



# Ocean alkalinity enhancement pelagic impact in the Northwest Iberian Upwelling System under nutrient limited conditions

Marcos Fontela<sup>1</sup>, María Froján<sup>1</sup>, Belén Arbones<sup>1</sup>, María Jesús Álvarez-Fernández<sup>1</sup>, Caio Cesar-Ribeiro<sup>2</sup>, Marylo Doval<sup>3</sup>, José Luís Garrido<sup>1</sup>, Sara Groppelli<sup>4</sup>, María López-Acosta<sup>1</sup>, María López-Rodríguez<sup>1</sup>, Celeste L. Hinojo<sup>1</sup>, Blanca Marigómez<sup>1,5</sup>, Laura Moreno<sup>6</sup>, Fíz F. Pérez<sup>1</sup>, Isabel Gomes Teixeira<sup>1</sup>, Antón Velo<sup>1</sup>, Xosé Antonio Padín<sup>1</sup>

<sup>1</sup>Instituto de Investigaciones Marinas (IIM), CSIC, 36208 Vigo, Spain

<sup>2</sup>CCMAR Centre of Marine Sciences, Universidade do Algarve, Campus de Gambelas, 8005-139 Faro, Portugal.

<sup>3</sup>INTECMAR

<sup>4</sup>University of Milano-Bicocca Department of Earth and Environmental Sciences (DISAT), Milano, Piazza della Scienza 20126, Italy

<sup>5</sup>Universidade de Vigo, Vigo, Spain.

<sup>6</sup>University of Aveiro, Aveiro, Portugal.

Correspondence to: Marcos Fontela (mfontela@iim.csic.es)

**Abstract.** Ocean Alkalinity Enhancement (OAE) is a promising strategy for marine carbon dioxide removal, yet its ecological effects remain largely unexplored in highly dynamic upwelling ecosystems. Here, we examine the response of OAE on a natural plankton community from the NW Iberian Upwelling System (Ría de Vigo) during a diatom bloom in May 2025. Natural *in situ* plankton communities were sampled aboard R/V Mytilus (May 9<sup>th</sup>) and enclosed in nine replicated microcosms exposed to two hydroxide-based OAE treatments and a control (n=3 per group). Microcosms were monitored for 20 consecutive days (9<sup>th</sup>-28<sup>th</sup> May). Total alkalinity, pH, dissolved inorganic nutrients, chlorophyll-*a*, biogenic silica, particulate organic carbon and nitrogen were measured, and samples for light microscopy and flow cytometry were collected. All microcosms showed rapid nutrient drawdown, synchronous declines in particulate organic matter, and a transition from a *Chaetoceros*-dominated diatom assemblage to a more diverse community with increasing contributions of smaller taxa. Microplankton dynamics were characterized by a rapid collapse of the diatom bloom due to inorganic nutrient exhaustion independent of OAE treatments. Only within the smallest size classes there was contrasting OAE responses: while nanoeukaryotes and heterotrophic bacteria remain unaffected, autotrophic picoeukaryotes were negatively influenced by alkalization, and *Synechococcus* abundance increased in the OAE treatments. Under nutrient-limited late diatom-bloom conditions, OAE does not modify microplankton succession nor alter biomass or the potential efficiency of the biological carbon pump. Pelagic ecological impacts to OAE remain low when resource limitation controls phytoplankton community structure. While OAE did not fundamentally alter the upwelling-driven diatom-bloom dynamics in this highly dynamic ecosystem, the ecological outcome under contrasting hydrographic and seasonal scenarios remains to be evaluated.



## 1 Introduction

Reducing anthropogenic carbon dioxide emissions is no longer sufficient to meet the temperature goals of the Paris Agreement, and future climate scenarios consistent with the 1.5 °C target require the deployment of marine-based Carbon Dioxide Removal (mCDR) at meaningful scales (IPCC, 2021). Within the mCDR portfolio, Ocean Alkalinity Enhancement (OAE) has emerged as a promising approach to increase the ocean's long-term capacity to store atmospheric CO<sub>2</sub> (National Academies of Sciences, Engineering, and Medicine (NASEM), 2022). The OAE approach involves increasing the total alkalinity of seawater, thereby shifting the marine carbonate system toward enhanced CO<sub>2</sub> uptake. Electrochemical approaches (electrodialysis, electrolytic) or the addition of different alkaline mineral feedstocks have been proposed, including silicate (olivine) and/or carbonate minerals (quicklime, limestone, sodium or calcium hydroxide), each differing in solubility, reactivity, and potential environmental side effects (National Academies of Sciences, Engineering, and Medicine (NASEM), 2022). Furthermore, OAE has been proposed as a mitigation strategy against ocean acidification, because an increase in alkalinity counteracts the progressive decline in seawater pH and carbonate ion concentrations, which are critical for calcifying organisms (Kroeker et al., 2013). As OAE advances toward field-scale deployment, Monitoring, Reporting and Verification (MRV) frameworks and predictive modelling tools will be essential (Ho and Bopp, 2024). An OAE deployment will only be successful if it strengthens CO<sub>2</sub> uptake through the modification of the physical carbon pump without any drawback in the biological carbon pump neither the ecosystem services.

Pelagic plankton communities are cornerstone to the biological carbon pump (Boyd et al., 2019), and their structure and functioning can be sensitive to changes in carbonate chemistry mediated through OAE. Previous studies have shown that OAE can influence phytoplankton composition, with effects ranging from mild shifts in dominant groups to changes in nutrient drawdown dynamics (Ferderer et al., 2022). Diatoms, in particular, appear susceptible to carbonate-system perturbations (Ferderer et al., 2022), whereas other taxa that are negatively affected by Ocean Acidification may respond positively under elevated alkalinity scenarios (Kousoulas et al., 2025). Rapid chemical shifts associated with OAE have also been shown to stimulate bacterial groups and enzymatic activities, altering short-term microbial processing of organic matter (de Castro et al., 2025). At the same time, mesocosm experiments suggest that OAE may not compromise microbial metabolic rates and photosynthetic efficiency (Oberlander et al., 2025), or the export of nutrients and organic matter in oligotrophic conditions (Marín-Samper et al., 2024; Oberlander et al., 2025). These contrasting results emphasize the need to examine pelagic responses across diverse ecosystems and natural conditions, especially coastal regions characterized by strong seasonality and rapid biogeochemical turnover. The resilience of plankton assemblages, structured by physical forcing, nutrient availability and ecological interactions, remains insufficiently constrained under OAE conditions (Bach et al., 2024).

The plankton community in the coastal Northwest Iberian Upwelling System is a highly-diverse system, typically diatom-dominated during spring and summer (Arbones et al., 2008; Cermeño et al., 2006). Seasonal succession patterns align with Margalef's mandala, alternating between turbulence-driven diatom blooms and stratification-favoured flagellate communities (Margalef, 1978), shaped by wind-driven upwelling events, nutrient pulses, and stratification cycles (Figueiras



et al., 2020; Tilstone et al., 2000). Beyond its ecological relevance, the coastal area supports intense aquaculture activities dominated by calcifying organisms, making the area socially and economically sensitive to ocean acidification (Labarta and Fernández-Reiriz, 2019). Long-term time-series observations have documented the seasonal variability of plankton communities in this system (Bode et al., 2015), though their response to abrupt alkalinity perturbations remains unexplored. Within this context, the goal of this study is to assess the biogeochemical and ecological responses of natural coastal plankton communities to hydroxide-based OAE under diatom bloom conditions. Specifically, we aim to compare two different alkalinity additions treatments (equilibrated with inorganic carbon and unequilibrated, sensu Ferderer et al., (2022) to determine whether transient chemical extremes can disrupt bloom development, community composition, or particle dynamics. Our hypothesis is that the initial status of the community, in terms of size structure and inorganic nutrient availability, will constrain the pelagic response to OAE effects, leading to minimal divergence between treatments despite contrasting initial pH and pCO<sub>2</sub> conditions.

## 2 Methods

The experimental design and analytical procedures followed, as closely as possible, the methodological framework established by the Ocean Alkalinity Enhancement Pelagic Impact Intercomparison Project (OAEPIIP) technical note (Bach et al., 2024). The methodological consistency with the broader OAEPIIP community allows direct comparison with experiences conducted under the same protocol. The subsections below only provide the specific experimental details unique to this study.

### 2.1 Experimental setup

The enclosure of in-situ plankton communities with surface seawater collected from the central Ría de Vigo was done on 9<sup>th</sup> May 2025 during a survey aboard R/V Mytilus (Fig. A1). A complete biogeochemical characterization of the water column was performed before filling (Fig. A2). Each microcosm (54.5 L) was filled gently from the base to minimize shear stress and avoid damaging cells, and the filling process was completed in approximately 70 minutes to ensure comparable initial conditions (Table A1). At the base of each microcosm, a 200 µm mesh was installed to prevent large zooplankton inside the microcosm at time zero.

The experimental design consisted of nine replicate microcosms ( $n = 3$  per treatment), distributed across three conditions: a control, an unequilibrated OAE treatment, and an equilibrated OAE treatment. The chemical reagents added to establish both treatments followed the OAEPIIP technical specifications and were introduced at target doses designed to increase total alkalinity by approximately +500 µmol kg<sup>-1</sup> assuming that each microcosm contains a volume of 54.5 L of seawater (Table 1). The two OAE scenarios differed in their chemical settling: the unequilibrated treatment involved the immediate addition of sodium hydroxide (27.25 mL of 1 molar NaOH, Fisher Scientific S/4920/60 Lot 2525551). In the equilibrated treatment, we added a combination of sodium bicarbonate (NaHCO<sub>3</sub>, Fisher Scientific S/4240/60 Lot 2411754) and sodium hydroxide (NaOH), calculated beforehand so the resulting seawater was in carbonate-system equilibrium with sea surface pCO<sub>2</sub> upon amendment. For the establishment of the equilibrated treatment the observed *in situ* surface seawater pCO<sub>2</sub> (~360 µatm, 4H-



Jena HydroC CO<sub>2</sub>-FT, Fig. A3) and a modelled alkalinity were considered. Background total alkalinity (TA<sub>0</sub>) of the source seawater was estimated from an empirical salinity relationship characteristic for the surface waters of the sampling area (Padin et al., 2020):

$$TA_0 = (66 \times \text{Salinity}) \quad (1)$$

100 where S is the observed salinity of the enclosed seawater (34.3, Fig. A2). The target alkalinity after enhancement is then

$$TA_{0+500} = TA_0 + \Delta TA \quad (2)$$

with  $\Delta TA$  being +500  $\mu\text{mol kg}^{-1}$ . Therefore, we computed the inorganic carbon system for both the initial and target alkalinities at the observed temperature ( $T^a$ , 17°C) and salinity (Sal, 34.3) using the carb() function of the R package seacarb (Gattuso et al., 2003) with constant pCO<sub>2</sub> (360  $\mu\text{atm}$ ) and varying TA as the input pair:

$$105 \quad DIC_0 = \text{carb}(pCO_2, TA_0, \text{Salinity}, T^a) \quad (3)$$

$$DIC_{\text{equilibrated}} = \text{carb}(pCO_2, TA_{0+500}, \text{Salinity}, T^a) \quad (4)$$

The difference in DIC ( $\Delta DIC = DIC_{\text{equilibrated}} - DIC_0$ ) gives the amount of dissolved inorganic carbon that must accompany the alkalinity addition for the water to remain equilibrated with atmospheric pCO<sub>2</sub> after treatment addition. For the sampling conditions, the estimated  $\Delta DIC$  was 416.05  $\mu\text{mol kg}^{-1}$ . Considering the enclosed volume of seawater and since each added mole of NaHCO<sub>3</sub> contributes equally to TA and DIC (1:1), an addition of 22.67 mL 1 molar NaHCO<sub>3</sub> equals this  $\Delta DIC$  of 416.0  $\mu\text{mol kg}^{-1}$ . Since NaOH contributes to TA but not to DIC, the remainder of the target alkalinity increase (84  $\mu\text{mol kg}^{-1}$ , 500  $\mu\text{mol kg}^{-1}$  - 416.0  $\mu\text{mol kg}^{-1}$ ) was supplied with 4.58 mL of 1 molar NaOH (Table 1). In summary, the experiment was amended with 1 molar solutions of 27.25 mL of NaOH per microcosm for the unequilibrated treatment, and 22.67 mL NaHCO<sub>3</sub> plus 4.58 mL NaOH per microcosm for the equilibrated treatment.

115 Microcosms were maintained in a temperature-controlled room, where the system aimed to reproduce *in situ* temperature conditions at the time of enclosure. Illumination was provided by LED light strips, programmed to reproduce the natural photoperiod of May (11 dark: 13 light hours) at the study site.

120

| Treatment      | Addition                                             |                                                      | Measured $\Delta TA$                              |
|----------------|------------------------------------------------------|------------------------------------------------------|---------------------------------------------------|
|                | NaOH (1 M)                                           | NaHCO <sub>3</sub> (1 M)                             |                                                   |
| Control        | /                                                    | /                                                    | /                                                 |
| Unequilibrated | 27.25 mL (500 $\mu\text{mol} \cdot \text{kg}^{-1}$ ) | /                                                    | 499.7 ± 5.0 $\mu\text{mol} \cdot \text{kg}^{-1}$  |
| Equilibrated   | 4.58 mL (84 $\mu\text{mol} \cdot \text{kg}^{-1}$ )   | 22.67 mL (416 $\mu\text{mol} \cdot \text{kg}^{-1}$ ) | 529.2 ± 10.7 $\mu\text{mol} \cdot \text{kg}^{-1}$ |

**Table 1. Summary of treatment setup conditions.** Volumes are the nominal additions per microcosm, with the corresponding alkalinity increase given in parentheses ( $\mu\text{mol kg}^{-1}$ ). Measured  $\Delta TA$  is the difference in total alkalinity between the treated microcosms and the control at the start of the experiment (mean ± SD, n = 3).



## 2.2 Sampling and analysis

The experiment lasted 20 days, from 9<sup>th</sup> to 28<sup>th</sup> May 2025. Temperature and pH were sampled and measured daily (Fig. 1), whereas the sampling frequency for other biogeochemical parameters changed with time. Sampling intensity was highest during the initial phase of the experiment (days 0-4), followed by measurements every two days during the intermediate phase (days 6-10), and a lower sampling frequency thereafter (Fig. 1). Considered tracers included total alkalinity (n=7), dissolved inorganic nutrients (n=11), chlorophyll-*a* (*Chla*, n=11), particulate organic carbon and nitrogen (POC/PON; n=11), biogenic silica (BSi; n=11), flow cytometry (n=11), and light microscopy (n=8) analyses (Fig. 1). Salinity and irradiance were measured only at the start and end of the experiment (n=2).

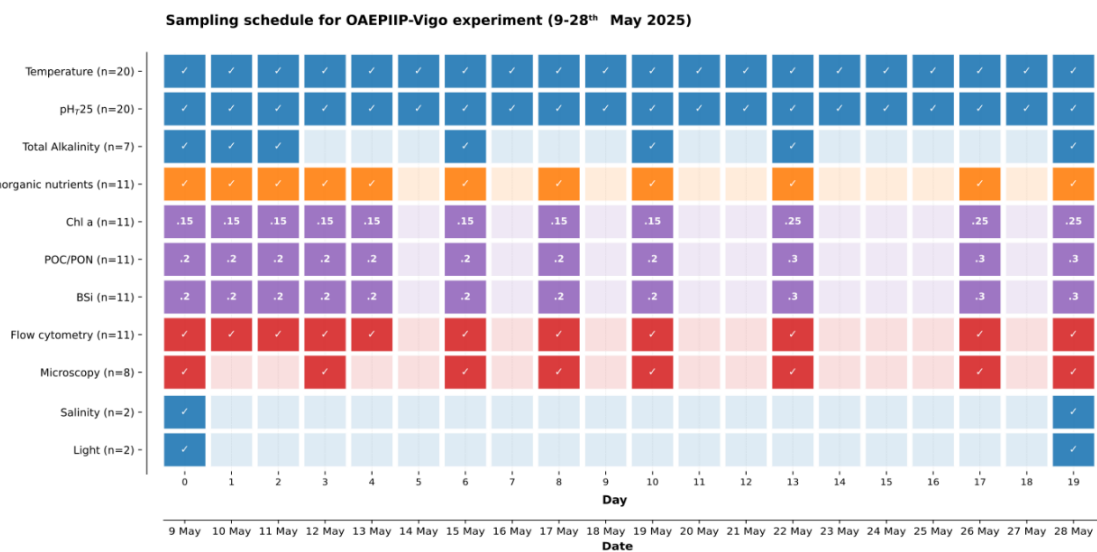
Temperature was measured at a depth 0.1 m within each microcosm using a precision thermometer sonde (Ebro Electronic<sup>TM</sup>. TFX430,  $\pm 0.05^{\circ}\text{C}$  accuracy). Inorganic carbon analysis for pH and total alkalinity followed best practices recommendations (Dickson et al., 2007). pH was measured spectrophotometrically on the total scale at 25  $^{\circ}\text{C}$  (pHT25, Clayton and Byrne, 1993) with unpurified mCP dye (Pérez et al., 2026). Total alkalinity (TA) was determined by single-point titration (Pérez & Fraga, 1987) following the methodology in Fontela et al. (2023). The methodological uncertainty of each pH measurement is 0.0055 pH units (Carter et al., 2013) and  $\pm 2 \mu\text{mol kg}^{-1}$  for total alkalinity (Fontela et al., 2023). Carbonate-system parameters (DIC,  $\text{pCO}_2$ , and aragonite saturation state,  $\Omega_{\text{ar}}$ ) were computed from TA and in-situ pH with *seacarb* package (Gattuso et al., 2003) assuming negligible (and constant) organic alkalinity contributions. Carbon system estimations followed best practices recommendations of Dickson et al. (2007), employing the  $\text{CO}_2$  dissociation constants of Lueker et al., (2000), the sulphate dissociation constant of Dickson, (1990), the fluoride association constant of Pérez & Fraga, (1987) and the total boron concentration of Lee et al., (2010).

Nutrient analyses resolved individual nitrogen species: nitrate ( $\text{NO}_3^-$ ), nitrite ( $\text{NO}_2^-$ ), and ammonium ( $\text{NH}_4^+$ ), as well as phosphate ( $\text{PO}_4^{3-}$ ) and dissolved silicate ( $\text{H}_4\text{SiO}_4$ ). Inorganic nutrients were analysed by continuous segmented flow analysis (CFA) with colorimetric detection, following UNE-EN ISO/IEC 17025:2025 quality standards, with precisions of  $\pm 0.1 \mu\text{mol L}^{-1}$  for  $\text{NO}_3^-$ ,  $\pm 0.02 \mu\text{mol L}^{-1}$  for  $\text{NO}_2^-$ ,  $\pm 0.05 \mu\text{mol L}^{-1}$  for  $\text{NH}_4^+$ ,  $\pm 0.01 \mu\text{mol L}^{-1}$  for  $\text{PO}_4^{3-}$  and  $\pm 0.06 \mu\text{mol L}^{-1}$  for  $\text{SiO}_4$ . We also report dissolved inorganic nitrogen (DIN) as the sum of all nitrogen species ( $\text{DIN} = \text{NO}_3^- + \text{NO}_2^- + \text{NH}_4^+$ ). Stoichiometric N:P ratio is estimated as  $\text{DIN}/(\text{PO}_4^{3-})$  and is presented in nondimensional units.

Filtration protocols for particulate matter (*Chla*, POC, PON, and BSi) balanced analytical sensitivity with the need to preserve microcosm volume. The filtered volume was increased towards the end of the experiment (Fig. 1) and larger volumes were used in late-experiment samples to improve signal-to-noise (Fig. 1). Chlorophyll-*a* was measured after pigments extraction in 90% acetone using the fluorometric method with a Turner Designs 10000 R fluorometer (Strickland & Parsons, 1972). Particulate organic matter (POC and PON) were measured with an elemental analyzer (Leco TruSpec CN) by sample combustion at high-temperature. BSi samples were leached in 10 mL of 0.2M NaOH at 95 $^{\circ}\text{C}$  in a shaking water bath for 3h to extract BSi, after which a 1mL subsample of the extract was collected and neutralized with 1M HCl. Dissolved Si in the

extracts was then quantified using the molybdate-blue colorimetric method with an Alliance FUTURA automatic continuous-  
155 flow analyzer.

Aliquots of 100 ml were preserved with Lugol's iodine solution for light microscopy counts, and the Utermöhl settling  
technique was used to count larger microplankton cells, such as diatoms, dinoflagellates, ciliates, small flagellates and small  
metazoan zooplankton. Organisms were identified to the lowest taxonomic level whenever possible using a Leica inverted  
microscope. In parallel, flow cytometry was used to resolve the smaller size fractions, including autotrophic picoeukaryotes,  
160 cyanobacteria and heterotrophic bacteria. Samples were processed in a FACScalibur flow cytometer as described in Calvo-  
Díaz and Morán, (2006).



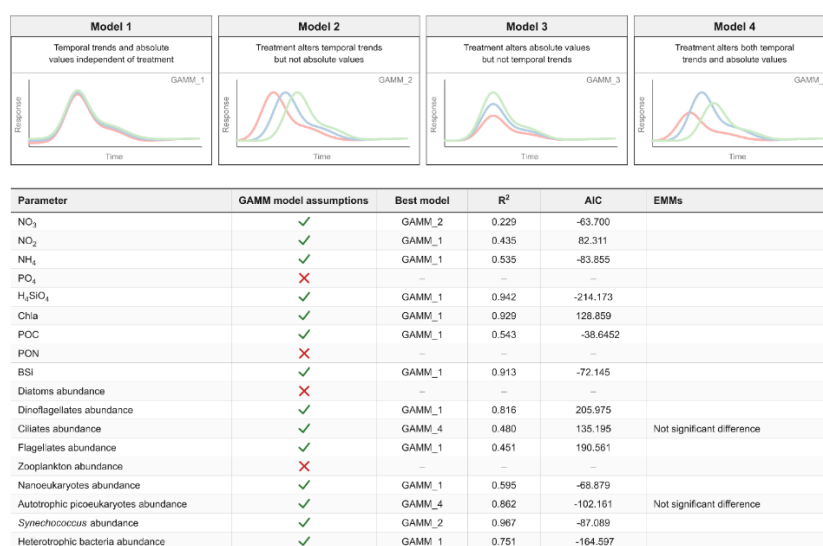
**Figure 1 Chronogram.** Sampling schedule over the experimental period. Number of different sampling days represented after the name of the parameter (n= X). Filtration volumes for biogeochemical parameters chlorophyll-*a* (*Chla*), POC/PON and BSi represented in L as white text inside the box. Parameter are color-coded: physical and chemical parameters (blue: temperature, pH<sub>T</sub>25, total alkalinity, salinity, light), inorganic nutrients (orange), biological productivity metrics (purple: *Chla*, POC/PON, BSi), and plankton community structure (red: flow cytometry, light microscopy).

### 2.3 Statistical analysis

Following Bach et al. (2024), we analysed temporal trajectories using generalized additive mixed models (GAMMs)  
165 formulations that differed in how they represented treatment effects and temporal dynamics (Fig. 2). All models included a  
smooth effect of time and a random smooth to capture replicate-level deviations. The first model assumed identical temporal



trajectories across treatments (GAMM\_1); another model allowed each treatment to follow its own temporal pattern while keeping their overall levels comparable (GAMM\_2); the third model permitted differences in mean values among treatments while constraining them to share a common temporal evolution (GAMM\_3); and the last model combined both types of contrasts, allowing treatments to differ simultaneously in their absolute values and in the their temporal trends (GAMM\_4). A visual explanation of model differences is depicted in Figure 2. For GAMM analyses, inorganic nutrient, particulate matter concentrations and flow cytometry abundances were log-transformed while microplankton counts were square root transformed. Model assumptions of heteroscedasticity and residual temporal autocorrelation were assessed for each tracer and model. Besides a visual assessment of the model residuals, heteroscedasticity was quantitatively tested with Spearman correlation and the GAMM assumptions related with the temporal pattern of the residuals was contrasted with autocorrelation function (ACF) values at lag +1. When model assumptions were met, GAMM results (AIC and  $R^2$ ) for each variable best model are available in Figure 2. If best model was GAMM\_1, then the response can be considered alike between treatments and no additional pairwise testing was executed. When GAMM\_2 type was the best model, we quantified time-varying treatment differences, i.e., the proportion of the experimental timeline during which pairwise treatment contrasts differed significantly (Simpson, 2024). Lastly, for variables best fitted by GAMM\_3 or GAMM\_4 models, post-hoc comparisons of treatment-level estimated marginal means (EMMs) using Šidák-adjusted pairwise contrasts ( $\alpha = 0.05$ ) were carried out (Lenth and Piaskowski, 2026) to discern treatment effects.



**Figure 2. Generalized additive mixed model (GAMM) results.** The upper panel is a schematic representation of the four candidate model structures. The table lists, for each considered parameter, whether the GAMM assumptions were met or not. If GAMM assumptions apply, the selected as best model, along with its adjusted  $R^2$  and its Akaike information criteria (AIC) are reported. For GAMM\_4 models, the result of the significant pairwise contrasts derived from estimated marginal means (EMMs column) is also shown.



### 3 Results

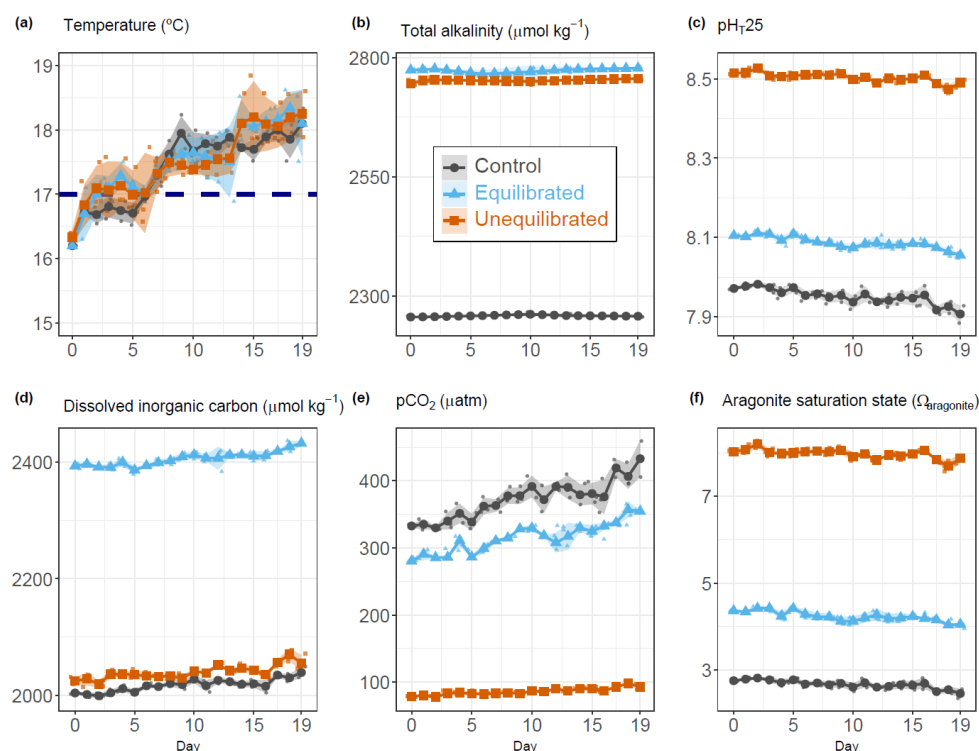
185 Overall, there were small variations between replicates in each treatment for most of the considered parameters. Despite minor temperature variability and an evident +1.5°C warming trend, all microcosms experienced comparable thermal trajectories, allowing robust comparative analyses across treatments.

#### 3.1 Stability of the inorganic carbon system

The alkalinity addition produced immediate and treatment-specific shifts in the inorganic carbon system (Fig. 3). Mean TA  
190 after treatment addition was  $2258.0 \pm 2.0 \mu\text{mol kg}^{-1}$ , and  $2757.5 \pm 3.2 \mu\text{mol kg}^{-1}$ ,  $2787.1 \pm 4.1 \mu\text{mol kg}^{-1}$ , for the control, unequilibrated and equilibrated treatment, respectively. The treatment manipulation achieved the target objective of  $\sim +500 \mu\text{mol kg}^{-1}$  (mean change of  $+499 \mu\text{mol kg}^{-1}$ , for the unequilibrated, and  $+529 \mu\text{mol kg}^{-1}$  for the equilibrated, Table 1). Alkalinity was persistently stable until the end of the experiment. The establishing of the treatments caused sharp increases in measured pH at 25°C (Fig. 3c) from initial values of  $7.97 \pm 0.01$  in the control until  $8.51 \pm 0.03$  in the unequilibrated and  $8.1 \pm 0.04$   
195 in the equilibrated. After an initial period of relatively constant pH values, from day 5 in advance there is a slight decrease in pH values that intensifies towards the end of the experiment. The final values of measured pH at 25°C are  $7.91 \pm 0.02$ ,  $8.49 \pm 0.01$  and  $8.05 \pm 0.01$  for the control, unequilibrated and equilibrated treatments, respectively. The difference between final and initial conditions is larger in the less buffered set of microcosms, i.e., the control. Following now with the description of the carbon parameters, the control had an initial DIC content of  $2002 \pm 2 \mu\text{mol kg}^{-1}$  that remains alike in the unequilibrated treatment  
200  $2024 \pm 5 \mu\text{mol kg}^{-1}$  and rise until  $2393 \pm 2 \mu\text{mol kg}^{-1}$  in the equilibrated treatment. The increase in carbon content in the equilibrated treatment with regard to the control was of only  $391 \mu\text{mol kg}^{-1}$ , a 5.9% lower than the target of  $416 \mu\text{mol kg}^{-1}$  aimed in the treatment setup. This  $-25 \mu\text{mol kg}^{-1}$  disagreement is likely related with inherent variability of the microcosms inorganic chemistry that was not taken into account, methodological uncertainties related with treatment dissolutions or a combination of both. Furthermore, it is close to the difference between DIC content of control and unequilibrated, that should  
205 be theoretically zero, and it is  $-22 \mu\text{mol kg}^{-1}$ . Nevertheless, the differences remain throughout the experiment and, in synchrony with pH, there is a slightly increasing trend after the day 5 onwards that becomes more pronounced in the last three days. The final values of DIC in the control, unequilibrated and equilibrated treatments are  $2030 \pm 10 \mu\text{mol kg}^{-1}$ ,  $2054 \pm 14 \mu\text{mol kg}^{-1}$  and  $2422 \pm 9 \mu\text{mol kg}^{-1}$ , respectively. The initial partial pressure of carbon dioxide ( $p\text{CO}_2$ ) at the control was  $332.5 \pm 2.6 \mu\text{atm}$ . Just after OAE manipulation,  $p\text{CO}_2$  was  $286.7 \pm 4.5 \mu\text{atm}$  at the equilibrated and decreased up to  $78.9 \pm 1.1 \mu\text{atm}$  in the unequilibrated  
210 treatment. All treatments showed a sustained increase in  $p\text{CO}_2$ , being faster in the last three days, reaching to the end-of-the experiment levels of  $408.5 \pm 24.3 \mu\text{atm}$ ,  $341.2 \pm 12.7 \mu\text{atm}$  and  $92.6 \pm 4.5 \mu\text{atm}$  in the control, equilibrated and unequilibrated treatments. Therefore, there was an increase of 76, 54 and 14  $\mu\text{atm}$  during the complete incubation in the control, equilibrated and unequilibrated treatments. Considering the temperature effect on  $p\text{CO}_2$  in isochemical conditions ( $+4.23\% \text{ } ^\circ\text{C}^{-1}$ ; Takahashi



et al., 1993), the rise in temperature between the initial and final days (around 1.5°C), would explain an increase in the control, equilibrated and unequilibrated treatments of 21.1, 18.2 and 5  $\mu\text{atm}$  respectively. Therefore, temperature was not the main driver of observed changes in the temporal evolution of inorganic carbon parameters. Considering that the atmospheric  $p\text{CO}_2$  concentration for May 2025 in the study region was around 430  $\mu\text{atm}$  (NOAA ESRL GML CCGG Group, 2019), the alkalinity addition will boost (equilibrated) or exacerbate (unequilibrated) the original uptake of  $\text{CO}_2$  that already occurs at *in situ* conditions (control). The saturation state for aragonite ( $\Omega_{\text{aragonite}}$ ) started at  $2.78 \pm 0.03$  in the control, and increased until maximum values of  $4.36 \pm 0.04$  in the equilibrated treatment and  $8.10 \pm 0.09$  in the unequilibrated treatment. Besides these high values for  $\Omega_{\text{aragonite}}$ , no runaway abiotic calcium carbonate precipitation was observed at any microcosms during the experiment. Differences between treatments remain through the experiment, showing a sustained small decreasing trend as seen in previous inorganic carbon parameters.



**Figure 3. Temporal evolution of temperature and inorganic carbon system through the experiment and across treatments.** Temporal daily evolution of (a) temperature ( $^{\circ}\text{C}$ ), (b) total alkalinity (TA,  $\mu\text{mol kg}^{-1}$ ), (c) pH in total scale measured at  $25^{\circ}\text{C}$ , ( $\text{pH}_{\text{T}25}$ ), (d) dissolved inorganic carbon (DIC,  $\mu\text{mol kg}^{-1}$ ), (e)  $p\text{CO}_2$  ( $\mu\text{atm}$ ), and (f) aragonite saturation state ( $\Omega_{\text{aragonite}}$ ) throughout the microcosm experiment for the Control (dark grey, circles), equilibrated (light blue, triangles) and unequilibrated (orange, squares) treatments. Shaded ribbons represent the standard deviation of the replicates (small points when visible,  $n = 3$  per treatment) with respect to the mean value (large point). Horizontal dashed blue line in (a) represents sea surface temperature at the time of microcosm filling.



### 3.2 Fast drawdown of low initial dissolved inorganic nutrients and subsequent remineralization

225 The temporal evolution of dissolved inorganic nutrients, including the relative distribution of nitrogen species, showed a consistent pattern (Fig. 4). Within nitrogen species, nitrate ( $\text{NO}_3^-$ ) started the experiment at low levels ( $<0.4 \mu\text{mol kg}^{-1}$ ) just after a sharp initial consumption if we assumed a shared *in situ* sampling content of  $0.8 \mu\text{mol kg}^{-1}$ . Then,  $\text{NO}_3^-$  remained very low ( $\sim 0.1 \mu\text{mol kg}^{-1}$ ) through the experiment in all the treatments, and concluded with a slight increase ( $0.51$  and  $0.43 \mu\text{mol kg}^{-1}$  in a control and unequilibrated treatment microcosm, respectively).  $\text{NO}_3^-$  was the only inorganic nutrient parameter that

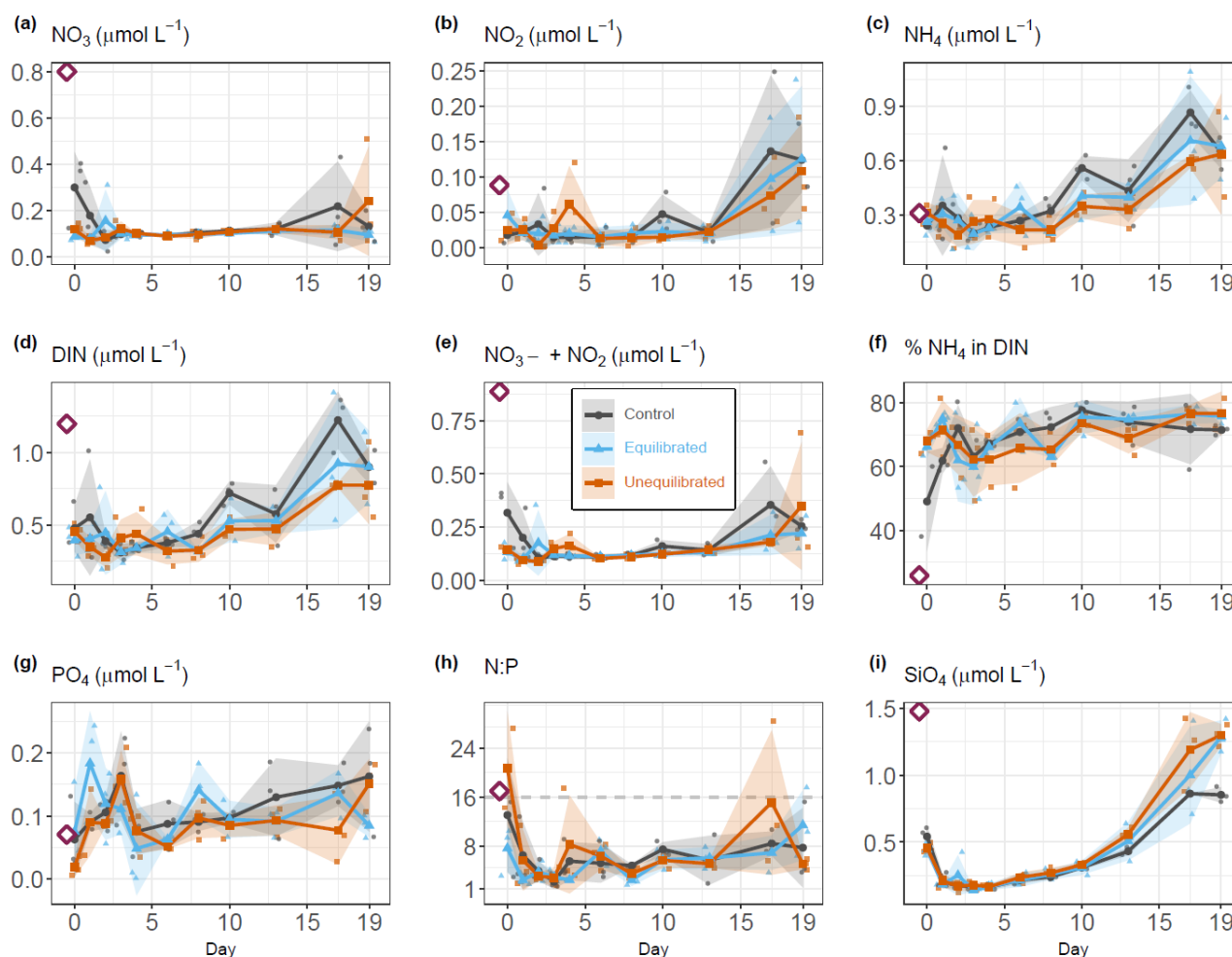
230 is better fitted with a GAMM\_2 model, i.e., the treatment altered temporal trends. Even so, it should be seen with cautious, as the adjustment is modest ( $R^2=0.23$ ) and significant pairwise divergence was confined to a small fraction of the experimental timeline (Fig A4). Nitrite ( $\text{NO}_2^-$ ) was also detectable (Fig. 4b) but mostly depleted until the final days of the experiment (GAMM\_1, Fig. 2) and ammonium ( $\text{NH}_4^+$ ) rise steadily from initial values of  $0.3 \mu\text{mol kg}^{-1}$ , similar to *in situ* conditions, until values larger than  $0.6 \mu\text{mol kg}^{-1}$ . The rising trend in  $\text{NH}_4^+$  was similar between treatments (GAMM\_1, Fig. 2) even if absolute

235 values were slightly higher in the control. All these changes in consumption/remineralization within the inorganic nitrogen chemical speciation causes a progressive increase of DIN and  $\text{NO}_3^- + \text{NO}_2^-$  (Fig. 4 d & e) after a fast initial consumption and a steady increase in the fraction of DIN that is in the form of ammonium (Fig. 4f), a signal of progressive remineralization. The amount of inorganic phosphorus, in the form of phosphate ( $\text{PO}_4$ , Fig 3g) remained pretty constant and quite low ( $0.098 \pm 0.05 \mu\text{mol kg}^{-1}$ ). This response appears independent of the treatment, even if  $\text{PO}_4$  data did not met GAMM model

240 assumptions to be adjusted (Fig. 2). Although  $\text{PO}_4$  initial conditions - ( $0.07 \mu\text{mol kg}^{-1}$ ) were also low, the *in situ* conditions shows N:P ratios slightly above 16 (Fig. 4h), meaning that the plankton community sampled was at equilibrium conditions with respect to Redfield ratio 16:1 (Anderson and Sarmiento, 1994) at the timing of sampling, i.e., that it does not had a nutrient limitation for nitrogen or phosphorus. Once enclosed, the planktonic community was persistently below the N:P value of 16, meaning a deficit of nitrogen with respect to phosphorus. Lastly, at the time of microcosm filling there was  $1.47 \mu\text{mol kg}^{-1}$  of

245 silicate ( $\text{H}_4\text{SiO}_4$ ) in the surface waters of Ría de Vigo while eight hours later, at the beginning of the experiments all the microcosms have a similar content of  $0.48 \pm 0.07 \mu\text{mol kg}^{-1}$  of  $\text{H}_4\text{SiO}_4$  (Fig. 4i). The inorganic content of  $\text{H}_4\text{SiO}_4$  decreased until  $0.18 \pm 0.03 \mu\text{mol kg}^{-1}$  during the first 5 days, followed by a sustained increase until the end of the experiment. Final mean  $\text{H}_4\text{SiO}_4$  concentrations ( $1.15 \pm 0.23 \mu\text{mol kg}^{-1}$ ) remained below *in situ* observed (Fig. 4i) but exceeded the  $\text{H}_4\text{SiO}_4$  concentrations measured at time zero, providing clear evidence of remineralization within the microcosms. Overall, the initial nutrient content

250 was low and became rapidly depleted within all microcosms with independence of the treatments. By the end of the experiment, there were clear remineralization signatures, like  $\text{NO}_2^-$  buildup, rising  $\text{NH}_4^+$  fractions, and  $\text{H}_4\text{SiO}_4$  content recovery.



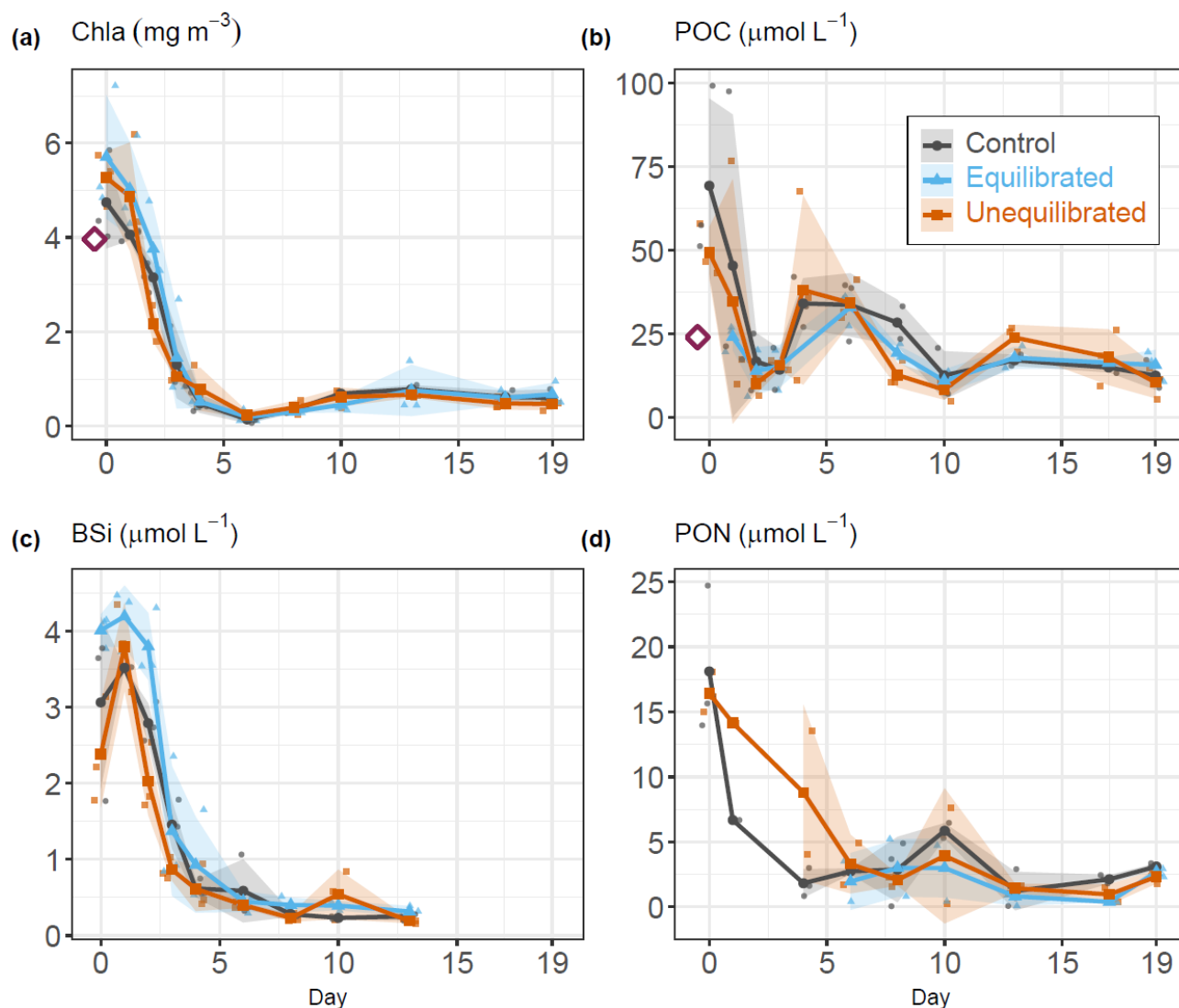
**Figure 4. Dissolved inorganic nutrient dynamics and stoichiometric ratios across treatments.**

Temporal daily evolution of (a) nitrate,  $\text{NO}_3^-$  ( $\mu\text{mol L}^{-1}$ ), (b) nitrite,  $\text{NO}_2^-$  ( $\mu\text{mol L}^{-1}$ ), (c) ammonium,  $\text{NH}_4^+$  ( $\mu\text{mol L}^{-1}$ ), (d) dissolved inorganic nitrogen,  $\text{DIN} = \text{NO}_3^- + \text{NO}_2^- + \text{NH}_4^+$  ( $\mu\text{mol L}^{-1}$ ), (e)  $\text{NO}_3^- + \text{NO}_2^-$  ( $\mu\text{mol L}^{-1}$ ), (f) percentage of  $\text{NH}_4^+$  in total DIN (% $\text{NH}_4^+$  in DIN, %), (g) phosphate,  $\text{PO}_4^{3-}$  ( $\mu\text{mol L}^{-1}$ ), (h) N:P ratio, and (i) dissolved silicate,  $\text{SiO}_4$  ( $\mu\text{mol L}^{-1}$ ) throughout the microcosm experiment for the control (dark grey, circles), equilibrated (light blue, triangles), and unequilibrated (orange, squares) treatments. Shaded ribbons represent the standard deviation of the replicates (small points when visible,  $n = 3$  per treatment) with respect to the mean value (large point). *In situ* conditions at the time of microcosm filling (Day 0) represented with a purple diamond.



### 3.3 Chlorophyll-*a* and particulate matter

Chlorophyll-*a* exhibited a consistent pattern across all treatments (GAMM\_1,  $R^2=0.93$ , Fig. 2), with maximum concentrations at the onset of the experiment:  $4.74 \pm 0.98 \text{ mg} \cdot \text{m}^{-3}$ ,  $5.71 \pm 1.31 \text{ mg} \cdot \text{m}^{-3}$  and  $5.27 \pm 0.56 \text{ mg} \cdot \text{m}^{-3}$  for the control, equilibrated and unequilibrated treatment (Fig. 5a). Initial values were slightly higher than the in-situ concentration measured at the time of collection ( $3.96 \text{ mg} \cdot \text{m}^{-3}$ ). The fluorescence sensor profile at sampling time shows that the *Chla* maximum was located in the surface layer from which the microcosms were filled (Fig. A2). The magnitude and timing of the *Chla* decrease were identical across treatments and at day 6 they reached minimum *Chla* values ( $0.19 \pm 0.05 \text{ mg} \cdot \text{m}^{-3}$ ). Afterwards, there is a slight increase during the second week of the experiment (days 8-13), to reach final relatively constant values of  $0.63 \pm 0.18 \text{ mg} \cdot \text{m}^{-3}$ . Prior to describe the POC and PON results (Fig. 5b,d), it should be noted that these two parameters, measured from the same filter sample, are strongly constrained by the filtered volume. Overall, the proportion of analysis below the limit of detection was 7% for POC and 39% for PON. The higher proportion of undetectable PON samples likely reflects the lower particulate nitrogen content of the samples and the greater nitrogen mass required for reliable CHN analysis (Verardo et al., 1990). Hence, PON observations during the first 5 days were sparse (13/45) including a data gap between days 2 and 3. The equilibrated treatment yielded no PON measurement until day 6. From day 13 onward, when the filtered volume was increased by up to 50% (and by 200% on the final day, Fig. 1), concentration estimates became consistent across treatments and exceeded the analytical detection limit in 26 of the 27 samples. Given these PON detection constraints, and considering that both parameters share the same filter, absolute POC values for the 0-5 day period should be interpreted with caution. POC echoed the *Chla* trajectory (Fig. 5b). Although substantial variability among replicates was observed, especially at the beginning of the experiment ( $4\text{--}99 \text{ } \mu\text{mol L}^{-1}$  range), the equilibrated treatment appeared to begin with slightly lower POC values. The retained POC model was GAMM\_1 (Fig. 2). In general, replicate variability for POC and PON was substantial during the first days, reflecting the sensitivity of these measurements to the volume of seawater filtered when particulate stocks were low. By the end of the experiment, when larger volumes could be filtered, POC concentrations converged across all treatments to  $12.9 \pm 4.5 \text{ } \mu\text{mol L}^{-1}$ . For reference, the *in situ* POC concentration at the time of collection was  $24 \text{ } \mu\text{mol L}^{-1}$ . Particulate organic nitrogen (PON) displayed a temporal pattern resembling those of *Chla* and POC (Fig. 5d), but the data did not meet the assumptions required for GAMM fitting (Fig. 2). The *in situ* PON signal was below the analytical detection limit, as were 39 % of all PON determinations over the course of the experiment. The PON record should therefore be regarded as qualitatively consistent with, rather than independent confirmation of the patterns described above. Biogenic silica (BSi) reproduced the rapid response and subsequent decline described for *Chla*, POC and PON (Fig. 5c), peaking at  $3.5\text{--}4 \text{ } \mu\text{mol L}^{-1}$  on day 1 and decreasing steadily thereafter until it stabilised at very low values ( $\approx 0.5 \text{ } \mu\text{mol L}^{-1}$ ) from day 6 onwards. There is no BSi data from day 13 onwards. BSi was the best-resolved of the particulate variables (GAMM\_1,  $R^2 = 0.91$ ; Fig. 2). Taken together, the models retained for this group of variables (Fig. 2, Fig. 5) indicate that OAE, whether equilibrated or unequilibrated, did not modify the timing or the shape of the bloom decay.



**Figure 5. Particulate matter dynamics across treatments.**

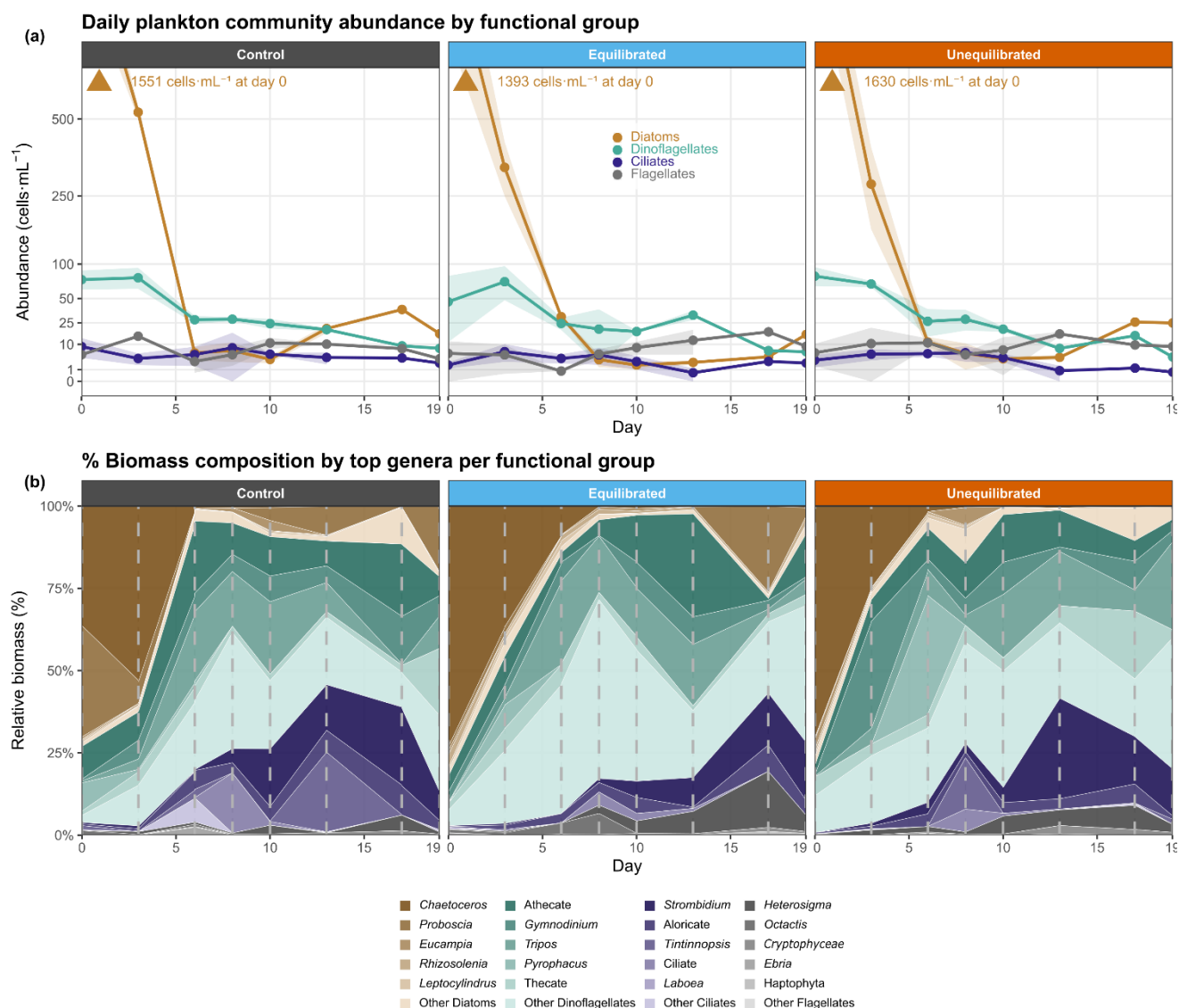
Temporal daily evolution of (a) chlorophyll a ( $\text{Chla}$ ,  $\text{mg m}^{-3}$ ), (b) particulate organic carbon (POC,  $\mu\text{mol L}^{-1}$ ), (c) biogenic silica (BSi,  $\mu\text{mol L}^{-1}$ ) and (d) particulate organic nitrogen (PON,  $\mu\text{mol L}^{-1}$ ) throughout the 20-day microcosm experiment for the control (dark grey, circles), equilibrated (light blue, triangles), and unequilibrated (orange, squares) treatments. Shaded ribbons, when present, represent the standard deviation of the replicates (small points when visible,  $n=3$  per treatment) with respect to the mean value (large point). *In situ* conditions at the time of microcosm filling (Day 0) represented with a purple diamond (data not available for subplot c and d). Note that BSi measurements are not available from day 13 onwards.



### 290 3.4 Plankton community composition

The initial plankton community was clearly dominated by a dense diatom bloom (Fig. 6a), with abundances an order of magnitude higher than any other functional group. *Chaetoceros* spp was the predominant genus with absolute abundance values around  $\sim 1500 \text{ cells} \cdot \text{mL}^{-1}$ . In all treatments, dinoflagellates exhibited a progressive reduction in abundance since the beginning of the experiment, albeit not as pronounced as that of diatoms. The abundance for ciliates is rarely above  $10 \text{ cells} \cdot \text{mL}^{-1}$  while flagellates abundance shows a maximum at days 13-17 with abundance between  $10\text{-}25 \text{ cells} \cdot \text{mL}^{-1}$ . As incubations progressed, the abundance curves converge at low-biomass conditions, with a subtle increase in the diatom abundance during the final days. Diatom abundance was excluded from the GAMM analysis because none of the candidate model structures fulfilled the assumption of residual homoscedasticity (Fig. 2). Dinoflagellate and flagellate abundances were best fitted by GAMM\_1, indicating no treatment effect, while ciliate abundance was best described by GAMM\_4, reflecting differences in both temporal patterns and absolute abundances. Ciliate results should be interpreted with caution, not only due to the limited model performance ( $R^2 = 0.48$ ), but also because, according to the estimated marginal means, no difference was observed (Fig. A5). Metazoan zooplankton ( $<200 \mu\text{m}$ ) abundance remained consistently low ( $< 1 \text{ cells} \cdot \text{mL}^{-1}$ ) and similar between microcosms (Fig. A6).

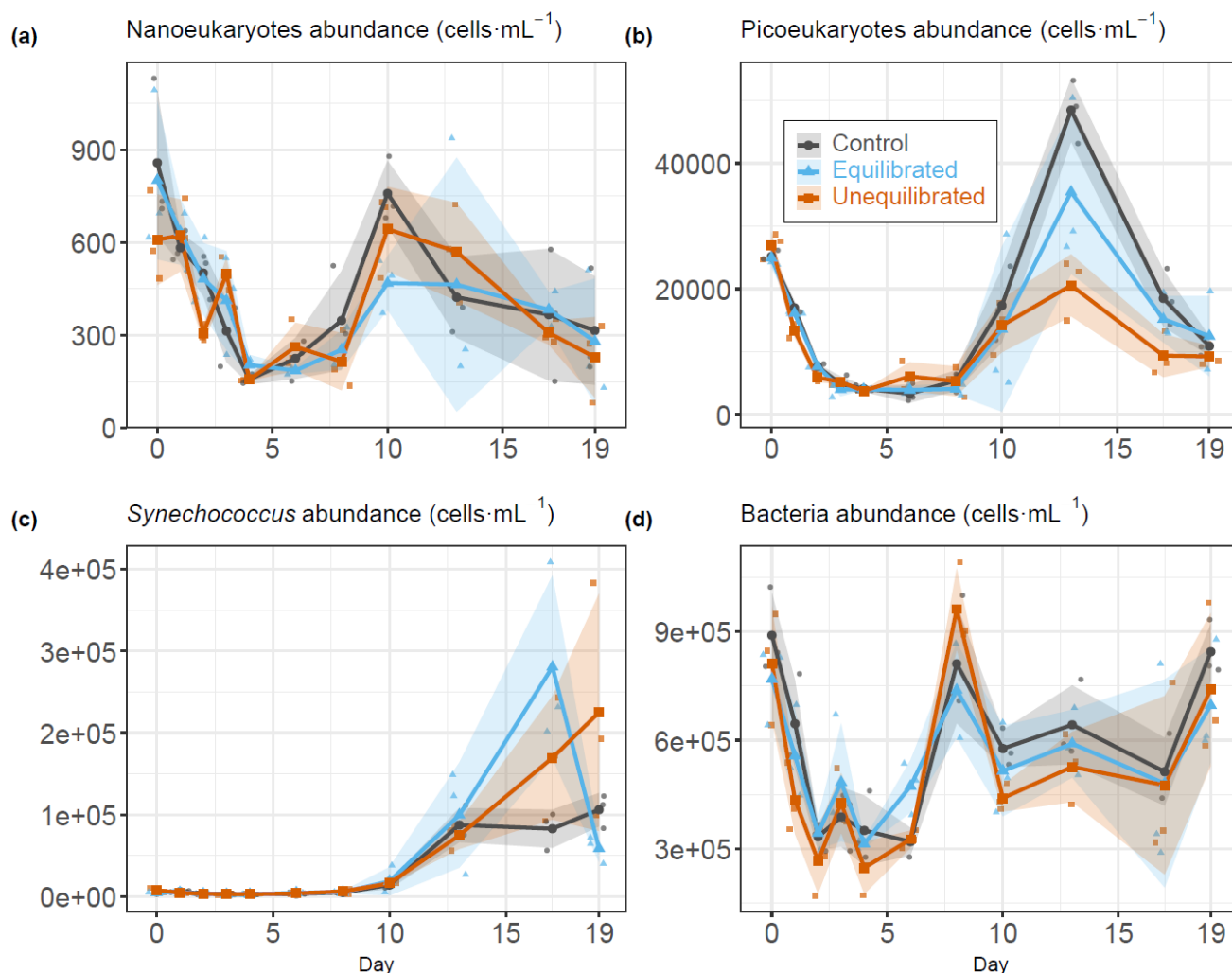
Plankton biomass composition by genus and functional group showed similar temporal dynamics across treatments (Fig. 6b). Across all treatments, the plankton community biomass underwent a rapid and synchronized shift in taxonomic composition, with the diatom-dominated assemblage collapsing at day 5, coinciding with the near-complete disappearance of *Chaetoceros* spp., the dominant genus in the early phase of the experiment. The collapse of *Chaetoceros* spp., generated a relative rise in dinoflagellate biomass that reflects the contraction of the whole community rather than an actual increase in absolute dinoflagellate biomass. The decline in diatom biomass occurred simultaneously in the control, equilibrated, and unequilibrated treatments. Following the diatom collapse, dinoflagellates increased their relative contribution to total biomass across all treatments. Unidentified athecate dinoflagellates accounted for the largest fraction of dinoflagellate biomass after day 5, followed by *Gymnodinium* spp and *Tripos* spp. From day 5 onward the contribution of Ciliates increased (*Strombidium* spp. as the main genera), accounting for  $\sim 33\%$  of total biomass between days 10-17. Small flagellated taxa, like *Heterosigma* spp. increased from day 10 until the end of the experiment. Across all treatments, the combined contribution of flagellates and ciliates continued to increase after the first week, reaching approximately 50% of total biomass by day 13. Collectively, these observations show a shared successional shift across treatments, marked by a diatom-driven decline in the initial days followed by a transition toward assemblages with increasing contributions of dinoflagellates, ciliates and flagellates.



**Figure 6. Microplankton abundance and biomass evolution across experimental period.** a) Microplankton community abundance by functional group. Note that the y-scale is not linear and that the upper limit still lags behind the maximum value observed at day 0 for diatom abundance, expressed as text for each subplot. b) Plankton biomass composition by genus and functional group. Relative biomass (%) of the dominant phytoplankton genera over the 19-day microcosm experiment for the control, equilibrated, and unequilibrated treatments. Genera are grouped into four functional groups, each represented by a distinct colour family: gold-brown for diatoms, blue for dinoflagellates, purple for ciliates, and grey for flagellates. The grey dashed vertical lines indicate the specific sampling days on which light-microscopy observations were done, corresponding to timepoints with direct taxonomic identification.



With regard to the flow cytometry analysis (Fig. 7), small autotrophic nanoeukaryotes abundance remained relatively low (600±200 cells mL<sup>-1</sup>) and showed no differences among treatments throughout the experiment (Fig. 7a, GAMM\_1, Fig. 2). Following an initial decline during the first 5 days, abundance recovered to approximately initial levels by day 10 and then remained relatively stable, with moderate fluctuations, until the end of the experiment. Autotrophic picoeukaryote (<2 µm) abundance (Fig. 7b) declined sharply during the first days in all treatments, followed by a pronounced increase that peaked at day 13, showing treatment-specific differences in their absolute and temporal response (GAMM\_4, Fig. 2). The highest abundance was observed in the control treatment, exceeding 48,000 cells mL<sup>-1</sup>, whereas middle peak abundances were observed in the equilibrated (~35,000 cells mL<sup>-1</sup>) and the lowest in the unequilibrated treatment (20,000 cells mL<sup>-1</sup>). Following the peak phase, picoeukaryote abundance declined and converged among treatments toward the end of the experiment. The abundance of *Synechococcus*, a picoplankton- sized cyanobacterium (0.2-2 µm), unequivocally increased from day 10 onwards, reaching values above 4×10<sup>5</sup> cells·mL<sup>-1</sup> in the unequilibrated treatment (Fig. 7c). However, temporal trajectories differed among treatments (GAMM\_2, Fig. 2). In the equilibrated treatment, *Synechococcus* abundance increased sharply and reached its maximum around day 17 (3 × 10<sup>5</sup> cells mL<sup>-1</sup>), followed by a pronounced decline by the end of the experiment. In contrast, abundance in the control and unequilibrated treatments were still increasing at the ending. Consequently, *Synechococcus* pairwise contrasts revealed that these differences were restricted to a short portion of the incubation, towards the experiment final days (Fig. A4). The equilibrated treatment differed significantly from both the control and unequilibrated treatments during approximately 20% of the experimental period, whereas no significant differences were detected between the control and unequilibrated treatments. Finally, heterotrophic bacteria (Fig. 7d) followed a trajectory characterised by an abrupt decline over the first two days (from ~9 × 10<sup>5</sup> to ~3 × 10<sup>5</sup> cells mL<sup>-1</sup>), a subsequent low plateau that persisted until day 6, followed by a pronounced peak at day 8, when abundances returned to initial values. Heterotrophic bacteria abundance then declined and remained stable before increasing again at the end of the experiment. Although the day-8 peak was highest in the unequilibrated treatment, heterotrophic bacteria abundances in this treatment tended to be the lowest and no significant treatment effect was considered (GAMM 1, Fig. 2).



**Figure 7. Dynamics of plankton groups resolved by flow cytometry across treatments.** Temporal daily evolution of (a) nanoeukaryote abundance (cells·mL<sup>-1</sup>), (b) picoeukaryote abundance (cells·mL<sup>-1</sup>) (c) *Synechococcus* abundance (cells·mL<sup>-1</sup>) and (d) heterotrophic bacteria abundance (cells·mL<sup>-1</sup>) throughout the 20-day microcosm experiment for the control (dark grey, circles), equilibrated (light blue, triangles), and unequilibrated (orange, squares) treatments. Shaded ribbons represent the standard deviation of the replicates (small points when visible, n = 3 per treatment) with respect to the mean value (large point).



## 4 Discussion

### 4.1 Biogeochemical response to OAE

#### 345 4.1.1 Temperature issues does not prevent OAE interpretation

A temperature increase ( $\sim 1.5^{\circ}\text{C}$ ) was observed during the experiment. We sustain that this similar warming across treatments does not affect the attribution of biological responses to OAE as all microcosms experienced the same room-controlled conditions of temperature and light. In fact, temperature ranges remained within Ría de Vigo sea surface temperature variability. First, climatologically, mean surface temperature in the middle zone of the Ría de Vigo increases from  
350 approximately 14 to 18  $^{\circ}\text{C}$  during spring (Padin et al., 2020). Second, observations from the nearest time-series observatories (Fig. A1) recorded during the same period showed a comparable warming trend, with daily temperature fluctuations that could exceed the total increase observed in the experiment (Fig. A7). Furthermore, when temperature is incorporated into a GAMM model as an experimental parameter no significant differences in its temporal evolution were found among treatments (not shown).

#### 355 4.1.2 OAE does not alter inorganic nutrient consumption and remineralization

Dissolved inorganic nutrients followed the same sequence across all treatments: a rapid drawdown from initially low nutrient levels. This low initial nutrient content aligns with the seasonal values observed in the Ría de Vigo during spring, where surface concentrations of nitrate, phosphate and silicate are typically low (Figueiras et al., 2020; Nogueira et al., 1997; Padin et al., 2020) leading to nitrogen limitation (Fontela et al., 2025; Martínez-García et al., 2010). Our findings agree with several Ría  
360 de Vigo mesocosm experiments with enclosed spring-summer phytoplankton communities that rapidly deplete inorganic nutrients, regardless of ancillary manipulations (Justel-Díez et al., 2025; López-Sandoval et al., 2025; Martínez-García et al., 2010; Teira et al., 2008). Previous mesocosm experiments in the same region with a comparable phytoplankton community depleted 6  $\mu\text{mol kg}^{-1}$  of  $\text{NO}_3^-$  in 48 hours (López-Sandoval et al., 2025) while initial  $\text{NO}_3^-$  concentrations in the present study were  $<1 \mu\text{mol kg}^{-1}$ . Our results suggest that OAE treatment could alter  $\text{NO}_3^-$  temporal trends, as seen in previous experiments  
365 (Kousoulas et al., 2025). Even so, the modest statistical support ( $R^2=0.23$ ), together with the fact that the differences were restricted to a short interval of the experiment (Fig. A4), suggests that they likely arose from stochastic processes during microcosm setup (Riebesell et al., 2023) rather than from sustained treatment-driven changes in  $\text{NO}_3^-$  dynamics. Heterotrophic remineralization progressively increased inorganic nutrient pools, with  $\text{NH}_4^+$  building up faster than  $\text{NO}_2^-$  and  $\text{NO}_3^-$ , following the expected sequence whereby  $\text{NH}_4^+$  is the initial inorganic product of nitrogen regeneration before oxidizing to  $\text{NO}_3^-$  (Garber,  
370 1984; Pérez et al., 2000). As seen here, ammonium accumulation over weekly timescales is a typical response in unamended coastal microcosms (Justel-Díez et al., 2025, their Fig. S1) and consequently, the  $\text{NH}_4^+$  fraction of DIN also increased. Thus, OAE did not alter the timing of nutrient exhaustion nor the onset of remineralization. The stability of stoichiometric ratios indicates that, on experimental timescales, OAE does not disrupt the fundamental efficiency of the biological carbon pump (Suessle et al., 2025).



375 Under identical approach, previous experiments with coastal Tasmania plankton communities find silicate to be a treatment-  
sensitive inorganic nutrient (Ferderer et al., 2022; Kousoulas et al., 2025) and reported that OAE led to slower silicate  
consumption. We do not observe such response. This discrepancy is likely explained by the substantially lower initial silicate  
concentration in our experiment ( $0.5 \mu\text{mol kg}^{-1}$  versus  $\sim 10 \mu\text{mol kg}^{-1}$  in Tasmania), together with concurrent nitrogen limitation  
of diatom growth, which reduced the potential for differential silicate dynamics among treatments. Here, significant early  
380 nitrogen and silicate limitation combined with the rapid diatom collapse prevented the sustained diatom growth necessary for  
OAE to influence silicate uptake dynamics. The growth limitation of large, silica-dependent phytoplankton potentially  
attributed to OAE (Ferderer et al., 2022) is not developed here because nitrogen and silicate became limiting factor during the  
experiment. Our results aligns with nutrient availability being the main driver of response in OAE treatment experiments (Liu  
et al., 2026). In nutrient-depleted systems, plankton community experiences nutrient limitation and is therefore less sensitive  
385 to carbonate chemistry changes (Marín-Samper et al., 2024) compared to nutrient-rich environments (Ferderer et al., 2022;  
Kousoulas et al., 2025). In summary, despite clear chemical differences between equilibrated and unequilibrated OAE and the  
control microcosms, nutrient dynamics converged across treatments: consumption and remineralization drive the  
biogeochemical response, suggesting that carbonate chemistry shifts had limited influence on community scale responses  
under nutrient competition.

#### 390 **4.1.3 OAE does not prevent organic particulate matter peak and decline**

Initial *Chla* levels ( $\sim 4 \text{ mg m}^{-3}$ ) are within the expected range for May in Ría de Vigo (Nogueira et al., 1997; Padin et al., 2020)  
but are notably lower than during typical peak spring bloom values ( $\sim 12 \text{ mg m}^{-3}$ , Cermeño et al., 2006). Our observations,  
coupled with the low initial nutrient inventory, are indicative of a late spring-bloom state. Besides, the vertical fluorescence  
structure was characterized by a surface maximum (Fig. A2), contrasting with the subsurface maximum associated with  
395 summer stratification (Cermeño et al., 2006). Chlorophyll-*a* increased between the microcosm filling step and the treatment  
setup (Fig. 5a), which can be partially explained by the short-term relaxation from grazing after the  $200 \mu\text{m}$  pre-filtration step  
rather than an OAE effect. This rapid biomass build-up may also explain the lower  $\text{pCO}_2$  in the control microcosm at time zero  
( $332.5 \pm 2.6 \mu\text{atm}$ ) than under in situ conditions ( $\sim 360 \mu\text{atm}$ ), due to the drawdown of inorganic carbon associated with primary  
production.

400 Initial BSi content ( $2\text{--}4 \mu\text{mol L}^{-1}$ ) are also within the reported range for Ría de Vigo (Ríos et al., 1998). The strong BSi peak  
and decline reflects the collapse of *Chaetoceros* spp., the dominant silicifier at initial conditions. Since inorganic nutrient  
limitation developed at day 1, diatom growth was constrained almost immediately and no mechanistic pathway existed for  
OAE to influence silica uptake or frustule production. Consequently, and in contrast with previous experiments (Ferderer et  
al., 2022), the BSi trajectory was indistinguishable among treatments. The absence of late-experiment BSi data does not affect  
405 interpretation: the system had already transitioned away from a diatom-supported particulate silica pool before any potential  
OAE effect could materialize.



Across all treatments, *Chla* and BSi declined rapidly and synchronously. This pattern is much more robust than the trajectories of POC and PON, even if they all decreased sharply. Such coherent decline across all particulate pools reveals that OAE did not delay, accelerate, or modulate the collapse of organic matter stocks, which was driven by nutrient limitation and diatom decline. POC-PON dynamics provide an additional constraint that must be seen with cautious. After an initial signal characterized by analytical noise likely related with insufficient filtered volumes, particulate organic matter converged to similar end-of-experiment concentrations in all treatments, indicating that organic carbon export potential declined at comparable rates irrespective of OAE perturbations. An alternative approach, to overcome volume limitation issues in future experiments, could be to assess dissolved organic matter (DOC/DON) as proxies of POC/PON, as they can be measured from smaller volume samples. Overall, organic particulate matter behaved consistently across the treatments, reflecting the dynamics of a diatom bloom collapse rather than any inhibitory or stimulatory effect mediated by alkalinity additions (Gately et al., 2023).

## 4.2 Planktonic response to OAE

### 4.2.1 A characteristic *Chaetoceros* bloom collapse after nutrient exhaustion

The initial dominance of *Chaetoceros* spp. is usual within spring bloom dynamics in the NW Iberian Upwelling System, where medium-sized *Chaetoceros* species frequently dominate spring phytoplankton assemblages in nutrient-replete surface waters (Bode et al., 2015; Bode and Varela, 1998; Nogueira and Figueiras, 2005). *Chaetoceros* spp. are favoured during upwelling pulses due to their high growth rates, efficient light utilization in mixed layers, and capacity to store inorganic nutrients in vacuoles (luxury nutrient uptake) (Kemp and Villareal, 2018; Stolte and Riegman, 1996). Their morphology, including chain formation and the production of extracellular polymers, enhances buoyancy and aggregate formation under low turbulence conditions (Kjørboe and Hansen, 1993; Lancelot, 1983). These traits can explain the large initial abundances observed at the beginning of the experiment. The rapid collapse of *Chaetoceros* spp. during the first five days may reflect also a density-dependent shift in life-history strategy. Experimental evidence has shown that *Chaetoceros socialis* can form spores not only under nutrient limitation but also at high cell densities through chemical-mediated intraspecific signals (Pelusi et al., 2020). This process promotes the formation of heavily silicified resting spores that rapidly sink out of the surface layer, contributing to abrupt decreases in observed diatom abundance. This process could imply a peak in BSi, before diatom decline, just as we observed. Therefore, the sharp decline observed after the initial bloom peak could also be explained by the activation of density-dependent sporulation mechanisms (Pelusi et al., 2020). From an upwelling perspective, the OAE experiment represented an abrupt ending of upwelling or a transient stratification state where no nutrient intermittency through vertical upwelling pulses occurred. In that moment, the *Chaetoceros* bloom started to collapse after enclosure. Similar to oligotrophic regions, the observed decline in diatom abundance was likely driven by nutrient limitation rather than from cellular stress (Ramírez et al., 2025). Strong nitrogen and silicate limitation from day 1, coupled with the absence of renewed nutrient supply from upwelling, constrained primary production and diatom growth. This decline was consistent across all treatments,



providing evidence that OAE did not suppress diatom growth, induce stress responses, or accelerate mortality. Unlike  
440 mineral-based OAE feedstocks such as olivine or steel slag, hydroxide additions did not introduce essential trace metals that  
might stimulate diatom physiology (Guo et al., 2024). Thus, no positive fertilization pathway existed, and the diatom trajectory  
was solely driven by nutrient depletion. The negative OAE effect in diatoms observed in other experiments (Ferderer et al.,  
2022) is unfeasible when nutrient limitation is the predominant factor. To assess whether OAE can influence diatom success,  
nutrient-replete experiments during active upwelling or controlled nutrient-addition designs that maintain diatom growth  
445 windows long enough for alkalinity effects on silica cycling or ballasting to manifest are required.

#### 4.2.2 Small-sized cells and heterotrophs leverage nutrient exhaustion

We observe a classical response after nutrient exhaustion, with shifts in the phytoplankton size structure from large cells  
decline towards a community dominated by small-sized cells (Cermeno et al., 2006). Following the diatom collapse,  
dinoflagellates, small flagellates, and ciliates increased consistently in relative contribution across all treatments. The rise of  
450 bacteria and these microplankton heterotrophic groups also fits the expected trajectory of an enclosed, nutrient-exhausted  
system: when strict photoautotrophs disappear and organic matter is still abundant for heterotrophic processing. The increase  
of small flagellates, observed from days 10–13 onward, matches the expected post-bloom succession in upwelling systems  
once nutrient recycling becomes the dominant source of inorganic nitrogen (Bode and Varela, 1998). This behaviour is  
consistent with mesocosm studies in the same region, where heterotrophic biomass rapidly increases after bloom collapse  
455 regardless of experimental manipulation (Teira et al., 2008, 2011). The mid-experiment heterotrophic bacteria maximum was  
short-lived, and likely eroded by microzooplankton grazing since these consumers remove a substantial fraction of the daily  
bacterial and picoplankton production in the Ría de Vigo (Teixeira et al., 2011). Bacterial abundance showed no significant  
treatment effect, indicating that heterotrophic bacterial dynamics were also governed by the post-bloom successional stage  
rather than by the alkalinity manipulation. The lack of an OAE effect on bacterial succession agrees with Kousoulas et al.  
460 (2025) and contrasts with Ferderer et al. (2022), suggesting that current evidence remains inconclusive to establish a general  
pattern. The uniform behaviour across treatments shows that OAE neither modifies the rhythm nor the structure of  
microplankton and heterotrophic bacteria succession under nutrient limited conditions.

Although the resilience of picoplankton to OAE perturbation and their ability to exploit regenerated nutrients are documented  
in subtropical and oligotrophic systems (Marín-Samper et al., 2024; Suessle et al., 2025; Xin et al., 2024), here we show that  
465 after a diatom bloom that exhausted inorganic nutrient content, the picoplankton groups assessed did show an OAE-dependent  
alteration. Smallest sized groups resolved by flow cytometry, autotrophic picoeukaryotes and *Synechococcus*, displayed a  
response in-line with the progress of remineralization and secondary production processes but with dynamics affected by OAE  
treatments. Although OAE treatment in autotrophic picoeukaryotes modifies both the temporal trend and the absolute values,  
none of the pairwise contrasts were significant when the complete experiment timeline is considered (Šidák-adjusted  $p > 0.05$ ,  
470 Fig. A5). Most of the difference in picoeukaryote abundance happens at day 13 peak, when abundances decrease with the  
extent of the carbonate-chemistry shift. An identical picoeukaryote response under OAE treatment has been seen in similar



experiments (Ferderer et al., 2022; Kousoulas et al., 2025). If picoeukaryotes are 'winners' under ocean acidification conditions (Sala et al., 2016; Schulz et al., 2017), they would be 'losers' in alkalinization situations and the more extreme the shift (unequilibrated), the worse (Ferderer et al., 2022; Kousoulas et al., 2025).

475 *Synechococcus* also displayed a shift in the temporal pattern associated with OAE treatments. Here we shown the same model response than Ferderer et al. (2022), although with an opposite dynamic: their population declined whereas ours showed a marked increase near its conclusion. Our observed response is more similar to Kousoulas et al. (2025) and Guo et al. (2024), who found an increase in *Synechococcus* abundance towards the end of their experiments. *Synechococcus* responses to carbonate-chemistry manipulation have revealed contrasting results (Sala et al., 2016; Schulz et al., 2017) likely related to top-  
480 down effects transmitted through the grazing pressure (Bach et al., 2017; Kousoulas et al., 2025; Traboni et al., 2025) rather than direct physiological responses (Ramírez et al., 2025).

In summary, after a strong alkalinization event at nutrient limited conditions, the succession of the pelagic plankton community in the NW Iberian upwelling system was only altered within the picoplankton size-class. Whether it modifies the bottom-up transfer of carbon and energy through the microbial food web remains an open question.

#### 485 **4.3 Experimental constraints, open questions and future work: is it the OAE response succession-dependent?**

This study provides a snapshot of the NW Iberian Upwelling pelagic ecosystem during a spring diatom bloom event. Therefore, its ecological relevance depends on how representative the initial conditions were. Fortunately, the initial phytoplankton community assemblage and inorganic nutrient content were typical of the seasonal cycle. Even so, the temporal structure of plankton assemblages in this region can shift rapidly due to changes in wind forcing, stratification, and nutrient delivery (Buttay  
490 et al., 2022; Otero et al., 2018). Consequently, a proper characterization of hydrography, ecology and biogeochemistry during the days preceding any future OAE deployment should be required. A significant limitation of the current experiment to reproduce OAE response in an upwelling ecosystem is the lack of nutrient additions during several weeks. In a highly dynamic coastal bay such as the Ría de Vigo, where upwelling and downwelling events alternate on short temporal scales (Gilcoto et al., 2017), a period exceeding 15 days without external nutrient inputs is an anomalous situation. The controlled addition of  
495 nutrient inputs during OAE treatments, particularly nitrate and silicate pulses mimicking upwelling intermittency, would prolong diatom growth, and therefore primary production, enabling evaluation of potential pelagic OAE impacts. Certainly, our main OAE-mediated effects with statistical support were the altered abundances in the smallest sized classes. Both processes were transient and concentrated in the last week of the experimental timeline, precisely when enclosure artefacts and "bottle effects" become most usual (Carpenter, 1996; Riebesell et al., 2023). The envisioned synthesis meta-analysis study of  
500 OAEPIIP experiments could give a more robust answer (Bach et al., 2024).

Future OAE research in the region should prioritize seasonal assessments across winter mixed and summer stratified regimes, include contrasting upwelling and downwelling conditions, and extend sampling sites across the full shelf-to-inner bay continuum. Such designs would capture the full range of natural plankton variability and test whether OAE effects emerge only under nutrient-replete or diatom-favourable conditions. Moreover, even small variations in environmental conditions may



determine which pioneer species initiates the first bloom (Nogueira and Figueiras, 2005). This is particularly relevant because previous studies have suggested that the identity of early colonizers can generate priority effects, thereby influencing community assembly and potentially altering long-term successional trajectories (Stroud et al., 2024). It is therefore a priority to determine whether OAE responses differ under alternative successional stages. Finally, future experiments should consider the ecological implications of OAE for mussel aquaculture, a key economic sector in the study area (Labarta and Fernández-Reiriz, 2019), particularly given its potential to alleviate the regional threat posed by ocean acidification (Cameselle et al., 2024; Fontela et al., 2020) and the limited understanding of species-specific physiological responses of marine invertebrates to OAE (Jones et al., 2025). Understanding how OAE interacts with natural variability in food quality, phytoplankton size structure, and particulate export will be essential for assessing environmental safety of OAE or any mCDR technique. From a methodological perspective, the inclusion of additional biogeochemical (e.g., size-fractionated chlorophyll-*a*, DOC, DON), photophysiological (e.g., PAM fluorometry), or metabolic indicators (e.g., community metabolism, bacterial heterotrophic production, or microbial respiration) would strengthen the interpretation of ecosystem functioning under OAE.

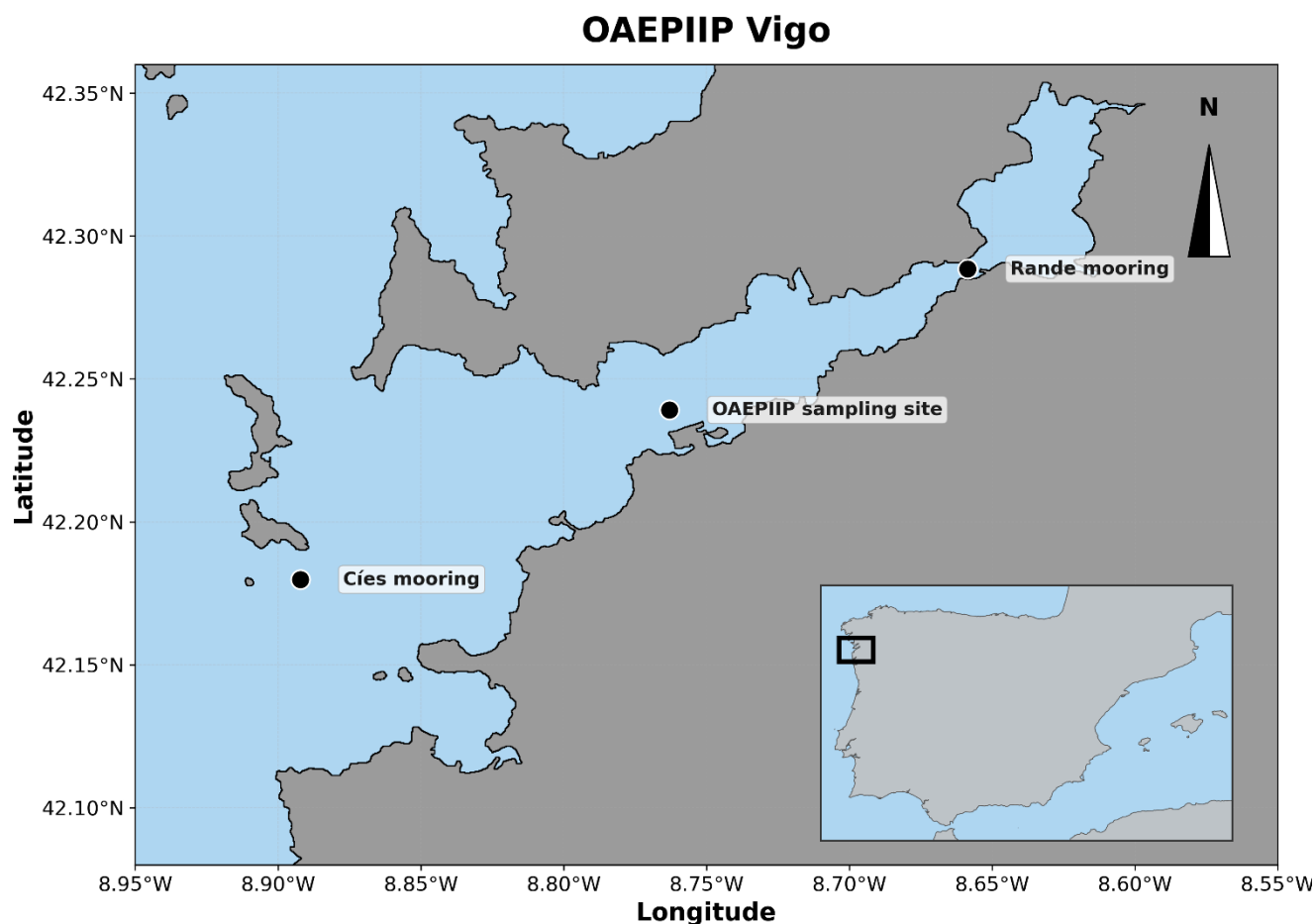
## 5 Conclusions

Here we show that OAE produced limited effects on the plankton community in the surface waters of the Ría de Vigo just after a diatom bloom event, with responses largely restricted to the smallest size classes. Despite abrupt changes in inorganic carbon chemistry, most variables showed no differential response between equilibrated and unequilibrated treatments or relative to the unperturbed control. Although the abundance of the small-sized classes picoeukaryotes and *Synechococcus* appears to be affected by OAE, the export potential in terms of biological carbon pump of the pelagic ecosystem remains unaltered. At the final stages of a diatom bloom when inorganic nutrients become limiting, if the NW Iberian phytoplankton community composition is dominated by medium-size diatoms, it can withstand the environmental shifts associated with OAE. As plankton community resilience to OAE is highly conditioned by the initial status, the ecological pelagic impacts of OAE could be strongly succession- and nutrient-regime dependent. Through OAEPIIP framework we build capacity to evaluate the pelagic response for each combination of initial planktonic community structure and ambient inorganic nutrient content. Future studies should conduct seasonal and spatial (shelf-inner bay gradient) assessments, include nutrient-addition mimicking upwelling pulses and diverse OAE feedstocks to evaluate the ecological safety and scalability of potential future OAE deployments. Under the tested conditions, OAE does not compromise pelagic plankton ecosystem services in this productive coastal upwelling system yet the safe operational limit of OAE is still uncertain. In this ecosystem, pelagic microplankton community is so finely tuned to nutrient competition that it shows remarkable resilience toward carbon chemistry changes.



## Appendix A

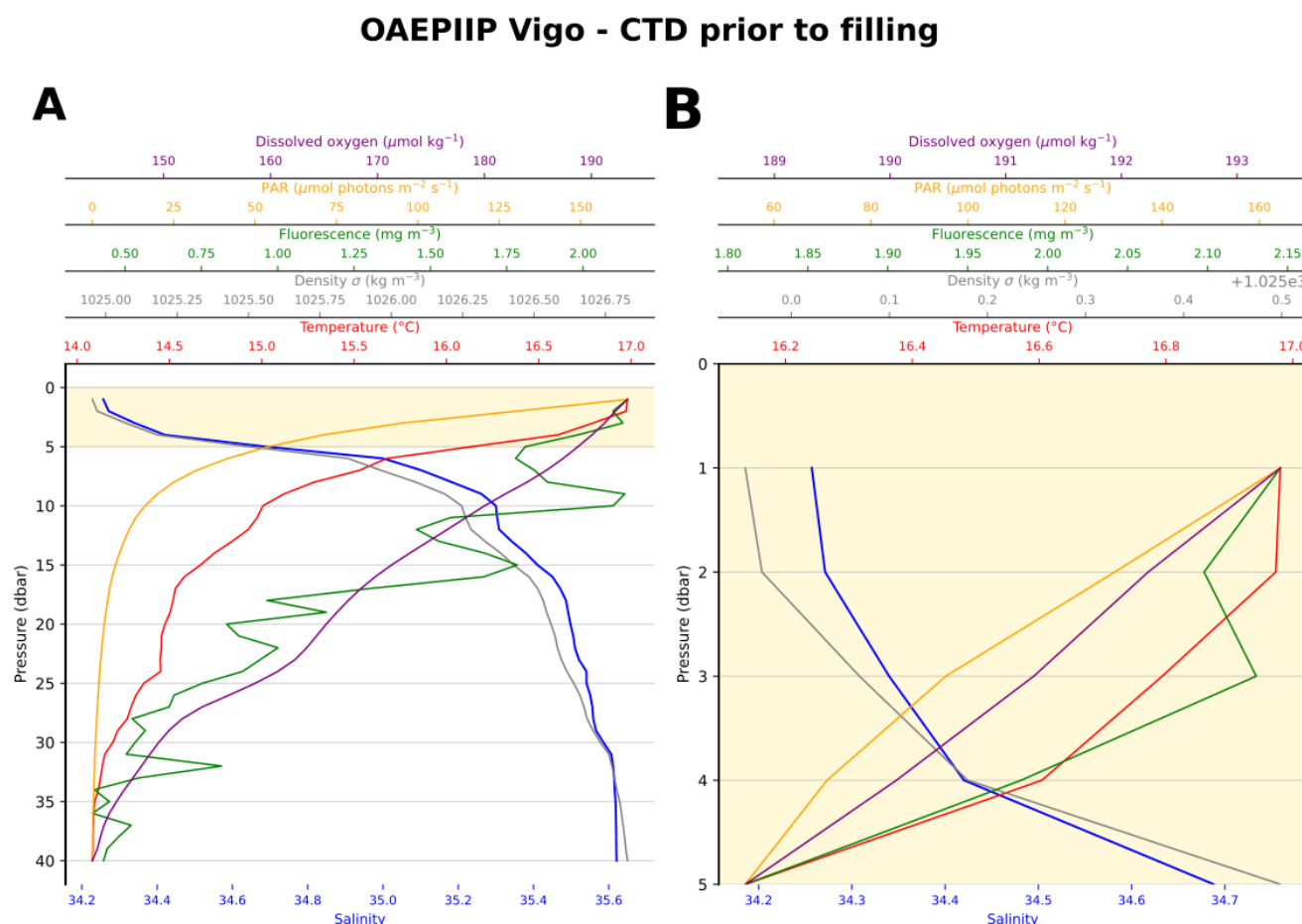
**Figure A1. OAEPIIP Vigo sampling site map**



**Figure A1.** Ría de Vigo map. The OAEPIIP sampling site (42.239°N, 8.763°W) where microcosms were filled and the Cíes and Rande moorings are represented with black circles. The inset in the lower-right corner shows the location of the study area within the Northwest Iberian Upwelling System.



**Figure A2. CTD profiles**



**Figure A2.** CTD profile in the Ría de Vigo OAEPIIP sampling site (42.239°N, 8.763°W) on 9th May 2025 (06:41 UTC), immediately before microcosms filling. (A) Full water-column (1–40 dbar) showing salinity (blue, bottom axis), *in situ* temperature (°C, red), density ( $\sigma$ ,  $\text{kg m}^{-3}$ , gray), fluorescence ( $\text{mg m}^{-3}$ , green), photosynthetically active radiation (PAR,  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , orange) and dissolved oxygen ( $\mu\text{mol kg}^{-1}$ , purple), each plotted against pressure (dbar). The shaded band (0–5 dbar) delimits the surface layer zoomed in (B). (B) Near-surface zoom of the same variables over the top 5 dbar, with axis ranges rescaled to the range of values observed within this interval. The microcosm filling procedure took place surely in the first 2 dbar pressure layer. All profiles correspond to the downcast CTD cast.



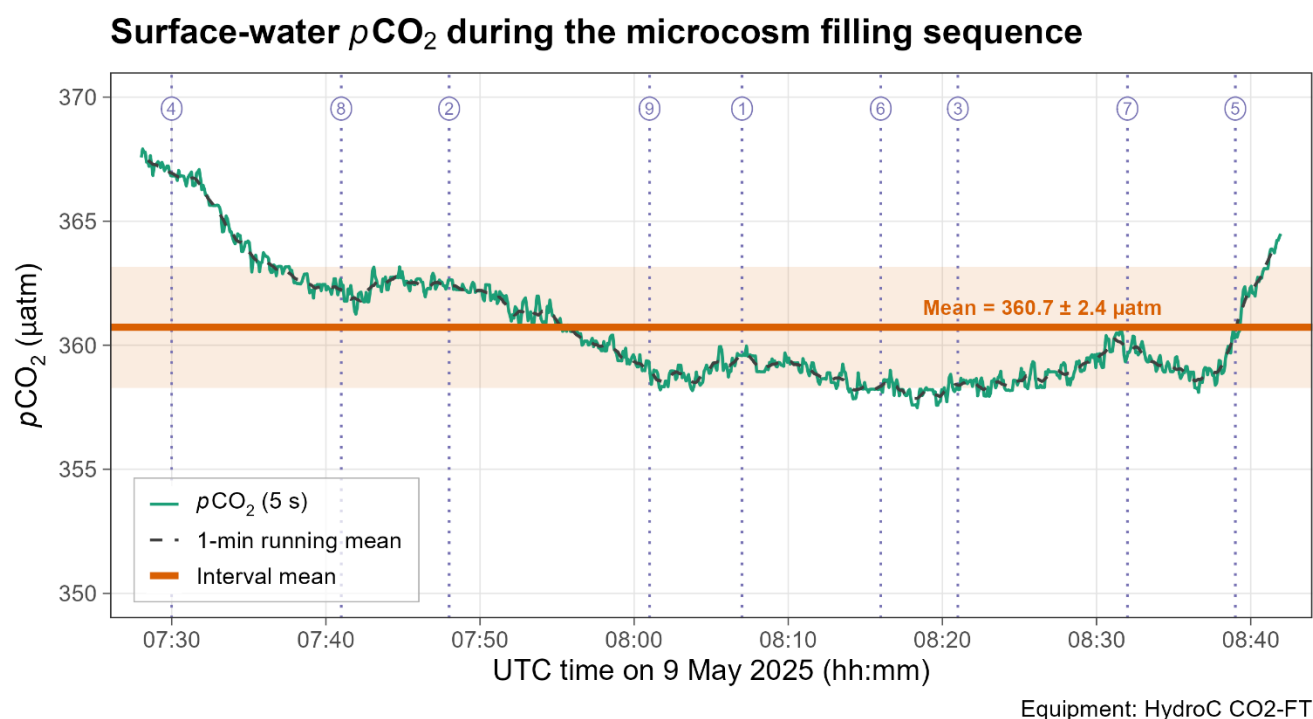
### Table A1 Microcosm filling time

Table A1. The start time (UTC hour, 9<sup>th</sup> May 2025) and the time interval (in minutes) for the microcosm filling process. Microcosms were filled sequentially, one at a time in a random order. Time difference (minute) is the interval between the start of a microcosm filling and that of the previous one. The full sequence (n = 9) was completed in 69 min (07:30–08:39 UTC).

| Microcosm number   | Filling start time (UTC) | Time difference (minute) |
|--------------------|--------------------------|--------------------------|
| 4                  | 07:30                    |                          |
| 8                  | 07:41                    | 11                       |
| 2                  | 07:48                    | 7                        |
| 9                  | 08:01                    | 13                       |
| 1                  | 08:07                    | 6                        |
| 6                  | 08:16                    | 9                        |
| 3                  | 08:21                    | 5                        |
| 7                  | 08:32                    | 11                       |
| 5                  | 08:39                    | 7                        |
| Total filling time |                          | 69                       |



**Figure A3. Surface pCO<sub>2</sub> at filling time**



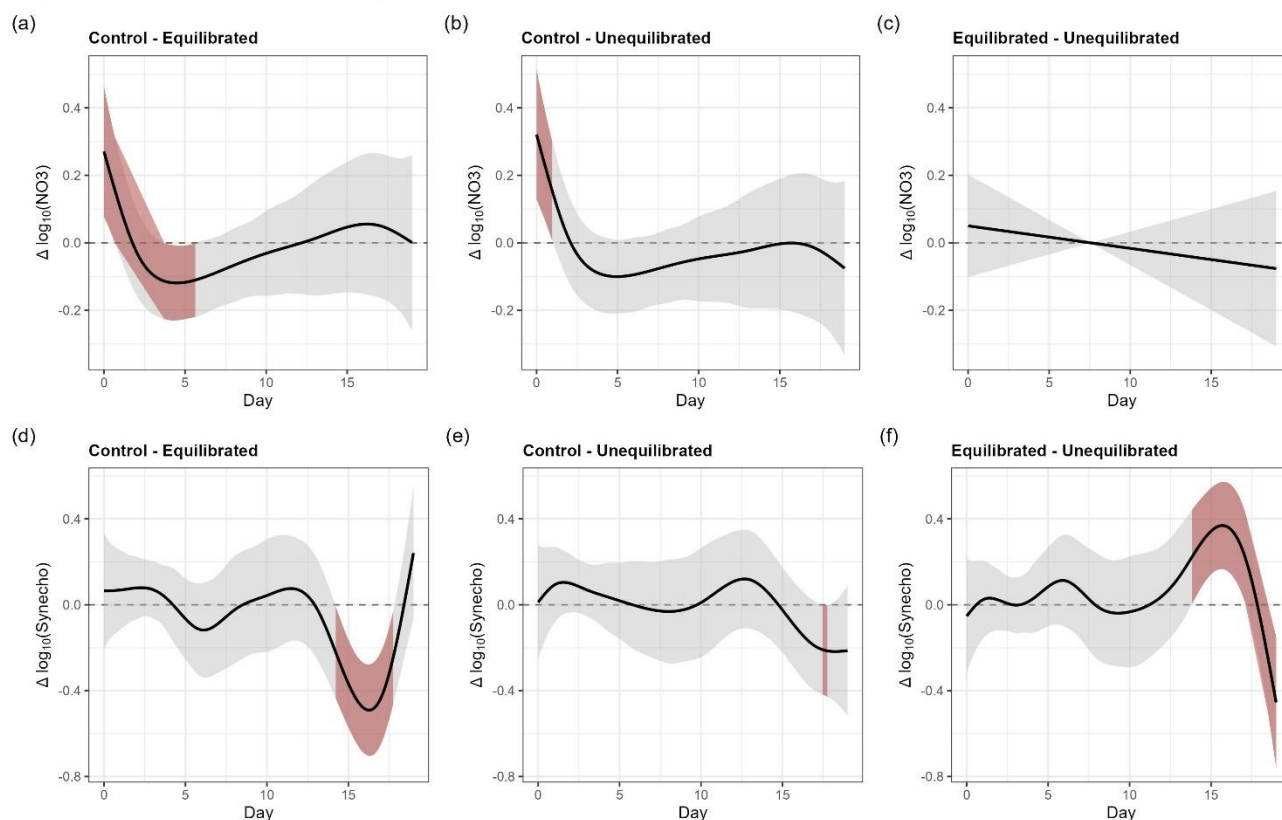
**Figure A3.** Temporal evolution of surface-water partial pressure of carbon dioxide (pCO<sub>2</sub>) measured during the microcosm-filling sequence. Measurements were recorded every 5 s (green line) with a HydroC CO<sub>2</sub>-FT membrane sensor in the underway system of R/V Mytilus. The corresponding 1-min running mean is shown in dashed black. Vertical dashed lines mark the filling of individual microcosms, identified by numbered labels. The mean and standard deviation of sea surface pCO<sub>2</sub> during the filling period ( $360.7 \pm 2.4$  µatm) is represented with an orange horizontal line and a shaded band.



**Figure A4.**

Pairwise treatment difference smooths (gamm\_2 models)

Grey band = 95% CI, red = CI excludes zero (significant divergence)

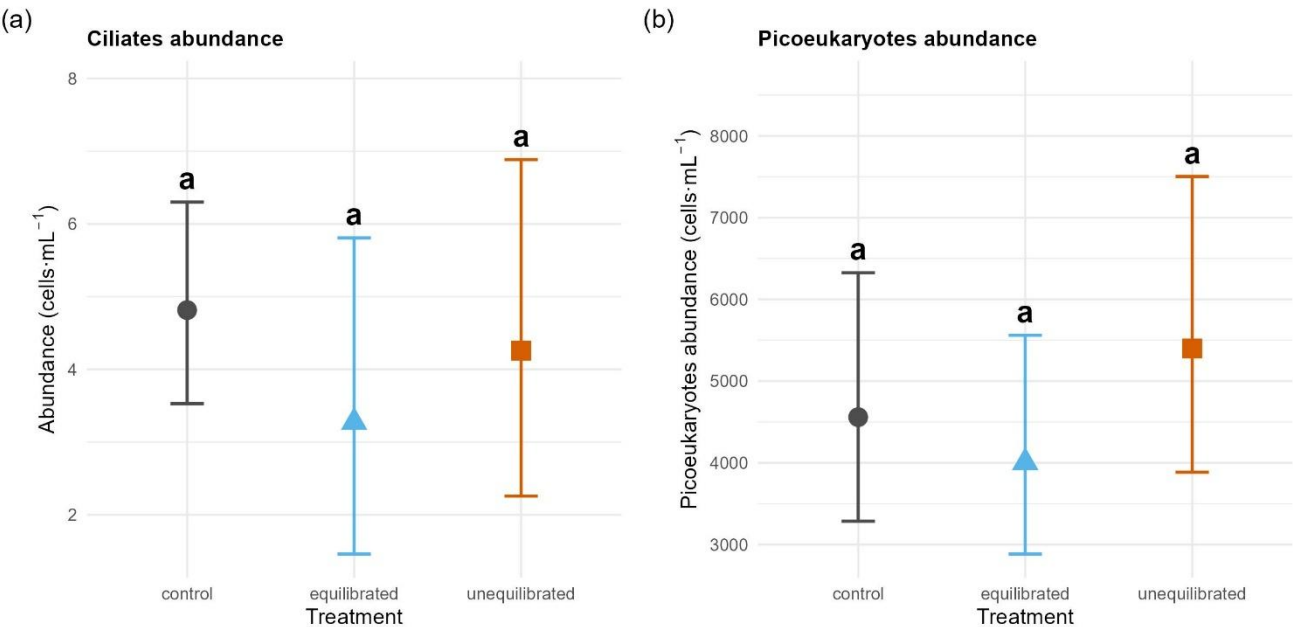


**Figure A4.** Pairwise treatment difference smooths for the variables whose best-supported model retained a treatment-specific temporal smooth without a parametric treatment effect (GAMM\_2<sub>2</sub>): (a–c)  $\text{NO}_3$  and (d–f)  $\text{Synechococcus}$ . Each panel shows the estimated difference between two treatment-specific  $s(\text{Day})$  smooths on the  $\log_{10}$ -transformed scale (solid black line) together with its 95% confidence interval (shaded band) across the 20-day incubation. Grey shading indicates periods where the confidence interval includes zero (no significant divergence between treatments); red shading indicates periods where the interval excludes zero, denoting a statistically significant difference between the two treatments at that time point. The dashed horizontal line marks zero difference. Because both variables were modelled on the  $\log_{10}$  scale,  $\Delta \log_{10}$  values correspond to the  $\log_{10}$  of the fold-change ratio between the two treatments being compared.



550 **Figure A5.**

Treatment effect on estimated marginal means using Šidák-adjusted pairwise contrasts ( $\alpha = 0.05$ )



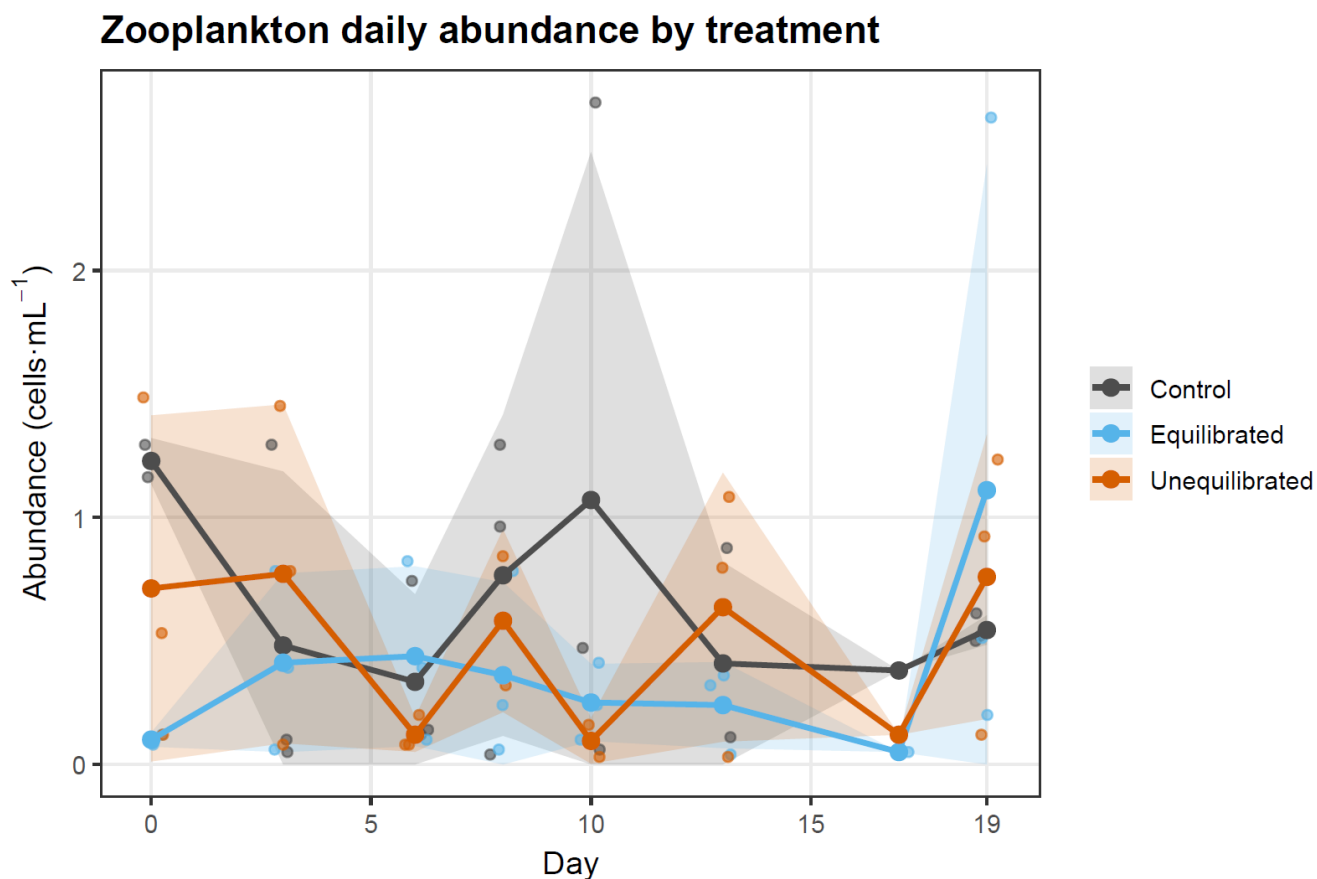
**Figure A5. Time-averaged treatment effects** on (a) ciliate group abundance, and (b) picoeukaryote abundance. For each variable, estimated marginal means (EMMs) and 95% confidence intervals were computed from their best-supported GAMM\_4 model and back-transformed from the scale on which the model was fitted (square-root for ciliate abundance, log<sub>10</sub> for Picoeuk) to the original measurement units. Points and error bars show back-transformed EMMs ± 95% CI, averaged over the experimental period for each treatment (control, equilibrated, unequilibrated). Letters denote a compact letter display (CLD) from pairwise post-hoc comparisons of EMMs ( $\alpha = 0.05$ , Šidák-adjusted); treatments sharing a letter are not significantly different.

555

560



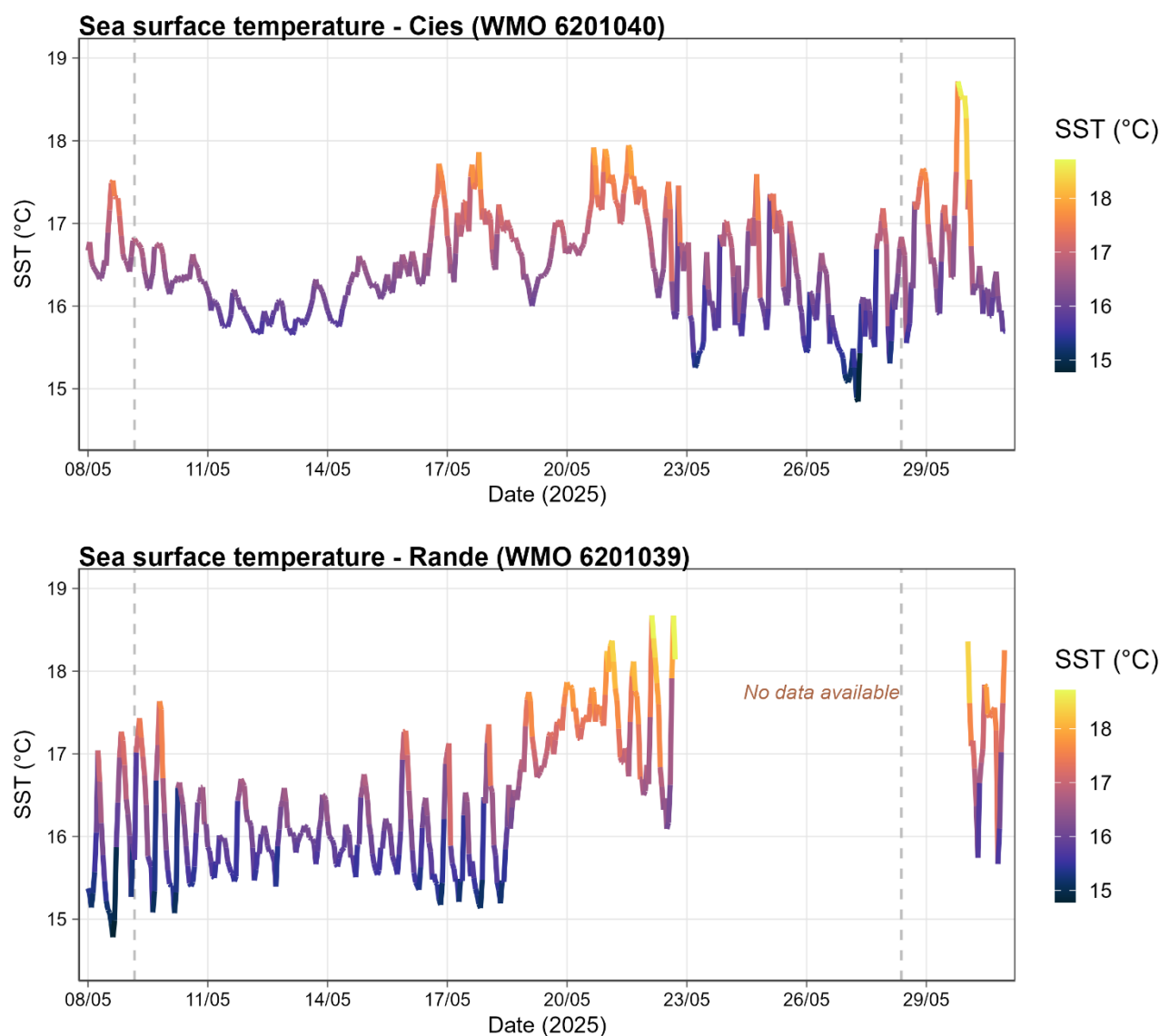
**Figure A6.**



**Figure A6. Daily meatazoan zooplankton abundance by treatment.** Small points show individual microcosm replicates (horizontally jittered for visibility); solid points and lines show the mean across replicates, and shaded bands show  $\pm 1$  SD ( $n = 2-3$  replicates per treatment and day, except day 17,  $n = 1$ ). Colors indicate treatment: control (dark grey, circles), equilibrated (light blue, triangles), unequilibrated (brown)."



**Figure A7.** *In situ* temperature in the Ría de Vigo



**Figure A7.** Time series of sea surface temperature (°C) recorded at the Cíes (WMO 6201040; upper panel) and Rande (WMO 6201039; lower panel) mooring stations during May 2025 (8<sup>th</sup>-31<sup>th</sup>). The dashed vertical lines delimit the study period. A gap in observations at the Rande station between 23 and 29 May indicates a period with no data availability. Data have been transferred free of charge by the Observatorio Costeiro da Xunta de Galicia ([www.observatoriocosteiro.gal](http://www.observatoriocosteiro.gal)) for their use. The Costeiro da Xunta de Galicia Observatory is part of the RAIA Observatory ([www.marnaraia.org](http://www.marnaraia.org)).



## 570 **Code and data availability**

The Ocean Alkalinity Enhancement Pelagic Impact Intercomparison Project (OAEPiIP) Vigo May 2025 experiment data report is available at (temporary link): <https://co2.iim.csic.es/seafile/d/916d13d4e7864924bd73/>. The code to reproduce the results is available at <https://github.com/mfontela/OAEPiIP>.

## **Author contributions**

575 MF conceptualized the study, acquired the funding and administered the project, curated the data, prepared the figures, performed the formal analysis and the software development, and supervised and validated the work. MF, MFr., SG, LM, CCR, CLH, MLR, MD and IGT developed the methodology and performed the analytical determinations. MF prepared the original draft, with review and editing contributions from all co-authors, who read and approved the final manuscript.

## **Competing interests**

580 None declared.

## **Disclaimer**

Copernicus Publications remains neutral with regard to jurisdictional claims made in the text, published maps, institutional affiliations, or any other geographical representation in this paper. While Copernicus Publications makes every effort to include appropriate place names, the final responsibility lies with the authors. Views expressed in the text are those of the authors and  
585 do not necessarily reflect the views of the publisher.

## **Acknowledgements**

M. Fontela was funded by PTA2022-021307-I, MCIN/AEI/10.13039/501100011033 and by FSE+. F. F. Pérez and X. A. Padin were supported by the FICARAM+ project (PID2023-148924OB-I00) funded by MICIU/AEI/10.13039/501100011033 and FEDER, UE. L. Moreno was supported by FCT — Fundação para a Ciência e a Tecnologia, I.P., PRT/BD/154754/2023. C.  
590 Cesar-Ribeiro was supported by FCT contracts UID/04326/2025, UID/PRR/04326/2025, LA/P/0101/2020 and CEECINSTLA/00028/2022/CP2990/CT0002. M. López-Acosta was supported by a GAIN postdoctoral fellowship (IN606C-2023/001) funded by Xunta de Galicia and by a Ramón y Cajal fellowship (RYC2024-050991-I) funded by the Spanish Ministry of Science, Innovation and Universities. The authors thank the SACUIM unit at IIM-CSIC (Rubén Chamorro, Xoán Martínez, Félix Álvarez) for their valuable help with the experimental setup, and the R/V *Mytilus* crew for their invaluable  
595 collaboration and expertise during the microcosm filling process.



## Financial support

Support funds and grant agreement numbers are listed as specified upon manuscript registration and reported to FundRef upon publication.

## Review statement

- 600 The review statement will be added by Copernicus Publications listing the handling editor as well as all contributing referees according to their status anonymous or identified.

## References

- Anderson, L. A. and Sarmiento, J. L.: Redfield ratios of remineralization determined by nutrient data analysis, *Glob. Biogeochem. Cycles*, 8, 65–80, <https://doi.org/10.1029/93GB03318>, 1994.
- 605 Arbones, B., Castro, C., Alonso-Pérez, F., and Figueiras, F.: Phytoplankton size structure and water column metabolic balance in a coastal upwelling system: the Ría de Vigo, NW Iberia, *Aquat. Microb. Ecol.*, 50, 169–179, <https://doi.org/10.3354/ame01160>, 2008.
- Bach, L. T., Alvarez-Fernandez, S., Hornick, T., Stuhr, A., and Riebesell, U.: Simulated ocean acidification reveals winners and losers in coastal phytoplankton, *PLoS ONE*, 12, e0188198, <https://doi.org/10.1371/journal.pone.0188198>, 2017.
- 610 Bach, L. T., Ferderer, A. J., LaRoche, J., and Schulz, K. G.: Technical note: Ocean Alkalinity Enhancement Pelagic Impact Intercomparison Project (OAPEIIP), *Biogeosciences*, 21, 3665–3676, <https://doi.org/10.5194/bg-21-3665-2024>, 2024.
- Bode, A. and Varela, M.: Primary production and phytoplankton in three Galician Rias Altas (NW Spain): seasonal and spatial variability, *Sci. Mar.*, 62, 319–330, <https://doi.org/10.3989/scimar.1998.62n4319>, 1998.
- Bode, A., Estévez, M. G., Varela, M., and Vilar, J. A.: Annual trend patterns of phytoplankton species abundance belie homogeneous taxonomical group responses to climate in the NE Atlantic upwelling, *Mar. Environ. Res.*, 110, 81–91, <https://doi.org/10.1016/j.marenvres.2015.07.017>, 2015.
- 615 Boyd, P. W., Claustre, H., Levy, M., Siegel, D. A., and Weber, T.: Multi-faceted particle pumps drive carbon sequestration in the ocean, *Nature*, 568, 327–335, <https://doi.org/10.1038/s41586-019-1098-2>, 2019.
- Buttay, L., Vasseur, D. A., González-Quirós, R., and Nogueira, E.: Nutrient limitation can explain a rapid transition to synchrony in an upwelling-driven diatom community, *Limnol. Oceanogr.*, 67, S298–S311, <https://doi.org/10.1002/lno.12033>, 2022.
- 620 Calvo-Díaz, A. and Morán, X.: Seasonal dynamics of picoplankton in shelf waters of the southern Bay of Biscay, *Aquat. Microb. Ecol.*, 42, 159–174, <https://doi.org/10.3354/ame042159>, 2006.
- Cameselle, S., Velo, A., Doval, M. D., Broullón, D., and Pérez, F. F.: Long-term trends of pH, alkalinity, and hydrogen ion concentration in an upwelling-dominated coastal ecosystem: Ría de Vigo, NW Spain, *Sci. Rep.*, 14, 17929, <https://doi.org/10.1038/s41598-024-68694-z>, 2024.
- 625



- Carpenter, S. R.: Microcosm Experiments have Limited Relevance for Community and Ecosystem Ecology, *Ecology*, 77, 677–680, <https://doi.org/10.2307/2265490>, 1996.
- 630 Carter, B. R., Radich, J. A., Doyle, H. L., and Dickson, A. G.: An automated system for spectrophotometric seawater pH measurements, *Limnol. Oceanogr. Methods*, 11, 16–27, <https://doi.org/10.4319/lom.2013.11.16>, 2013.
- de Castro, I., Ribeiro, S. C., Louvado, A., Gomes, N. C. M., Cachão, M., Brito de Azevedo, E., and Barcelos e Ramos, J.: Ocean liming effect on a North Atlantic microbial community: changes in composition and rates, *Front. Mar. Sci.*, Volume 12-2025, <https://doi.org/10.3389/fmars.2025.1602158>, 2025.
- 635 Cermeño, P., Marañón, E., Pérez, V., Serret, P., Fernández, E., and Castro, C. G.: Phytoplankton size structure and primary production in a highly dynamic coastal ecosystem (Ría de Vigo, NW-Spain): Seasonal and short-time scale variability, *Estuar. Coast. Shelf Sci.*, 67, 251–266, <https://doi.org/10.1016/j.ecss.2005.11.027>, 2006.
- Clayton, T. D. and Byrne, R. H.: Spectrophotometric seawater pH measurements: total hydrogen ion concentration scale calibration of m-cresol purple and at-sea results, *Deep Sea Res. Part Oceanogr. Res. Pap.*, 40, 2115–2129, [https://doi.org/10.1016/0967-0637\(93\)90048-8](https://doi.org/10.1016/0967-0637(93)90048-8), 1993.
- 640 Dickson, A. G.: Standard potential of the reaction:  $\text{AgCl(s)} + 1/2 \text{H}_2\text{(g)} = \text{Ag(s)} + \text{HCl(aq)}$ , and the standard acidity constant of the ion  $\text{HSO}_4^-$  in synthetic sea water from 273.15 to 318.15 K, *J. Chem. Thermodyn.*, 22, 113–127, [https://doi.org/10.1016/0021-9614\(90\)90074-Z](https://doi.org/10.1016/0021-9614(90)90074-Z), 1990.
- Dickson, A. G., Sabine, C. L., and Christian, J. R.: Guide to best practices for ocean  $\text{CO}_2$  measurements, North Pacific Marine Science Organization Sidney, British Columbia, 191 pp., <https://doi.org/10.25607/OBP-1342>, 2007.
- 645 Ferderer, A., Chase, Z., Kennedy, F., Schulz, K. G., and Bach, L. T.: Assessing the influence of ocean alkalinity enhancement on a coastal phytoplankton community, *Biogeosciences*, 19, 5375–5399, <https://doi.org/10.5194/bg-19-5375-2022>, 2022.
- Figueiras, F. G., Teixeira, I. G., Froján, M., Zúñiga, D., Arbones, B., and Castro, C. G.: Seasonal Variability in the Microbial Plankton Community in a Semienclosed Bay Affected by Upwelling: The Role of a Nutrient Trap, *Front. Mar. Sci.*, Volume 7-2020, <https://doi.org/10.3389/fmars.2020.578042>, 2020.
- 650 Fontela, M., Pérez, F. F., Carracedo, L. I., Padín, X. A., Velo, A., García-Ibañez, M. I., and Lherminier, P.: The Northeast Atlantic is running out of excess carbonate in the horizon of cold-water corals communities, *Sci. Rep.*, 10, 14714, <https://doi.org/10.1038/s41598-020-71793-2>, 2020.
- Fontela, M., Velo, A., Brown, P. J., and Pérez, F. F.: Carbonate System Species and pH, in: *Marine Analytical Chemistry*, edited by: Blasco, J. and Tovar-Sánchez, A., Springer International Publishing, Cham, 1–37, [https://doi.org/10.1007/978-3-031-14486-8\\_1](https://doi.org/10.1007/978-3-031-14486-8_1), 2023.
- 655 Fontela, M., Fernández-Román, D., Broullón, E., Farnelid, H., Fernández-Carrera, A., Marañón, E., Martínez-García, S., Rodríguez-Ramos, T., Varela, M. M., and Mouriño-Carballido, B.: Puzzling out the ecological niche construction for nitrogen fixers in a coastal upwelling system, *ISME Commun.*, 5, ycaf018, <https://doi.org/10.1093/ismeco/ycaf018>, 2025.
- Garber, J. H.: Laboratory study of nitrogen and phosphorus remineralization during the decomposition of coastal plankton and seston, *Estuar. Coast. Shelf Sci.*, 18, 685–702, [https://doi.org/10.1016/0272-7714\(84\)90039-8](https://doi.org/10.1016/0272-7714(84)90039-8), 1984.
- 660 Gately, J. A., Kim, S. M., Jin, B., Brzezinski, M. A., and Iglesias-Rodriguez, M. D.: Coccolithophores and diatoms resilient to ocean alkalinity enhancement: A glimpse of hope?, *Sci. Adv.*, 9, eadg6066, <https://doi.org/10.1126/sciadv.adg6066>, 2023.



- Gattuso, J.-P., Epitalon, J.-M., Lavigne, H., and Orr, J.: seacarb: Seawater Carbonate Chemistry, <https://doi.org/10.32614/CRAN.package.seacarb>, 2003.
- 665 Gilcoto, M., Largier, J. L., Barton, E. D., Piedracoba, S., Torres, R., Graña, R., Alonso-Pérez, F., Villaceros-Robineau, N., and de la Granda, F.: Rapid response to coastal upwelling in a semienclosed bay, *Geophys. Res. Lett.*, 44, 2388–2397, <https://doi.org/10.1002/2016GL072416>, 2017.
- Guo, J. A., Strzepek, R. F., Swadling, K. M., Townsend, A. T., and Bach, L. T.: Influence of ocean alkalinity enhancement with olivine or steel slag on a coastal plankton community in Tasmania, *Biogeosciences*, 21, 2335–2354,   
670 <https://doi.org/10.5194/bg-21-2335-2024>, 2024.
- Ho, D. T. and Bopp, L.: Marine carbon dioxide removal may be a future climate solution, *Dialogues Clim. Change*, 1, 56–62, <https://doi.org/10.1177/29768659241293223>, 2024.
- IPCC, 2021: Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Masson-Delmotte, V., P. Zhai, A. Pirani, S.L. Connors, C. Péan,   
675 S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou (eds.)], Cambridge University Press, Cambridge, UK and New York, NY, USA, 2391 pp., <https://doi.org/10.1017/9781009157896>, 2021.
- Jones, K., Hemery, L. G., Ward, N. D., Regier, P. J., Ringham, M. C., and Eisaman, M. D.: Biological response of eelgrass epifauna, Taylor's Sea hare (*Phyllaplysia taylori*) and eelgrass isopod (*Idotea resicata*) to elevated ocean alkalinity,   
680 *Biogeosciences*, 22, 1615–1630, <https://doi.org/10.5194/bg-22-1615-2025>, 2025.
- Justel-Díez, M., Delgadillo-Nuño, E., Costas-Selas, C., Martínez-García, S., Fuentes-Lema, A., Álvarez-Salgado, X. A., Fernández, E., and Teira, E.: Effect of bacteria on the phytoplankton response to P-replete and P-deplete riverine water inputs, *Mar. Environ. Res.*, 211, 107400, <https://doi.org/10.1016/j.marenvres.2025.107400>, 2025.
- Kemp, A. E. S. and Villareal, T. A.: The case of the diatoms and the muddled mandalas: Time to recognize diatom adaptations to stratified waters, *Prog. Oceanogr.*, 167, 138–149, <https://doi.org/10.1016/j.pocean.2018.08.002>, 2018.
- Kjørboe, T. and Hansen, J. L. S.: Phytoplankton aggregate formation: observations of patterns and mechanisms of cell sticking and the significance of exopolymeric material, *J. Plankton Res.*, 15, 993–1018, <https://doi.org/10.1093/plankt/15.9.993>, 1993.
- Kousoulas, K., Ferderer, A., Eriksen, R., and Bach, L. T.: Winners and losers under hydroxide-based ocean alkalinity enhancement in a Tasmanian plankton community, *J. Phycol.*, 61, 989–1006, <https://doi.org/10.1111/jpy.70052>, 2025.
- 690 Kroeker, K. J., Kordas, R. L., Crim, R., Hendriks, I. E., Ramajo, L., Singh, G. S., Duarte, C. M., and Gattuso, J.-P.: Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming, *Glob. Change Biol.*, 19, 1884–1896, <https://doi.org/10.1111/gcb.12179>, 2013.
- Labarta, U. and Fernández-Reiriz, M. J.: The Galician mussel industry: Innovation and changes in the last forty years, *Ocean Coast. Manag.*, 167, 208–218, <https://doi.org/10.1016/j.ocecoaman.2018.10.012>, 2019.
- 695 Lancelot, C.: Factors affecting phytoplankton extracellular release in the Southern Bight of the North Sea, *Mar. Ecol. Prog. Ser.*, 12, 115–121, <https://doi.org/10.3354/meps012115>, 1983.
- Lee, K., Kim, T.-W., Byrne, R. H., Millero, F. J., Feely, R. A., and Liu, Y.-M.: The universal ratio of boron to chlorinity for the North Pacific and North Atlantic oceans, *Geochim. Cosmochim. Acta*, 74, 1801–1811, <https://doi.org/10.1016/j.gca.2009.12.027>, 2010.



- 700 Lenth, R. V. and Piaskowski, J.: emmeans: Estimated Marginal Means, aka Least-Squares Means, R package version 2.0.4, <https://doi.org/10.32614/CRAN.package.emmeans>, 2026.
- Liu, Y., Wang, X., Niu, R., Huang, X., Zhou, X., Li, H., Li, G., Hopwood, M. J., and Hou, S.: Resilience to Alkalinity Perturbations Reveals Ecosystem Stability under Ocean Alkalinity Enhancement, *Ocean-Land-Atmos. Res.*, 5, 0157, <https://doi.org/10.34133/olar.0157>, 2026.
- 705 López-Sandoval, D. C., Fernández-González, C., González-García, C., and Marañón, E.: Warming Accelerates Phytoplankton Bloom Dynamics and Differentially Affects the Fluxes of Carbon, Nitrogen, and Oxygen Through a Coastal Microbial Community, *Microb. Ecol.*, 88, 117, <https://doi.org/10.1007/s00248-025-02643-9>, 2025.
- Lueker, T. J., Dickson, A. G., and Keeling, C. D.: Ocean pCO<sub>2</sub> calculated from dissolved inorganic carbon, alkalinity, and equations for K<sub>1</sub> and K<sub>2</sub>: validation based on laboratory measurements of CO<sub>2</sub> in gas and seawater at equilibrium, *Mar. Chem.*, 70, 105–119, [https://doi.org/10.1016/S0304-4203\(00\)00022-0](https://doi.org/10.1016/S0304-4203(00)00022-0), 2000.
- 710 Margalef, R.: Life-forms of phytoplankton as survival alternatives in an unstable environment, *Oceanol. Acta*, 1, 493–509, <https://archimer.ifremer.fr/doc/00123/23403/>, 1978.
- Marín-Samper, L., Arístegui, J., Hernández-Hernández, N., Ortiz, J., Archer, S. D., Ludwig, A., and Riebesell, U.: Assessing the impact of CO<sub>2</sub>-equilibrated ocean alkalinity enhancement on microbial metabolic rates in an oligotrophic system, *Biogeosciences*, 21, 2859–2876, <https://doi.org/10.5194/bg-21-2859-2024>, 2024.
- 715 Martínez-García, S., Fernández, E., Álvarez-Salgado, X.-A., González, J., Lønborg, C., Marañón, E., Morán, X.-A. G., and Teira, E.: Differential responses of phytoplankton and heterotrophic bacteria to organic and inorganic nutrient additions in coastal waters off the NW Iberian Peninsula, *Mar. Ecol. Prog. Ser.*, 416, 17–33, <https://doi.org/10.3354/meps08776>, 2010.
- National Academies of Sciences, Engineering, and Medicine (NASEM): A Research Strategy for Ocean-based Carbon Dioxide Removal and Sequestration, The National Academies Press, Washington, DC, <https://doi.org/10.17226/26278>, 2022.
- 720 NOAA ESRL GML CCGG Group: Earth System Research Laboratory Carbon Cycle and Greenhouse Gases Group Flask-Air Sample Measurements of CO<sub>2</sub> at Global and Regional Background Sites, 1967–Present, <https://doi.org/10.15138/WKGJ-F215>, 2019.
- Nogueira, E. and Figueiras, F. G.: The microplankton succession in the Ría de Vigo revisited: species assemblages and the role of weather-induced, hydrodynamic variability, *J. Mar. Syst.*, 54, 139–155, <https://doi.org/10.1016/j.jmarsys.2004.07.009>, 2005.
- 725 Nogueira, E., Pérez, F. F., and Ríos, A. F.: Seasonal Patterns and Long-term Trends in an Estuarine Upwelling Ecosystem (Ría de Vigo, NW Spain), *Estuar. Coast. Shelf Sci.*, 44, 285–300, <https://doi.org/10.1006/ecss.1996.0119>, 1997.
- Oberlander, J. L., Burke, M. E., London, C. A., and MacIntyre, H. L.: Assessing the impacts of simulated ocean alkalinity enhancement on viability and growth of nearshore species of phytoplankton, *Biogeosciences*, 22, 499–512, <https://doi.org/10.5194/bg-22-499-2025>, 2025.
- 730 Otero, J., Bode, A., Álvarez-Salgado, X. A., and Varela, M.: Role of functional trait variability in the response of individual phytoplankton species to changing environmental conditions in a coastal upwelling zone, *Mar. Ecol. Prog. Ser.*, 596, 33–47, <https://doi.org/10.3354/meps12542>, 2018.
- 735 Padin, X. A., Velo, A., and Pérez, F. F.: ARIOS: a database for ocean acidification assessment in the Iberian upwelling system (1976–2018), *Earth Syst. Sci. Data*, 12, 2647–2663, <https://doi.org/10.5194/essd-12-2647-2020>, 2020.



- Pelusi, A., Margiotta, F., Passarelli, A., Ferrante, M. I., Ribera d'Alcalà, M., and Montresor, M.: Density-dependent mechanisms regulate spore formation in the diatom *Chaetoceros socialis*, *Limnol. Oceanogr. Lett.*, 5, 371–378, <https://doi.org/10.1002/lol2.10159>, 2020.
- 740 Pérez, F. F. and Fraga, F.: Association constant of fluoride and hydrogen ions in seawater, *Mar. Chem.*, 21, 161–168, [https://doi.org/10.1016/0304-4203\(87\)90036-3](https://doi.org/10.1016/0304-4203(87)90036-3), 1987.
- Pérez, F. F., Álvarez-Salgado, X. A., and Rosón, G.: Stoichiometry of the net ecosystem metabolism in a coastal inlet affected by upwelling. The Ría de Arousa (NW Spain), *Mar. Chem.*, 69, 217–236, [https://doi.org/10.1016/S0304-4203\(99\)00107-3](https://doi.org/10.1016/S0304-4203(99)00107-3), 2000.
- 745 Pérez, F. F., López-Mozos, M., Fontela, M., García-Ibáñez, M. I., Fajar, N., Padín, X. A., Castaño-Carrera, M., de la Paz, M., Carracedo, L. I., Álvarez, M., Mercier, H., Lherminier, P., and Velo, A.: Two decades of pH<sub>T</sub> measurements along the GO-SHIP A25 section in the North Atlantic, *Earth Syst. Sci. Data*, 18, 801–821, <https://doi.org/10.5194/essd-18-801-2026>, 2026.
- Ramírez, L., Pozzo-Pirotta, L. J., Trebec, A., Manzanares-Vázquez, V., Díez, J. L., Arístegui, J., Riebesell, U., Archer, S. D., and Segovia, M.: Ocean alkalinity enhancement (OAE) does not cause cellular stress in a phytoplankton community of the subtropical Atlantic Ocean, *Biogeosciences*, 22, 1865–1886, <https://doi.org/10.5194/bg-22-1865-2025>, 2025.
- 750 Riebesell, U., Basso, D., Geilert, S., Dale, A. W., and Kreuzburg, M.: Mesocosm experiments in ocean alkalinity enhancement research, *State Planet*, 2-oae2023, 1–14, <https://doi.org/10.5194/sp-2-oae2023-6-2023>, 2023.
- Ríos, A. F., Fraga, F., Pérez, F. F., and Figueiras, F. G.: Chemical composition of phytoplankton and Particulate Organic Matter in the Ría de Vigo (NW Spain), *Sci. Mar.*, 62, 257–271, <https://doi.org/10.3989/scimar.1998.62n3257>, 1998.
- 755 Sala, M. M., Aparicio, F. L., Balagué, V., Boras, J. A., Borrell, E., Cardelús, C., Cros, L., Gomes, A., López-Sanz, A., Malits, A., Martínez, R. A., Mestre, M., Movilla, J., Sarmiento, H., Vázquez-Domínguez, E., Vaqué, D., Pinhassi, J., Calbet, A., Calvo, E., Gasol, J. M., Pelejero, C., and Marrasé, C.: Contrasting effects of ocean acidification on the microbial food web under different trophic conditions, *ICES J. Mar. Sci.*, 73, 670–679, <https://doi.org/10.1093/icesjms/fsv130>, 2016.
- Schulz, K. G., Bach, L. T., Bellerby, R. G. J., Bermúdez, R., Büdenbender, J., Boxhammer, T., Czerny, J., Engel, A., Ludwig, A., Meyerhöfer, M., Larsen, A., Paul, A. J., Sswat, M., and Riebesell, U.: Phytoplankton Blooms at Increasing Levels of Atmospheric Carbon Dioxide: Experimental Evidence for Negative Effects on Prymnesiophytes and Positive on Small Picoeukaryotes, *Front. Mar. Sci.*, 4, 64, <https://doi.org/10.3389/fmars.2017.00064>, 2017.
- 760 Simpson, G. L.: gratia: An R package for exploring generalized additive models, *J. Open Source Softw.*, 9, 6962, <https://doi.org/10.21105/joss.06962>, 2024.
- 765 Stolte, W. and Riegman, R.: A Model Approach for Size-Selective Competition of Marine Phytoplankton for Fluctuating Nitrate and Ammonium, *J. Phycol.*, 32, 732–740, <https://doi.org/10.1111/j.0022-3646.1996.00732.x>, 1996.
- Stroud, J. T., Delory, B. M., Barnes, E. M., Chase, J. M., De Meester, L., Dieskau, J., Grainger, T. N., Halliday, F. W., Kardol, P., Knight, T. M., Ladouceur, E., Little, C. J., Roscher, C., Sarneel, J. M., Temperton, V. M., van Steijn, T. L. H., Werner, C. M., Wood, C. W., and Fukami, T.: Priority effects transcend scales and disciplines in biology, *Trends Ecol. Evol.*, 39, 677–688, <https://doi.org/10.1016/j.tree.2024.02.004>, 2024.
- 770 Suessele, P., Taucher, J., Goldenberg, S. U., Baumann, M., Spilling, K., Noche-Ferreira, A., Vanharanta, M., and Riebesell, U.: Particle fluxes by subtropical pelagic communities under ocean alkalinity enhancement, *Biogeosciences*, 22, 71–86, <https://doi.org/10.5194/bg-22-71-2025>, 2025.



- 775 Takahashi, T., Olafsson, J., Goddard, J. G., Chipman, D. W., and Sutherland, S. C.: Seasonal variation of CO<sub>2</sub> and nutrients  
in the high-latitude surface oceans: A comparative study, *Glob. Biogeochem. Cycles*, 7, 843–878,  
<https://doi.org/https://doi.org/10.1029/93GB02263>, 1993.
- 780 Teira, E., Gasol, J. M., Aranguren-Gassis, M., Fernández, A., González, J., Lekunberri, I., and Álvarez-Salgado, X. A.:  
Linkages between bacterioplankton community composition, heterotrophic carbon cycling and environmental conditions in a  
highly dynamic coastal ecosystem, *Environ. Microbiol.*, 10, 906–917, <https://doi.org/10.1111/j.1462-2920.2007.01509.x>,  
2008.
- Teira, E., Martínez-García, S., Carreira, C., and Morán, X.-A. G.: Changes in bacterioplankton and phytoplankton community  
composition in response to nutrient additions in coastal waters off the NW Iberian Peninsula, *Mar. Ecol. Prog. Ser.*, 426, 87–  
104, <https://doi.org/10.3354/meps09008>, 2011.
- 785 Tilstone, G., Míguez, B., Figueiras, F., and Fermín, E.: Diatom dynamics in a coastal ecosystem affected by upwelling:  
coupling between species succession, circulation and biogeochemical processes, *Mar. Ecol. Prog. Ser.*, 205, 23–41,  
<https://doi.org/10.3354/meps205023>, 2000.
- Traboni, C., Nocera, A. C., Romano, F., Courboulès, J., Chantzaras, C., Magiopoulos, I., Varliero, S., Basso, D., and Pitta, P.:  
Plankton do not care: Minimal effects of ocean liming on plankton growth and grazing in the Eastern Mediterranean, *Limnol.*  
*Oceanogr.*, 70, e70136, <https://doi.org/10.1002/lno.70136>, 2025.
- 790 Verardo, D. J., Froelich, P. N., and McIntyre, A.: Determination of organic carbon and nitrogen in marine sediments using the  
Carlo Erba NA-1500 analyzer, *Deep Sea Res. Part Oceanogr. Res. Pap.*, 37, 157–165, [https://doi.org/10.1016/0198-0149\(90\)90034-S](https://doi.org/10.1016/0198-0149(90)90034-S), 1990.
- 795 Xin, X., Goldenberg, S. U., Taucher, J., Stühr, A., Arístegui, J., and Riebesell, U.: Resilience of Phytoplankton and  
Microzooplankton Communities under Ocean Alkalinity Enhancement in the Oligotrophic Ocean, *Environ. Sci. Technol.*, 58,  
20918–20930, <https://doi.org/10.1021/acs.est.4c09838>, 2024.