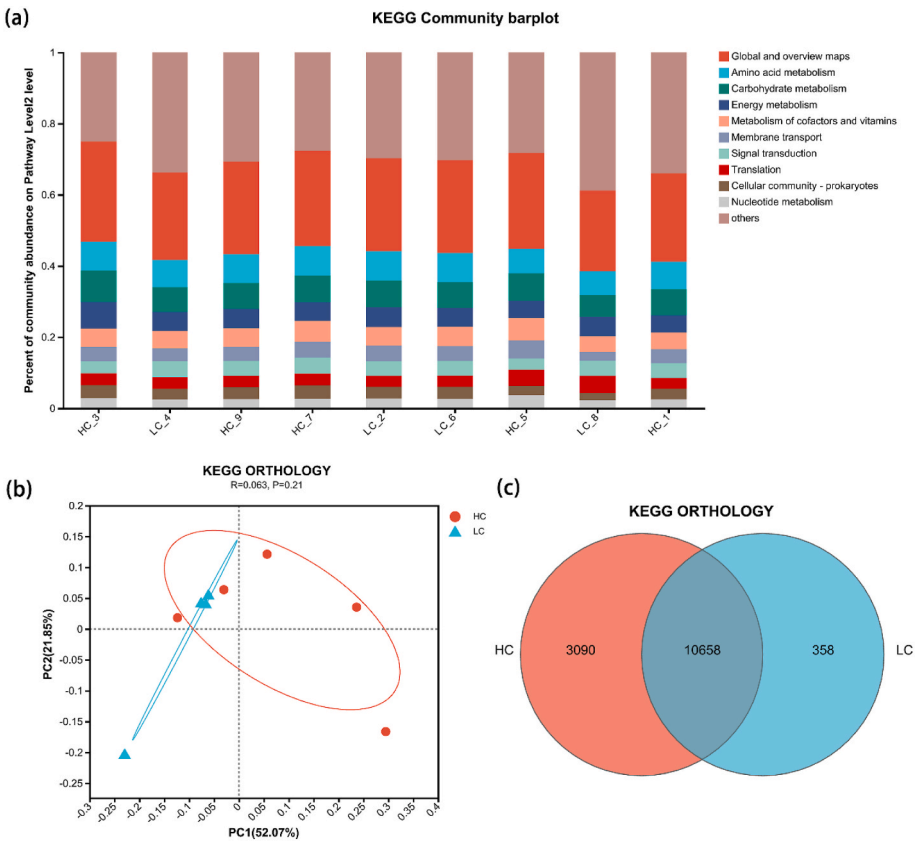

Fig. 3. Relative abundance of KEGG pathways in each sample **(a)**. PCoA analysis of KO between HC and LC (ANOSIM, $p = 0.21$, R = 0.063) **(b)**. The Venn diagram of unique KO and shared KO under HC and LC **(c)**.

under LC than HC, though not statistically significant (Fig. 3 b). The Venn diagram showed that the number of shared KOs between the two treatment groups was 10,658, accounting for 75.6% of the total KOs, and the HC treatment group had many more unique KOs than the LC treatment group (Fig. 3 c).

We further analyzed the genes associated with photosynthesis, focusing on four categories: photosystems, photosynthetic pigments, carbonic anhydrase, and bicarbonate transporters. We identified 10 KOs related to light in photosynthesis and 9 KOs related to photosynthetic pigments, with 3 KOs overlapping between the two categories (Fig. 4 a). In general, the KOs related to light system in photosynthesis and photosynthetic pigments were reduced under HC compared to LC (Wilcoxon rank-sum test, $p < 0.05$). The relative contribution of each taxon to each KEGG ontology is illustrated in Fig. 4 b. At KEGG Pathway level 3, we identified a decrease in the relative abundance of genes related to carotenoid biosynthesis at the plastic interface. To further investigate the impact of high CO_2 on photosynthesis related genes, we analyzed genes associated with photosynthesis at the KEGG Module level. We identified five pathways related to photosynthesis with significant differences in gene relative abundance. These pathways include photorespiration, photosystem II, photosystem I, beta-Carotene biosynthesis, and Cytochrome *b*6f complex, all of which play crucial roles in microbial photosynthesis (Supplementary Table 2). The relative abundance of genes in these pathways exhibited a consistent trend, with lower gene relative abundance under high CO_2 conditions (Wilcoxon rank-sum test, $p < 0.05$) (Supplementary Table 2).

Furthermore, the HC group exhibited a significantly higher relative abundance of functional genes related to Glycerophospholipid metabolism, Vancomycin resistance, and Zeatin biosynthesis compared to the LC group (Supplementary Figure 5). On the other hand, functional genes related to Tuberculosis, Carotenoid biosynthesis, and GABAergic synapse showed significantly lower abundance in the HC group (Supplementary Fig. 5). The top fifteen KEGG Modules with the largest differences in gene relative abundance are shown in Supplementary Figure 6. Noteworthy, genes involved in nitrate the assimilation was lower in the HC treatment group than in the control group at the KEGG Module level (Supplementary Fig. 6). Further exploration revealed that this phenomenon may be attributed to a decrease in the relative abundance of a gene encoding NADH-dependent nitrate reductase (EC1.7.1.1).

3.3. *The effects of ocean acidification on gene functions based on GO database*

GO annotations were utilized to categorize the functional genes. At GO Term level 1, biological process accounted for 63.8%, cellular component accounted for 19.7%, and molecular function accounted for 16.5%. At Term level 2, there were 23 functional gene categories, and the relative abundance of each category is displayed in Fig. 5 a.

Based on LEfSe analysis at GO Term level 3, specific functional categories were associated with either the HC or LC treatment (LDA >2). The GO terms involved in RNA catalytic activity and cell wall organization or biogenesis were associated with the HC treatment, while the photosynthetic membrane was associated with the LC treatment (Supplementary Figure 7).

At GO Term level 4, the HC group had 176 unique terms, the LC group had 42 unique terms, and both groups shared 92 terms (Supplementary Figure 8). PCoA showed greater divergence in HC versus LC samples, though not significant (Fig. 5 b). Significantly higher β-diversity at the level 4 hierarchy of GO Terms under HC compared to LC was detected (Fig. 5 c). In the HC group, there were significant differences (Wilcoxon rank-sum test, $p < 0.05$) in the relative abundance of GO terms related to intrinsic components of the plasma membrane, transferase activity (transferring glycosyl groups), external

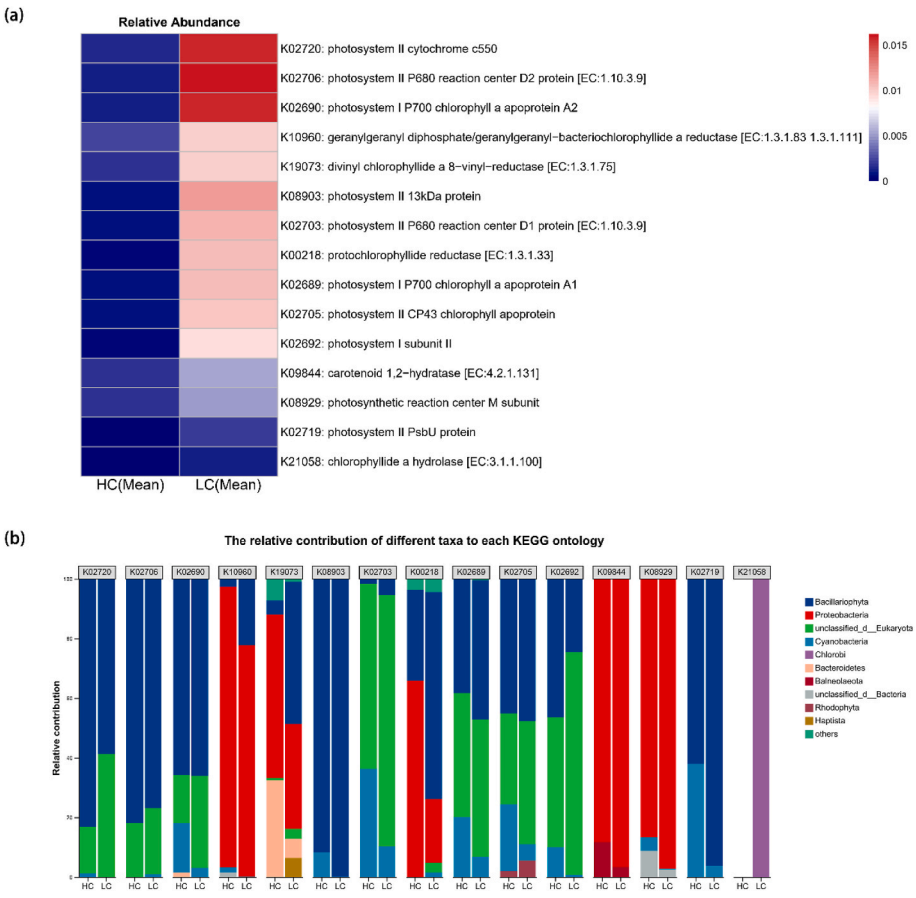

Fig. 4. Heatmap showing photosynthetic pathways with significant differences (Wilcoxon rank-sum test, $p < 0.05$) in relative abundance between HC and LC, numbers in the legend represent relative abundance **(a)**. The relative contribution of different taxa to each KEGG ontology as shown in Fig. 5a. The values on the y-axis represent the relative contribution, indicating the proportion of functional gene abundance within each KEGG category that is attributed to a given taxon **(b)**.

encapsulating structure organization, cell wall organization, cellular aldehyde metabolic process, ribonuclease activity, catalytic activity (acting on rRNA), thylakoid part, thylakoid membrane, plastid part, and photosynthesis (Fig. 5 d). GO Terms associated with photosynthesis showed a decrease in gene abundance under HC (Supplementary Table 3).

4. Discussion

In this study, we employed metagenomic sequencing within a mesocosm experimental framework to investigate OA-induced modifications in both community structure and functional gene repertoire of the plastisphere on drinking water bottles made of PET. This controlled approach enabled mechanistic analysis of how sustained OA may fundamentally reshape plastisphere ecology. Our study revealed that HC conditions drastically reduced eukaryotic reads within the plastisphere by 75.3%, with a particularly severe decline of roughly 95.6% in diatom abundance (Fig. 1, Supplementary Table 4). Moreover, the genes related to photosynthetic processes including light capture, light-dependent reactions, and pigment biosynthesis were decreased in relative abundance under HC (Fig. 3).

Planktonic diatom responses to OA have been found to vary with species and environmental conditions (Bach and Taucher, 2019; Gao and Campbell, 2014; Li et al., 2017; Shi et al., 2019). However, the response of benthic diatoms to OA, which are controlled by their microenvironment, protected by biofilms, and endowed with distinct life-history adaptations, remains understudied. Previous studies have shown that diatoms are the first colonizers of plastic biofilms, particularly those exposed to sunlight, and contribute significantly to the abundance and biomass of the biofilm (Amaral-Zettler et al., 2020; Delacuvellerie et al., 2022; Zhao et al., 2021). As major producers of glycoprotein 'slime' (Rosic, 2021), diatoms have the potential to affect the physical structure and resilience of the biofilm (Wright et al., 2020), and to potentially affect the biofilm's attractiveness and palatability to marine animals which may swallow the plastics (Savoca et al., 2016). Therefore, this dramatic reduction in diatoms within the plastisphere under high CO_2 (HC) could have profound implications for plastisphere dynamics and marine food chains involving plastisphere. Our study suggests that OA may potentially influence the dynamics of community structure of the plastisphere. Typically, plastisphere succession begins with diatom dominance, followed by a gradual decline in their relative abundance over time (Amaral-Zettler et al., 2020). However, we observed significantly lower relative abundance of diatoms within the plastisphere after 32 days under OA, indicating that OA may accelerate the transition from a diatom dominated community to one dominated by other taxa, thus leading to a more rapid decrease in the relative abundance of diatoms within the plastisphere. This shift is likely driven by a combination of reduced recruitment and intensified microbial competition. First, the lower abundance of planktonic diatoms in the surrounding mesocosm seawater under OA at the late stage may have limited the "seed pool" available for plastisphere colonization (Rao et al., 2025). Second, we observed a significant increase in Actinobacteria—a group renowned for degrading complex organic compounds, such as polysaccharides and refractory carbon (Sutaria et al., 2021). We hypothesize that OA potentially altered the bioavailability of carbon leached from the plastic substrates (Huang and Xia, 2024), creating a metabolic niche that favored these heterotrophic decomposers over autotrophic diatoms. Together, these factors suggest

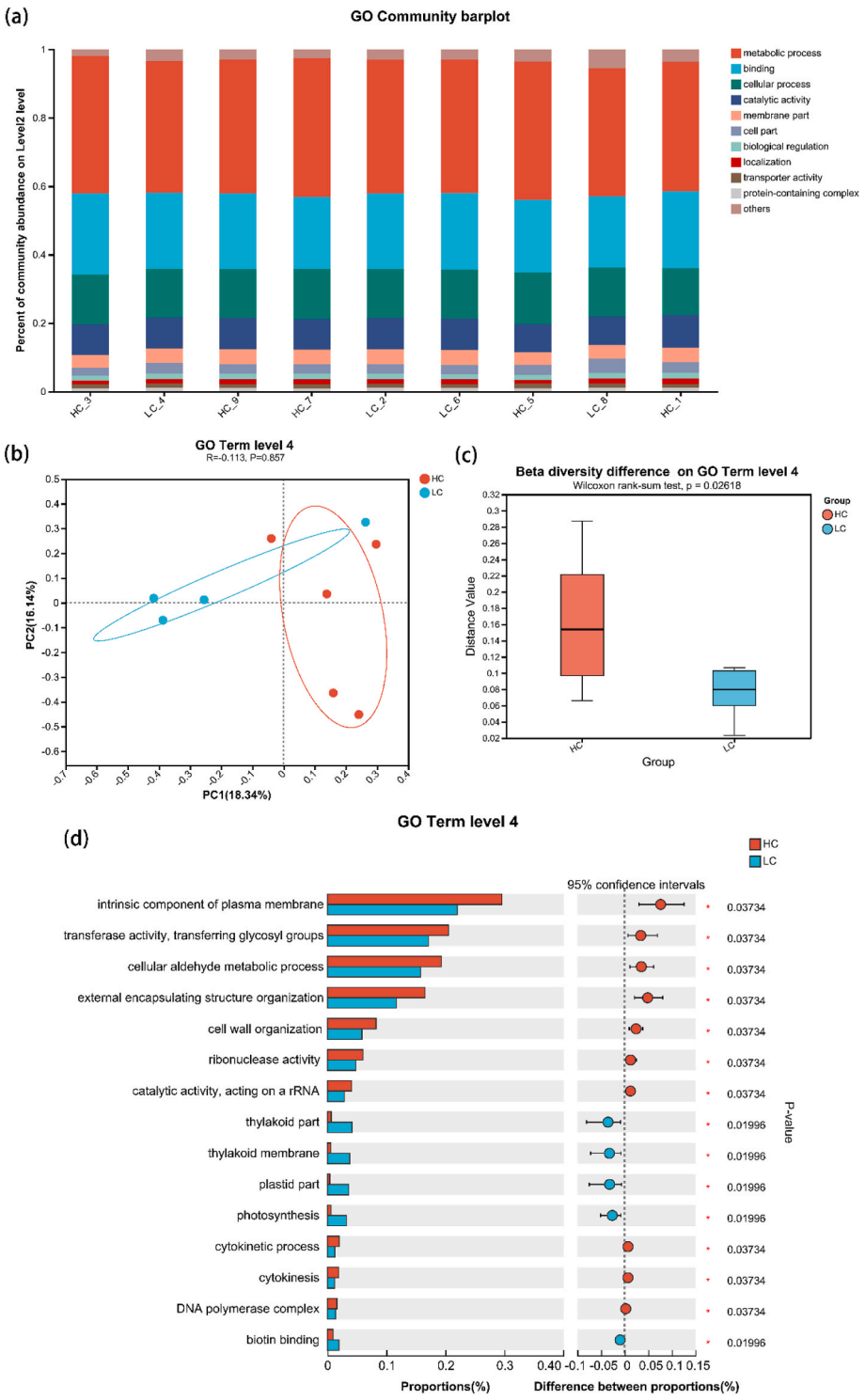

Fig. 5. Relative abundance of GO terms in each sample **(a)**. PCoA analysis of GO terms between HC and LC in level 4 (ANOSIM, $p = 0.857$, $R = 0.113$) **(b)**. Difference in beta diversity between HC and LC under GO term level 4 **(c)**. The fifteen terms with the largest relative abundance differences between HC and LC under GO term level 4 **(d)**.

that OA accelerated the successional transition of the plastisphere from a diatom-dominated community to a heterotroph-dominated one, ultimately leading to the observed loss of diatom dominance. However, further in-depth research is needed to elucidate the underlying mechanisms driving the observed shift.

In contrast to our findings, previous studies have demonstrated that elevated CO_2 levels increased the abundance of diatoms. Kerfahi et al. (2023) found an increase in the relative abundance of diatoms colonizing plastic debris at higher CO_2 concentrations at a natural CO_2 seep in coastal waters off Japan. Other studies on biofilms or benthic mats on natural or artificial substrata also showed an increase in diatom relative abundance under OA. In a coastal CO_2 gradient around a shallow water cold vent system off the island of Vulcano (NE Sicily, Italy), high CO_2 levels with pH values of 8.05 and 7.49 increased the abundance of diatoms in biofilms on perspex slides (Johnson et al., 2013). A study conducted along natural seawater CO_2 gradients in the

north Pacific Ocean basin demonstrated that growth of the large diatom *Biddulphia biddulphiana* - which attaches to benthic substrata and forms mats - was markedly enhanced by higher pCO_2 levels (Harvey et al., 2019). These discrepancies may stem from variations in environmental conditions, such as light intensity, nutrient availability, and temperature, as well as top-down control (e.g., microzooplankton herbivory). For instance, studies have shown that nutrient levels and grazing pressure jointly modulate benthic diatom responses to short-term ocean acidification and warming (Baure et al., 2024; Johnson et al., 2013). Therefore, regional differences in plastisphere responses to ocean acidification are a critical factor, making it imperative to expand research into different ocean areas and habitats.

Our finding of decreased diatom abundance under high CO_2 conditions provides a more nuanced perspective compared to our previous study (Zhang et al. (2023). While our earlier work detected no significant OA-induced changes in diatom relative abundance and other major eukaryotic groups using 18S rDNA amplicon sequencing (Supplementary Figure 9). This discrepancy likely stems from the inherent methodological differences between amplicon sequencing and metagenomics: the universal 18S V9 primers may reduce efficiency for benthic eukaryotes within the plastisphere due to sequence variation and database limitations, while metagenomics avoids these PCR biases and better captures rare taxa and total diversity (Liu et al., 2021; Rausch et al., 2019). Thus, metagenomics might offer a different, and potentially more ecologically relevant, perspective on OA-induced community changes by reflecting shifts in genomic potential and avoiding amplification biases.

In addition to changes in taxonomic community composition, metagenomic sequencing can offer more information in terms of functional genes. Our results based on the KEGG annotation showed decreases in genes related photosynthetic processes under HC, including light capture, light-dependent reactions, and pigment biosynthesis, indicating a potential decline in the photosynthetic light reactions within the plastisphere under OA conditions. Furthermore, our results showed that plasma membrane and cell wall related genes were reduced under OA based on GO database, which were also potentially associated with photosynthesis. The reduced abundance of gene related to photosynthesis may suggest a potential downregulation of this pathway and could be interpreted as a indicating weakening of the photosynthetic capability in the plastisphere community under high CO_2 conditions (Fig. 4 a). Under OA, the community appears to be moving away from a phototrophic foundation towards a more exclusively heterotrophic state, probably driven by the degradation of the plastic polymer and consumption of dissolved organic carbon. Consequently, OA may fundamentally steer the plastisphere more towards a 'degradation consortium'. While a decrease in photosynthesis gene abundance does not necessarily equate to reduced activity, this genomic downregulation nonetheless points to a potential contraction in the energetic investment toward autotrophy. Concurrently, we also found that decreased relative abundance of genes for enzymes related to nitrate assimilation decreased, which may be directly linked to reduced photosynthetic activity, as lower photosynthetic output diminishes the demand for nitrogen-containing compounds (e.g., chlorophyll, photosynthetic enzymes, and proteins) (Supplementary Figure 6). Taken together, these findings support the notion that OA exerts a selective pressure shifting the PET plastisphere toward a more heterotrophic state. However, whether the reduction of photosynthesis genes under OA observed here is a universal phenomenon across other commonly used plastics remains an area for future investigation.

In contrast to reported CO_2 concentration mechanisms (CCMs) downregulation in planktonic diatoms under OA (Gao and Campbell, 2014; Shi et al., 2019), our study found no significant changes in CCMs gene abundance (Fig. 2). This result indicates that the process of inorganic carbon assimilation in plastisphere photosynthetic organisms may be unaffected by OA. The majority of benthic diatoms within biofilms rely on photosynthesis, but some diatoms, such as *Cylindrotheca closterium* within biofilms have the capacity for mixotrophy, which allows them to absorb organic matter from their surroundings (Kumar et al., 2024; Paterson and Hope, 2021). We speculate that OA influences the capacity of diatoms within biofilms to assimilate organic matter, potentially resulting in diminished abundance of photosynthetic genes associated with light reactions and a reduction in diatom abundance under OA. This hypothesis requires further empirical examination in the future.

Our study suggests that OA may reduce photosynthesis in the plastisphere, which could decrease particulate organic carbon, therefore influencing the carbon cycle involving plastics. Additionally, OA triggers community shifts within the plastisphere, which might affect the buoyancy of plastic particles, potentially influencing their oceanic transport and the dispersal of associated organisms (Wright et al., 2020; Du et al., 2022). While these modifications could impact nutrient fluxes and food web interactions on a broader scale, their ecological significance remains to be fully quantified. Our findings stem from observations in the subtropical eutrophic coastal waters of the East China Sea. For better understanding of the interactions between global change and plastic pollution, research is needed in different marine regions, types and sizes of plastics, seawater temperatures, and different concentrations of CO_2.

Our findings should be interpreted within the specific environmental and temporal framework of this study. First, while OA is a gradual, long-term process, our 32-day experiment utilized an acute pH shift. Although this timeframe cannot fully replicate centennial processes, it offers a high-pressure scenario to reveal the immediate physiological sensitivity of the plastisphere and initial successional responses to pH stress. Second, samples were taken solely at the final time point due to logistical constraints, precluding a dynamic view of community succession. Third, plastic debris can remain afloat for years or even decades, accumulating distinct and diverse plastisphere communities across different regions. The long-term successional dynamics and the cumulative effects of chronic OA exposure may therefore differ from these early-phase observations. Fourth, the removal of macrozooplankton (180 μm) inherently reduced top-down grazing pressure in our study, which may have caused the community responses to deviate from those in natural systems.

CRediT authorship contribution statement

Zheng Chen: Writing – original draft. **Dorsaf Kerfahi:** Writing – original draft. **XueQian He:** Funding acquisition, Data curation. **Xu Zhang:** Methodology, Investigation. **Ping Zhang:** Investigation. **Guang Gao:** Conceptualization. **Kunshan Gao:** Investigation, Data curation, Conceptualization. **Jason M. Hall-Spencer:** Conceptualization. **Jonathan M. Adams:** Data curation, Conceptualization. **Xin Lin:** Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of generative AI and AI-assisted technologies in the manuscript preparation process

During the preparation of this work the authors used Gemini in order to polish English. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

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Declaration of competing interest

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

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2026.107917.

Data availability

Data will be made available on request.

References

Amaral-Zettler, L.A., Zettler, E.R., Mincer, T.J., 2020. Ecology of the plastisphere. Nat. Rev. Microbiol. 18, 139–151. https://doi.org/10.1038/s41579-019-0308-0.

Bach, L.T., Taucher, J., 2019. CO_2 effects on diatoms: a synthesis of more than a decade of ocean acidification experiments with natural communities. Ocean Sci. 15, 1159–1175. https://doi.org/10.5194/os-15-1159-2019.

Baure, J.G., Roleda, M.Y., Juinio-Menez, M.A., 2024. Benthic diatom response to short-term acidification and warming influenced by grazing and nutrients. Mar. Pollut. Bull. 208, 116956. https://doi.org/10.1016/j.marpolbul.2024.116956.

Bergmann, M., Tekman, M.B., Gutow, L., 2017. Marine litter: sea change for plastic pollution. Nature 544, 297. https://doi.org/10.1038/544297a.

Cressey, D., 2016. Bottles, bags, ropes and toothbrushes: the struggle to track ocean plastics. Nature 536, 263–265. https://doi.org/10.1038/536263a.

De Carvalho, C.C.C.R., 2018. Marine biofilms: a successful microbial strategy with economic implications. Front. Mar. Sci. 5, 126. https://doi.org/10.3389/fmars.2018.00126.

De Vos, L., Van de Voorde, B., Van Daele, L., Dubruel, P., Van Vlierberghe, S., 2021. Poly (alkylene terephthalate)s: from current developments in synthetic strategies towards applications. Eur. Polym. J. 161, 110840. https://doi.org/10.1016/j.eurpolymj.2021.110840.

Delacuvellerie, A., Geron, A., Gobert, S., Wattiez, R., 2022. New insights into the functioning and structure of the PE and PP plastispheres from the Mediterranean Sea. Environ. Pollut. 295, 118678. https://doi.org/10.1016/j.envpol.2021.118678.

Dixon, P., 2003. VEGAN, a package of R functions for community ecology. J. Veg. Sci. 14, 927–930. https://doi.org/10.1111/j.1654-1103.2003.tb02225.x.

Doney, S.C., Busch, D.S., Cooley, S.R., Kroeker, K.J., 2020. The impacts of ocean acidification on marine ecosystems and reliant human communities. Annu. Rev. Environ. Resour. 45, 83–112. https://doi.org/10.1146/annurev-environ-012320-083019.

Du, Y., Liu, X., Dong, X., Yin, Z., 2022. A review on marine plastisphere: biodiversity, formation, and role in degradation. Comput. Struct. Biotechnol. J. 20, 975–988. https://doi.org/10.1016/j.csbj.2022.02.008.

Erni-Cassola, G., Wright, R.J., Gibson, M.I., Christie-Oleza, J.A., 2020. Early colonization of weathered polyethylene by distinct bacteria in marine coastal seawater. Microb. Ecol. 79, 517–526. https://doi.org/10.1007/s00248-019-01424-5.

Fabricius, K.E., Langdon, C., Uthicke, S., Humphrey, C., Noonan, S., De'ath, G., Okazaki, R., Muehllehner, N., Glas, M.S., Lough, J.M., 2011. Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations. Nat. Clim. Change 1, 165–169. https://doi.org/10.1038/nclimate1122.

Franzellitti, S., Canesi, L., Auguste, M., Wathsala, R.H.G.R., Fabbri, E., 2019. Microplastic exposure and effects in aquatic organisms: a physiological perspective. Environ. Toxicol. Pharmacol. 68, 37–51. https://doi.org/10.1016/j.etap.2019.03.009.

Gao, K., Campbell, D.A., 2014. Photophysiological responses of marine diatoms to elevated CO_2 and decreased pH: a review. Funct. Plant Biol. 41, 449–459. https://doi.org/10.1071/FP13247.

Gao, K., Gao, G., Wang, Y., Dupont, S., 2020. Impacts of ocean acidification under multiple stressors on typical organisms and ecological processes. Mar. Life Sci. Technol. 2, 279–291. https://doi.org/10.1007/s42995-020-00048-w.

Gattuso, J.P., Hansson, L. (Eds.), 2011. Ocean Acidification. Oxford University Press, Oxford. https://doi.org/10.1093/oso/9780199591084.001.0001.

Guzzetti, E., Sureda, A., Tejada, S., Faggio, C., 2018. Microplastic in marine organism: environmental and toxicological effects. Environ. Toxicol. Pharmacol. 64, 164–171. https://doi.org/10.1016/j.etap.2018.10.009.

Hammill, E., Johnson, E., Atwood, T.B., Harianto, J., Hinchliffe, C., Calosi, P., Byrne, M., 2018. Ocean acidification alters zooplankton communities and increases top-down pressure of a cubozoan predator. Glob. Change Biol. 24, e128–e138. https://doi.org/10.1111/gcb.13973.

Harvey, B.P., Agostini, S., Kon, K., Wada, S., Hall-Spencer, J.M., 2019. Diatoms dominate and alter marine food-webs when CO_2 rises. Diversity 11, 242. https://doi.org/10.3390/d11120242.

Harvey, B.P., Kerfahi, D., Jung, Y., Shin, J.H., Adams, J.M., Hall-Spencer, J.M., 2020. Ocean acidification alters bacterial communities on marine plastic debris. Mar. Pollut. Bull. 161, 111749. https://doi.org/10.1016/j.marpolbul.2020.111749.

Huang, R., Sun, J., Yang, Y., Jiang, X., Wang, Z., Song, X., Wang, T., Zhang, D., Li, H., Yi, X., Chen, S., Bao, N., Qu, L., Zhang, R., Jiao, N., Gao, Y., Huang, B., Lin, X., Gao, G., Gao, K., 2021. Elevated pCO2 impedes succession of phytoplankton community from diatoms to dinoflagellates along with increased abundance of viruses and bacteria. Front. Mar. Sci. 8, 642208. https://doi.org/10.3389/fmars.2021.642208.

Huang, W., Xia, X., 2024. Element cycling with micro(nano)plastics. Science 385, 933–935. https://doi.org/10.1126/science.adr3421.

Huang, R., Zhang, P., Zhang, X., Chen, S., Sun, J., Jiang, X., Zhang, D., Li, H., Yi, X., Qu, L., Wang, T., Gao, K., Hall-Spencer, J.M., Adams, J., Gao, G., Lin, X., 2024. Ocean acidification alters microeukaryotic and bacterial food web interactions in a eutrophic subtropical mesocosm. Environmental Research 257, 119084. https://doi.org/10.1016/j.envres.2024.119084.

IPCC, 2023. Climate change 2023: synthesis report. In: core writing team. In: Lee, H., Romero, J. (Eds.), Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland, pp. 1–173. https://doi.org/10.59327/IPCC/AR6-9789291691647.

Johnson, V.R., Brownlee, C., Rickaby, R.E.M., Graziano, M., Milazzo, M., Hall-Spencer, J. M., 2013. Responses of marine benthic microalgae to elevated CO_2. Mar. Biol. 160, 1813–1824. https://doi.org/10.1007/s00227-011-1841-2.

Joint, I., Doney, S.C., Karl, D.M., 2011. Will ocean acidification affect marine microbes? ISME J. 5, 1–7. https://doi.org/10.1038/ismej.2010.79.

Kanehisa, M., Sato, Y., Kawashima, M., Furumichi, M., Tanabe, M., 2016. KEGG as a reference resource for gene and protein annotation. Nucleic Acids Res. 44, D457–D462. https://doi.org/10.1093/nar/gkv1070.

Kerfahi, D., Harvey, B.P., Kim, H., Yang, Y., Adams, J.M., Hall-Spencer, J.M., 2023. Whole community and functional gene changes of biofilms on marine plastic debris in response to ocean acidification. Microb. Ecol. 85, 1202–1214. https://doi.org/10.1007/s00248-022-01987-w.

Kroeker, K.J., Micheli, F., Gambi, M.C., 2012. Ocean acidification causes ecosystem shifts via altered competitive interactions. Nat. Clim. Change 3, 156–159. https://doi.org/10.1038/nclimate1630.

Kumar, M., Tibocha-Bonilla, J.D., Füssy, Z., Lieng, C., Schwenck, S.M., Levesque, A.V., Al-Bassam, M.M., Passi, A., Neal, M., Zuniga, C., Kaiyom, F., Espinoza, J.L., Lim, H., Polson, S.W., Allen, L.Z., Zengler, K., 2024. Mixotrophic growth of a ubiquitous marine diatom. Sci. Adv. 10, eado2623. https://doi.org/10.1126/sciadv.ado2623.

Li, F., Beardall, J., Collins, S., Gao, K., 2017. Decreased photosynthesis and growth with reduced respiration in the model diatom Phaeodactylum tricornutum grown under elevated CO_2 over 1800 generations. Glob. Change Biol. 23, 127–137. https://doi.org/10.1111/gcb.13340.

Li, Q., Wang, F., Wang, Z.A., Yuan, D., Dai, M., Chen, J., Dai, J., Hoering, K.A., 2013. Automated spectrophotometric analyzer for rapid single-point titration of seawater total alkalinity. Environ. Sci. Technol. 47, 11139–11146. https://doi.org/10.1021/es402421a.

Lin, X., Huang, R., Li, Y., Li, F., Wu, Y., Hutchins, D.A., Dai, M., Gao, K., 2018. Interactive network configuration maintains bacterioplankton community structure under elevated CO_2 in a eutrophic coastal mesocosm experiment. Biogeosciences 15, 551–565. https://doi.org/10.5194/bg-15-551-2018.

Liu, X., Li, Y., Wu, Y., Huang, B., Dai, M., Fu, F., Hutchins, D.A., Gao, K., 2017. Effects of elevated CO_2 on phytoplankton during a mesocosm experiment in the southern eutrophicated coastal water of China. Sci. Rep. 7, 7133. https://doi.org/10.1038/s41598-017-07196-1.

Liu, Y.X., Qin, Y., Chen, T., Lu, M., Qian, X., Guo, X., Bai, Y., 2021. A practical guide to amplicon and metagenomic analysis of microbiome data. Protein Cell 12, 315–330. https://doi.org/10.1007/s13238-020-00724-8.

Lott, C., Eich, A., Makarow, D., Unger, B., van Eekert, M., Schuman, E., Reinach, M.S., Lasut, M.T., Weber, M., 2021. Half-life of biodegradable plastics in the marine environment depends on material, habitat, and climate zone. Front. Mar. Sci. 8, 662074. https://doi.org/10.3389/fmars.2021.662074.

Ma, J., Li, P., Chen, Z., Lin, K., Chen, n., Jiang, Y., Chen, J., Huang, B., Yuan, D., 2018. Development of an integrated syringe-pump-based environmental-water analyzer (iSEA) and application of it for fully automated real-time determination of ammonium in fresh water. Anal. Chem. 90, 6431–6435. https://doi.org/10.1021/acs.analchem.8b00914.

Napper, I.E., Thompson, R.C., 2020. Plastic debris in the marine environment: history and future challenges. Glob. Chall. 4, 1900081. https://doi.org/10.1002/gch2.201900081.

P, G.C., Amila Sandaruwan, R., 2024. The world of plastic waste: a review. Clean. Mater. 11, 100220. https://doi.org/10.1016/j.clema.2024.100220.

Paterson, D.M., Hope, J.A., 2021. Diatom biofilms: ecosystem engineering and niche construction. In: Diatom Gliding Motility, pp. 135–158. https://doi.org/10.1002/9781119526483.ch6.

Qian, P.Y., Cheng, A., Wang, R., Zhang, R., 2022. Marine biofilms: diversity, interactions and biofouling. Nat. Rev. Microbiol. 20, 671–684. https://doi.org/10.1038/s41579-022-00744-4.

Rao, Y., Wang, N., Li, H., Sun, J., Jiang, X., Zhang, D., Qu, L., Fu, Q., Wang, X., Zhou, C., Deng, Z., Tian, Y., Yi, X., Huang, R., Gao, G., Lin, X., Gao, K., 2025. Ocean acidification alters phytoplankton diversity and community structure in the coastal water of the East China Sea. EGUsphere 1–26. https://doi.org/10.5194/egusphere-2024-3453 [Preprint].

Rausch, P., Ruhlemann, M., Hermes, B.M., Doms, S., Dagan, T., et al., 2019. Comparative analysis of amplicon and metagenomic sequencing methods reveals key features in

the evolution of animal metaorganisms. Microbiome 7, 133. https://doi.org/10.1186/s40168-019-0743-1.
Remple, K.L., Silbiger, N.J., Quinlan, Z.A., Fox, M.D., Kelly, L.W., Donahue, M.J., Nelson, C.E., 2021. Coral reef biofilm bacterial diversity and successional trajectories are structured by reef benthic organisms and shift under chronic nutrient enrichment. npj Biofilms Microbio. 7, 84. https://doi.org/10.1038/s41522-021-00253-0.
Rhodes, C.J., 2018. Plastic pollution and potential solutions. Sci. Prog. 101, 207–260. https://doi.org/10.3184/003685018X15294876706211.
Rodolfo-Metalpa, R., Houlbrèque, F., Tambutté, É., Boisson, F., Baggini, C., Patti, F.P., Jeffree, R., Fine, M., Foggo, A., Gattuso, J.P., Hall-Spencer, J.M., 2011. Coral and mollusc resistance to ocean acidification adversely affected by warming. Nat. Clim. Change 1, 308–312. https://doi.org/10.1038/nclimate1122.
Rosic, N.N., 2021. Recent advances in the discovery of novel marine natural products and mycosporine-like amino acid UV-absorbing compounds. Appl. Microbiol. Biotechnol. 105, 7053–7067. https://doi.org/10.1007/s00253-021-11532-w.
Ryan, P.G., Moloney, C.L., 1993. Marine litter keeps increasing. Nature 361, 23. https://doi.org/10.1038/361023a0.
Savoca, M.S., Wohlfeil, M.E., Ebeler, S.E., Nevitt, G.A., 2016. Marine plastic debris emits a keystone infochemical for olfactory foraging seabirds. Sci. Adv. 2, e1600395. https://doi.org/10.1126/sciadv.1600395.
Segata, N., Izard, J., Waldron, L., Gevers, D., Miropolsky, L., Garrett, W.S., Huttenhower, C., 2011. Metagenomic biomarker discovery and explanation. Genome Biol. 12, R60. https://doi.org/10.1186/gb-2011-12-6-r60.
Sharma, S., Chatterjee, S., 2017. Microplastic pollution, a threat to marine ecosystem and human health: a short review. Environ. Sci. Pollut. Res. 24, 21530–21547. https://doi.org/10.1007/s11356-017-9910-8.
Shi, D., Hong, H., Su, X., Liao, L., Chang, S., Lin, W., 2019. The physiological response of marine diatoms to ocean acidification: differential roles of seawater pCO_2 and pH. J. Phycol. 55, 521–533. https://doi.org/10.1111/jpy.12833.
Sutaria, D., Shah, K., Arora, S., Saxena, S., 2021. Actinomycetes as an environmental scrubber. In: Microbial Rejuvenation of Polluted Environment, pp. 237–261. https://doi.org/10.1007/978-981-15-4971-7_10.
Thompson, R.C., Moore, C.J., vom Saal, F.S., Swan, S.H., 2009. Plastics, the environment and human health: current consensus and future trends. Philos. Trans. R. Soc. B Biol. Sci. 364, 2153–2166. https://doi.org/10.1098/rstb.2009.0053.
Vaksmaa, A., Vielfaure, H., Polerecky, L., Kienhuis, M.V.M., van der Meer, M.T.J., Pflüger, T., Egger, M., Niemann, H., 2024. Biodegradation of polyethylene by the marine fungus *Parengyodontium album*. Sci. Total Environ. 934, 172819. https://doi.org/10.1016/j.scitotenv.2024.172819.
Van Sebille, E., Wilcox, C., Lebreton, L., Maximenko, N., Hardesty, B.D., van Franeker, J. A., Eriksen, M., Siegel, D., Galgani, F., Law, K.L., 2015. A global inventory of small floating plastic debris. Environ. Res. Lett. 10, 124006. https://doi.org/10.1088/1748-9326/10/12/124006.
Worm, B., Lotze, H.K., Jubinville, I., Wilcox, C., Jambeck, J., 2017. Plastic as a persistent marine pollutant. Annu. Rev. Environ. Resour. 42, 1–26. https://doi.org/10.1146/annurev-environ-102016-060700.
Wright, R.J., Erni-Cassola, G., Zadjelovic, V., Latva, M., Christie-Oleza, J.A., 2020. Marine plastic debris: a new surface for microbial colonization. Environ. Sci. Technol. 54, 11657–11672. https://doi.org/10.1021/acs.est.0c03057.
Wright, S.L., Thompson, R.C., Galloway, T.S., 2013. The physical impacts of microplastics on marine organisms: a review. Environ. Pollut. 178, 483–492. https://doi.org/10.1016/j.envpol.2013.02.031.
Zhang, S.H., Yu, J., Ding, Q.Y., Yang, G.P., Gao, K.S., Zhang, H.H., Pan, D.W., 2018. Effect of elevated pCO_2 on trace gas production during an ocean acidification mesocosm experiment. Biogeosciences 15, 6649–6658. https://doi.org/10.5194/bg-15-6649-2018.
Zhang, X., Zhang, P., Deng, Z., Huang, R., Zhang, D., Tian, Y., Wang, N., Li, H., Wang, X., Jiang, X., Sun, J., Fu, Q., Yi, X., Qu, L., Zhou, C., Rao, Y., Zeng, X., Hall-Spencer, J. M., Gao, G., Gao, K., Lin, X., 2023. Ocean acidification has a strong effect on communities living on plastic in mesocosms. Limnol. Oceanogr. Lett. 8, 675–684. https://doi.org/10.1002/lol2.10329.
Zhao, S., Zettler, E.R., Amaral-Zettler, L.A., Mincer, T.J., 2021. Microbial carrying capacity and carbon biomass of plastic marine debris. ISME J. 15, 67–77. https://doi.org/10.1038/s41396-020-00756-2.