



From Surface Warming to Vertical Phytoplankton Reorganization in the North Pacific Subtropical Gyre

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Abstract. The North Pacific Subtropical Gyre (NPSG) has experienced sustained warming and biological change in recent decades, yet how these changes through the water column is less well resolved. Here, we combined satellite observations from 1998-2024 with physical and biogeochemical Argo data and a long-term record from Station ALOHA to examine changes across the upper 300 m. Surface chlorophyll declined as sea-surface temperature increased. A marked physical transition around 2013-2014 involved changes in mixed-layer depth, ocean heat content, density structure, and the separation between the mixed layer and euphotic-zone depth. Subsequent biological changes were strongly depth-dependent, with chlorophyll declining most in the 75-105 m range, and the deep chlorophyll maximum deepened despite a comparatively stable euphotic-zone depth. These chlorophyll changes did not translate directly into changes in phytoplankton carbon biomass. In the upper water column, recent carbon biomass increased even as chlorophyll declined, while increases in chlorophyll relative to carbon at depth suggested that the deepening chlorophyll maximum did not simply represent a deeper biomass maximum. Station ALOHA observations also revealed depth-dependent changes in phytoplankton community composition that may have added to these patterns. Together, these results show that long-term warming in the NPSG has occurred alongside a reorganization of upper-ocean physical structure and phytoplankton vertical distribution, rather than a uniform decline in phytoplankton biomass through the water column.

1 Introduction

Phytoplankton productivity and community composition in the North Pacific Subtropical Gyre (NPSG) are strongly regulated by light, nutrient availability, temperature, mixing, and density stratification (Karl and Church, 2017; Wilson and Church, 2018; Dai et al., 2023). The oligotrophic NPSG is dominated by small phytoplankton, particularly *Prochlorococcus*, *Synechococcus* and picoeukaryotes (Letelier et al., 2004; Thompson et al., 2021; Sasai et al., 2022; Beckett et al., 2024; Winter et al., 2025). Chlorophyll is distributed unevenly through the water column. Surface waters receive abundant light but are nutrient-depleted, whereas irradiance decreases and nutrient availability generally increases with depth. This vertical contrast supports the devel-



opment of a deep chlorophyll maximum (DCM) near the upper pycnocline (Letelier et al., 2004; Rii et al., 2016b; Karl and Church, 2017; Letelier et al., 2017).

Chlorophyll concentration may not provide a direct measure of phytoplankton carbon biomass (C_{phyto}) (Baetge et al., 2024; Behrenfeld et al., 2005). Changes in chlorophyll can reflect changes in cellular pigment content associated with photoacclimation (Letelier et al., 2004; Corno et al., 2008; Behrenfeld and Boss, 2014; Rii et al., 2016b). Long-term observations in the NPSG further show that chlorophyll, phytoplankton production, particulate carbon, and export do not always vary synchronously (Karl et al., 2021; Dai et al., 2023; Behrenfeld et al., 2025). Therefore, a decline in surface chlorophyll does not necessarily indicate an equivalent decline in C_{phyto} throughout the euphotic zone (Z_{eu}). Conversely, high chlorophyll concentrations at depth do not necessarily indicate high biomass, as phytoplankton can increase their chlorophyll content per unit carbon under low-light conditions. Chlorophyll concentration can also remain relatively stable even when phytoplankton community composition changes.

Long-term observations from the Hawaii Ocean Time-series (HOT) programme at Station ALOHA provide evidence for variability in phytoplankton community composition. The oligotrophic community is dominated by picophytoplankton, but taxa are distributed differently with depth across gradients in light, nutrients, and density (Rii et al., 2016b, 2022; Beckett et al., 2024). For example, picoeukaryotes show pronounced vertical partitioning and can be redistributed by changes in mixing and displacement of the pycnocline, before reorganizing as stratification is re-established (Rii et al., 2022). Because *Prochlorococcus*, *Synechococcus*, and picoeukaryotes differ in their responses to light, temperature, and nutrient availability, changes in their relative abundance may occur without a proportional change in chlorophyll concentration (Thompson et al., 2021; Sasai et al., 2022; Winter et al., 2025). Thus, changes in chlorophyll can reflect not only changes in biomass and cellular pigmentation but also shifts in the phytoplankton community that contribute to the chlorophyll signal.

At the same time, the physical environment of the NPSG is changing as the ocean warms. Observations show widespread strengthening of upper-ocean stratification, primarily associated with surface warming, although salinity changes can also contribute (Cheng et al., 2025). In oligotrophic gyres, changes in mixed-layer depth (MLD) and density structure are particularly important because they alter the connection between nutrient-depleted surface waters and deeper nutrient reservoirs (Karl and Church, 2017; Letelier et al., 2017; Dai et al., 2023). These physical changes can therefore influence phytoplankton by changing nutrient supply and the vertical structure of the water column.

Ocean warming and stronger stratification have often been associated with declining surface chlorophyll in oligotrophic subtropical gyres (Behrenfeld et al., 2006; Volta et al., 2025). Satellite observations have reported long-term decreases in surface chlorophyll across the North Pacific subtropical gyre (Signorini et al., 2015; Dai et al., 2023; Volta et al., 2025). However, a surface chlorophyll decline does not necessarily describe the full biological response to a changing physical environment. Recent analyses of subtropical gyres show that declining chlorophyll can occur without an equivalent decline in phytoplankton carbon (Volta et al., 2025). Changes in mixing and density structure may also redistribute phytoplankton with depth and alter community composition (Rii et al., 2022; Winter et al., 2025). Understanding the response to warming therefore requires considering not only surface chlorophyll but also C_{phyto} , physiology, community composition, and vertical structure through the water column.



Here, we integrate 27 years (1998-2024) of satellite observations with physical and biogeochemical (BGC) Argo measurements and independent long-term observations from the HOT programme at Station ALOHA to investigate physical and biological change across the NPSG. We examine changes in upper-ocean thermal and density structure together with C_{phyto} , chlorophyll relative to carbon, vertical chlorophyll structure, DCM position, and phytoplankton community composition. We hypothesize that long-term physical change in the NPSG is associated with a broader reorganization of phytoplankton structure rather than a uniform loss of C_{phyto} . By combining surface, lagrangian profiling, and fixed-station observations, we test whether declining surface chlorophyll represents widespread phytoplankton loss or forms part of a vertically structured physiological and taxonomic response.

2 Materials and Methods

2.1 Study Area

The region of interest (ROI) spans 14-28°N and 160°E-160°W (Figs.1a & S1.a, c, e), encompassing the central oligotrophic interior of the NPSG. This domain was selected to represent the relatively stable, strongly stratified, and nutrient-depleted subtropical gyre, where large-scale wind-driven convergence and Ekman downwelling contribute to the characteristic deep thermocline and low surface nutrient concentrations (Kleeman et al., 2000; Karl and Church, 2017). The northern and western limits of the ROI were also chosen to reduce the direct influence of the more dynamically variable North Pacific transition zone and the energetic Kuroshio-Oyashio Extension system, where strong currents, fronts, and mesoscale eddies generate substantial spatial and temporal variability in upper-ocean properties (Qiu et al., 2007; Kavanaugh et al., 2018).

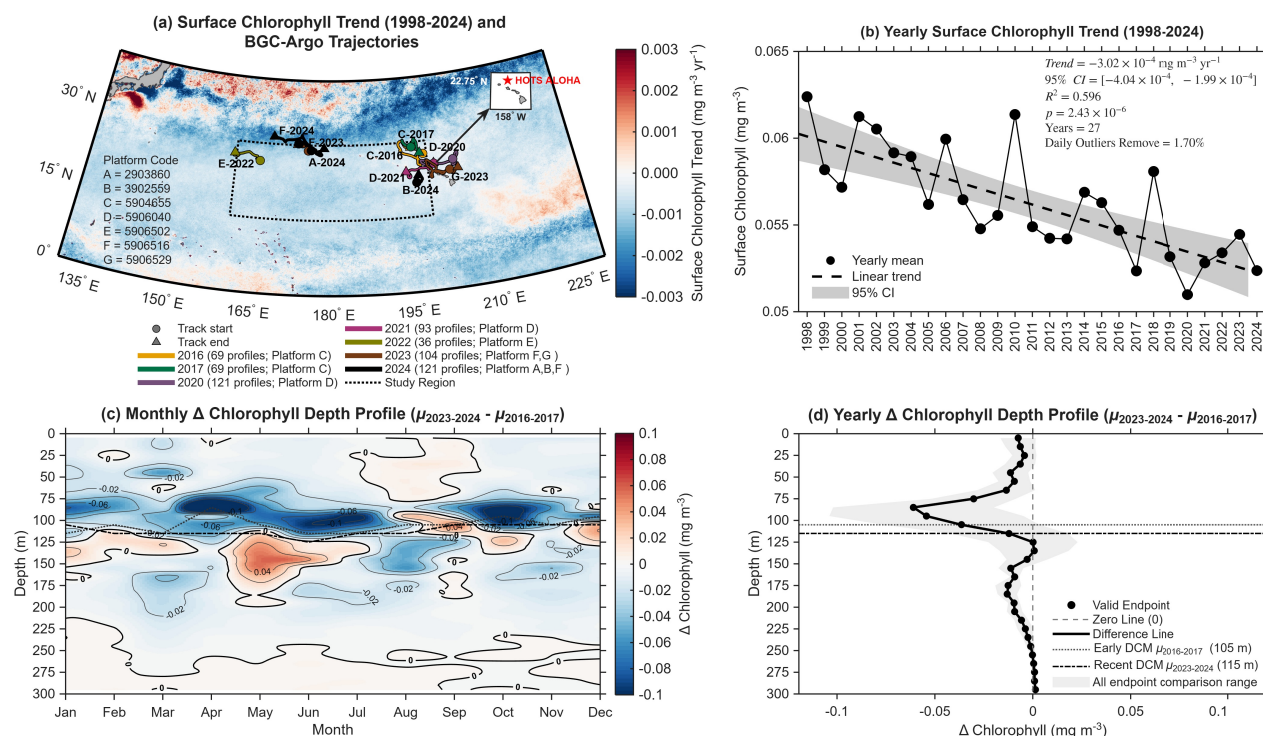


Figure 1. Long-term changes in surface and vertical chlorophyll structure in the North Pacific Subtropical Gyre (NPSG). (a) Trends in monthly satellite surface chlorophyll during January 1998–December 2024 across 0–40°N and 130–230°E, overlaid with retained bio-geochemical Argo (BGC-Argo) float trajectories. Grid-cell trends (mg m⁻³ yr⁻¹) were estimated by ordinary least-squares regression after removing invalid observations and values exceeding three standard deviations from the temporal mean, at least 10 valid observations were required. The dashed rectangle marks the study region (14–28°N, 160–200°E), and the inset locates Station ALOHA of the Hawaii Ocean Time-series (HOT) programme (22.75°N, 158°W). Trajectories cover 2016, 2017, and 2020–2024, retaining profiles with at least 10 unique depth levels within 0–300 m and platform-year records spanning at least 10 calendar months. Track colours indicate year; circles and triangles mark the first and last retained profiles, and letters identify platforms. (b) Annual mean surface chlorophyll in the study region during 1998–2024. Same-day observations were combined using their median. Outliers exceeding three robust standard deviations from a 61-observation moving median were removed using the median absolute deviation, requiring at least 15 observations per window. Annual means were calculated from the cleaned daily series; 1.70% of daily observations were excluded. Black circles and connecting lines show annual means; the dashed line and grey shading show the linear trend and its 95% confidence interval (CI). The slope, its 95% CI, R^2 , and p -value are reported. (c) Month-depth distribution of the chlorophyll difference between recent (2023–2024) and early (2016–2017) periods on a common grid: $\Delta\text{Chlorophyll} = \mu_{\text{recent}} - \mu_{\text{early}}$. Contours show difference magnitudes and the zero crossing. In (a) and (c), red and blue shading indicate positive and negative chlorophyll trends or differences, respectively. (d) Mean chlorophyll difference by depth (solid black line), with zero change marked by the vertical dashed line. Grey shading spans the four endpoint comparisons: 2023 minus 2016, 2023 minus 2017, 2024 minus 2016, and 2024 minus 2017. Filled circles and grey shading mark depth bins where all four differences have the same sign. Horizontal dotted and dash-dotted lines in (c) and (d) mark the early-period (105 m) and recent-period (115 m) deep chlorophyll maximum depths, respectively.



2.2 Datasets

75 Satellite surface chlorophyll and particulate backscattering at 443 nm (bbp443) were obtained from the European Space Agency Ocean Colour Climate Change Initiative (ESA OC-CCI) Version 6 merged product, combining SeaWiFS, MODIS, MERIS, VIIRS-SNPP, OLCI-S3A, and OLCI-S3B observations. We used the Level-3 product, 4 km spatial resolution, 1998-2024 (Sathyendranath et al., 2019). Z_{eu} and the diffuse attenuation coefficient at 490 nm (K_d490) were obtained from the Copernicus Marine multi-sensor Level-4 product at 4 km resolution over the same period (European Union-Copernicus Marine Service,
 80 2022).

Monthly SST was obtained from the NOAA Extended Reconstructed Sea Surface Temperature Version 6 (ERSSTv6) product at $2^\circ \times 2^\circ$ spatial resolution (Huang et al., 2025a, b). ERSSTv6 is a global monthly analysis based primarily on in situ ship and buoy observations from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) and Argo profiling floats, with spatial completeness enhanced through artificial-neural-network reconstruction, quality control, and large-scale spatial
 85 filtering. We used the complete monthly record from January 1998 to December 2024 to characterize long-term SST variability and trends.

We also used long-term observations from the HOT program at Station ALOHA (22.75°N , 158°W) (Fig. 1a), located approximately 100 km north of O'ahu and immediately east of the study domain, as an independent observational reference for chlorophyll and community composition variability. Chlorophyll was determined fluorometrically from discrete seawater
 90 samples collected at standard depths, filtered onto GF/F filters, and extracted in 100% acetone, while community composition was characterized by flow cytometry to determine the abundances of *Prochlorococcus*, *Synechococcus*, picoeukaryotes, and heterotrophic bacteria.

Physical and BGC-Argo data were retrieved through the Argopy Python API in expert mode (Maze and Balem, 2020). Adjusted values were used throughout, retaining observations with Argo quality-control flag 1. Argo temperature and salinity
 95 profiles were used to characterize the vertical thermal and density structure of the water column, MLD, and ocean heat content (OHC) over 0-300 m. Analyses were restricted to 2003-2024 and to the months January-November due to data availability. Profiles were analysed only if they contained at least 10 valid temperature-salinity (T-S) depth levels. After filtering, the physical Argo dataset comprised 37,679 unique profiles (Figs S1.e & f).

BGC Argo profiles were analysed independently for adjusted chlorophyll, bbp700, and dissolved oxygen (DOXY) because
 100 sensor availability differed among floats and years. Profiles were restricted to 0 to 300 m and required at least five valid depth levels. To reduce seasonal sampling bias, only platform-year combinations sampled during at least 10 distinct months and whose trajectories entered the NPSG ROI were retained.

For chlorophyll and bbp700, 616 unique profiles from seven World Meteorological Organization (WMO) floats were retained: 2903860, 3902559, 5904655, 5906040, 5906502, 5906516, and 5906529 (Fig. S1.a & b). For DOXY, 497 profiles from
 105 six WMO floats were retained, corresponding to the same set used for chlorophyll and bbp700, except that float 5904655 was excluded because DOXY observations were unavailable for this platform (Fig. S1.c & d). DOXY-derived apparent oxygen utilization (AOU) was used as a diagnostic of subsurface oxygen utilization rather than for trend or breakpoint analysis. Annual



AOU profiles were restricted to 2020, 2023, and 2024 because 2021 and 2022 had incomplete or uneven depth-month coverage. The trajectories and annual sampling frequencies of the physical and BGC-Argo observations are shown in Fig. S1.a-f.

110 Although the BGC-Argo observations were spatially distributed across the ROI rather than uniformly sampled (Figs. 1a, & S1.a, c), float selection was based on trajectories that passed through the ROI and on the availability of sufficiently complete vertical and temporal coverage, particularly in terms of depth range (0-300 m) and monthly sampling (10-12 months) (Table S2). To assess whether this spatially heterogeneous sampling introduced substantial platform-specific differences, we compared the mean vertical chlorophyll profiles among individual floats. Despite their different trajectories and sampling locations within
 115 the ROI, the platform-specific chlorophyll profiles were highly consistent (ranged from $r = 0.935$ to $r = 0.995$) (Table S3), with strong pairwise correlations among all floats. This consistency indicates that the major vertical chlorophyll structure was reproducible across independently sampled locations and was not driven by a single float trajectory. Therefore, although the BGC-Argo observations do not provide spatially uniform coverage of the entire ROI, their coherent vertical structure across geographically separated platforms supports their representativeness as an in situ observational basis for evaluating the broader
 120 basin-scale biological patterns identified in this study.

The observational framework of this study was structured to combine long-term surface records with progressively more detailed subsurface and in situ observations. Satellite observations were analysed over 1998-2024 to characterize long-term surface variability, while physical Argo observations over 2003-2024 were used to examine changes in upper-ocean thermal and density structure. BGC-Argo observations provided more detailed vertical biological and biogeochemical information but
 125 were available for a more limited set of years. Chlorophyll and C_{phyto} estimates were available for 2016, 2017, and 2020-2024, and DOXY observations used for AOU were available for 2020, 2023, and 2024. These observations were therefore used to characterize recent vertical biological and biogeochemical structure rather than long-term trends. Long-term observations from Station ALOHA year 1998-2024 were used as an independent fixed-station in situ reference to assess changes in phytoplankton vertical distribution and community composition within the NPSG.

130 2.3 Data Processing

To derive the datasets used in this study, we first spatially averaged the satellite surface chlorophyll, bbp443, K_d490 , and Z_{eu} within the ROI (Table S1, Method No. 1). C_{phyto} was then estimated from satellite bbp443 using Behrenfeld et al. (2005) model. The corresponding chlorophyll: C_{phyto} ratio was calculated by dividing chlorophyll concentration by the estimated C_{phyto} (Behrenfeld et al., 2005; Westberry et al., 2008; Behrenfeld and Boss, 2014) (Table S1, Method No. 2). Downwelling
 135 irradiance at depth (I_z) was subsequently reconstructed from satellite optical observations using the Beer-Lambert relationship following method from Ryther (1956) and Kirk (1994) (Table S1, Method No. 3).

Monthly SST from ERSSTv6 (Huang et al., 2025a, b) was similarly averaged over the ROI but using latitude-dependent area weighting to account for differences in grid-cell area with latitude. Spatial SST trends were calculated separately at each native ERSSTv6 grid cell before visualization (Table S1, Method No. 1).

140 The vertical biological structure of the water column was characterized using adjusted BGC-Argo chlorophyll, bbp700, and DOXY observations (Table S1, Method No. 4). Depth-resolved C_{phyto} was estimated from bbp700, from which the corre-



sponding Chlorophyll: C_{phyto} ratio was calculated at each depth (Table S1, Method No. 2 & 4). DCM depth was then identified from the vertical chlorophyll profile as the depth of maximum chlorophyll concentration (Table S1, Method No. 5), while apparent oxygen utilization (AOU) was calculated from the difference between oxygen saturation from Garcia and Gordon (1992) and Garcia et al. (2005) and observed DOXY by using method from Sarmiento and Gruber (2006) and Emerson and Bushinsky (2014) (Table S1, Method No. 6). Profiles were subsequently screened according to temporal and vertical-coverage criteria before being used in the depth-resolved analyses (Table S1, Method No. 4).

Physical Argo temperature and salinity observations were first converted to Conservative Temperature (CT) and Absolute Salinity (AS) and then aggregated by month and depth (Table S1, Method No. 7). Potential density anomaly referenced to the surface (σ_0) was calculated using the Gibbs SeaWater (GSW) Oceanographic Toolbox and the Thermodynamic Equation of Seawater 2010 (TEOS-10) (Table S1, Method No. 8). The resulting profiles were then used to characterize MLD and isopycnal structure (Table S1, Method No. 9), as well as OHC by using the method from Levitus et al. (2012) and Roemmich et al. (2015) (Table S1, Method No. 10).

After processing the raw datasets into the variables used in this study, we performed statistical analyses to evaluate their temporal changes and relationships. Before calculating annual means, anomalous monthly observations were identified separately within each year using a robust median-based outlier criterion. Observations lying more than three scaled median absolute deviations from the annual median were classified as outliers and removed. Outlier screening was applied only when at least four monthly observations were available within a given year, otherwise, all available observations were retained. If outlier removal resulted in no remaining observations, the original observations were retained to avoid an undefined annual mean (Table S1, Method No. 11).

Long-term temporal changes were evaluated using ordinary least-squares regression (Table S1, Method No. 12) and, where appropriate, a single-breakpoint framework (Table S1, Methods No. 13). Candidate breakpoints were identified by searching all permissible annual split points, with at least five annual observations required on each side of the breakpoint. Separate linear regressions were fitted before and after each candidate split, and the split minimizing the combined sum of squared errors (SSE) was selected as the best-fitting breakpoint location (Table S1, Methods No. 13).

A breakpoint was reported as statistically supported only when all three predefined criteria were met: (1) the Bai-Perron-style bootstrap sup- F test yielded $p < 0.05$, (2) the Davies-type bootstrap slope-change test yielded $p < 0.05$, and (3) comparison using the Bayesian information criterion (BIC) favoured the two-segment model, with $\Delta\text{BIC} \geq 2$. Akaike information criterion (AIC), corrected Akaike information criterion (AICc), and continuous segmented regression were used as additional supporting diagnostics but were not required for breakpoint acceptance (Table S1, Methods No. 14).

To further examine the mechanisms underlying changes in vertical biological structure, we evaluated the relationship between underwater light conditions and DCM variability by analysing z_{DCM} , I_z , and isolume depth together with MLD, Z_{eu} , and σ_0 . Their vertical variability across the available years was compared to assess whether changes in DCM depth were associated with changes in irradiance, light penetration, and upper-ocean physical structure.

To evaluate how changes in upper-ocean heat were distributed vertically, OHC was calculated over the upper 300 m and further partitioned into three dynamically defined layers: the surface to MLD, MLD to Z_{eu} , and Z_{eu} to 300 m. This partitioning



was used to identify where heat accumulated or was redistributed within the water column relative to changes in physical and optical structure. OHC calculation, anomaly estimation, and dynamic-layer partitioning are detailed in Supplementary Table S1 (Method No. 14 & 15).

180 Because the observations were spatially and temporally non-uniform, interpolation and smoothing were applied for visualization purposes only to generate continuous spatial and temporal fields and facilitate comparison among variables (Table S1, Method No. 15). These procedures did not alter the underlying observations used in the statistical analyses.

3 Results

3.1 Long-Term Surface Chlorophyll Decline and Vertical Changes

185 Surface chlorophyll declined across the NPSG ROI between 1998 and 2024 (Figs. 1a & b). Annual mean surface chlorophyll decreased at a rate of $-3.02 \times 10^{-4} \text{ mg m}^{-3} \text{ yr}^{-1}$ ($R^2 = 0.596$; $p = 2.43 \times 10^{-6}$) (Fig. 1b). BGC-Argo observations also show that the long-term surface chlorophyll decline was accompanied by marked changes in the vertical chlorophyll distribution (Figs. 1c, d & S2.b-h). Here, we compared chlorophyll on a monthly basis by calculating the difference between the mean concentrations for 2023-2024 and 2016-2017 for each calendar month and depth bin. To further assess the robustness of
190 these temporal changes, we also performed four pairwise endpoint comparisons by subtracting each early year (2016 and 2017) from each recent year (2023 and 2024), yielding the comparisons 2023-2016, 2023-2017, 2024-2016, and 2024-2017 (Table S4). This comparison showed that the strongest decreases were concentrated between approximately 75 and 105 m for about -0.03 to -0.06 mg m^{-3} (Figs. 1c & d; Table S4). These negative differences occurred during much of the year and were most pronounced during April-July and October, when they approached -0.10 mg m^{-3} (Fig. 1c). Decreases were also
195 evident during January-March and November-December, indicating that the reduction around the upper flank of the DCM was not limited to a single season (Fig. 1c). In contrast, positive chlorophyll differences occurred intermittently at greater depths, particularly around 125-135 m (Fig. 1d; Table S4). The clearest increase occurred in May near 125-150 m (Fig. 1c). The DCM showed variability around a deeper recent mean, shifting from approximately 105 m during 2016-2017 to 115 m during 2023-2024 (Fig. 1d). The BGC-Argo observations indicated a persistent tendency toward a deeper DCM in the more recent period.
200 The DCM was approximately 105 m in 2016-2017, shifted to 115 m in 2020, reached 125 m in 2021-2022, and remained at 115 m in 2023-2024 (Fig. S2). Because the DCM was identified using 10-m pressure bins, the difference between the early (105 m) and recent (115 m) endpoint means represents the minimum vertical shift resolvable by the method. Nevertheless, the repeated occurrence of the DCM in deeper bins after 2016-2017, including 125 m in 2021-2022, indicates that the result reflects interannual variability around a deeper recent DCM rather than a single-bin displacement in one year.

205 Observations from the HOT programme at Station ALOHA provided a long-term fixed-station comparison with the regional satellite and BGC-Argo observations (Fig. S3; Table S5). The five-year mean chlorophyll profiles indicated that the DCM deepened by approximately 25 m between 1998-2002 and 2020-2024 (Fig. S3.a). However, yearly chlorophyll trends at individual depths were not statistically significant after false-discovery-rate (FDR) correction, indicating no consistent long-term change in chlorophyll concentration at fixed depths (Table S5). This likely reflects strong seasonal variability, as significant increases



210 in chlorophyll concentration were observed only in March at approximately 45 m and in July and October at approximately 100-120 m (Fig. S3.f).

The phytoplankton community composition showed a distinct depth-dependent temporal patterns. *Prochlorococcus* showed positive relative trends in the upper 45 m water column which about 0.25 to 0.36 % yr⁻¹ (Table S5). Started from 75 m below, *Prochlorococcus* trends were generally negative, reaching -2.81% yr⁻¹ at 175 m (Table S5). However, none of these trends
 215 remained significant after FDR correction (Fig. S3.b; Table S5). Examination of the monthly trends showed that increasing trends throughout the water column were observed only in February and June (Fig. S3.g).

Synechococcus showed negative trends throughout the sampled water column, with relative rates of decline ranging from -1.56% yr⁻¹ at 5 m to -16.52% yr⁻¹ at 175 m (Fig. S3.c; Table S5). Although declines between 25 and 100 m were significant before multiple-testing correction, they did not remain significant after FDR adjustment. Statistically significant declines that
 220 remained significant after FDR correction were observed only at 150 m and 175 m. Examination of the monthly trends showed that the strongest increase occurred in February, whereas significant declines were observed across all months at depths below approximately 150 m (Fig. S3.h).

Similar to *Prochlorococcus*, picoeukaryotes and Heterotrophic bacteria showed no statistically significant annual trends after FDR correction. Picoeukaryotes relative trends were negative in the upper water column, ranging from -1.27% yr⁻¹ at 5 m
 225 to -0.65% yr⁻¹ at 75 m, became positive between 100 and 150 m, and were negative again at 175 m (Fig. S3.d; Table S5). Heterotrophic bacteria also showed negative annual trends across all evaluated depths, ranging from approximately -1.04% to -1.50% yr⁻¹ (Fig. S3.e; Table S5). Interestingly, despite the generally non-significant annual trends, the monthly analysis revealed a clearer seasonal pattern where both autotrophic microbial groups and heterotrophic bacteria showed increases throughout much of the water column in February (Figs. S3.g-j). This suggests that temporal changes in these microbial groups
 230 were seasonally dependent and may therefore be obscured when evaluated only as annual trends.

3.2 Changes in Phytoplankton Carbon Biomass and Chlorophyll-to-Carbon Ratio

At the surface, C_{phyto} and chlorophyll: C_{phyto} showed distinct long-term trajectories over 1998-2024 (Figs. 2a & d). Breakpoint analysis identified a statistically supported transition in C_{phyto} between 2015 and 2016 and a later transition in chlorophyll: C_{phyto} between 2017 and 2018 (Figs. 2a & d; Table S6.a), whereas surface chlorophyll itself did not show a significant struc-
 235 tural breakpoint. For C_{phyto} , the pre-breakpoint period was characterized by a significant increase of 0.52 mg C m⁻³ yr⁻¹ ($R^2 = 0.93$; $p < 0.001$), followed by a 21.2% decline across the breakpoint and a significant post-breakpoint decrease of -0.457 mg C m⁻³ yr⁻¹ ($R^2 = 0.459$; $p = 0.045$) (Fig. 2a; Table S6.a). In contrast, chlorophyll: C_{phyto} declined significantly before its breakpoint at -1.44×10^{-4} yr⁻¹ ($R^2 = 0.688$; $p < 0.001$), followed by a 69.76% increase across the breakpoint while no significant trend was detected thereafter (Fig. 2d; Table S6.a).

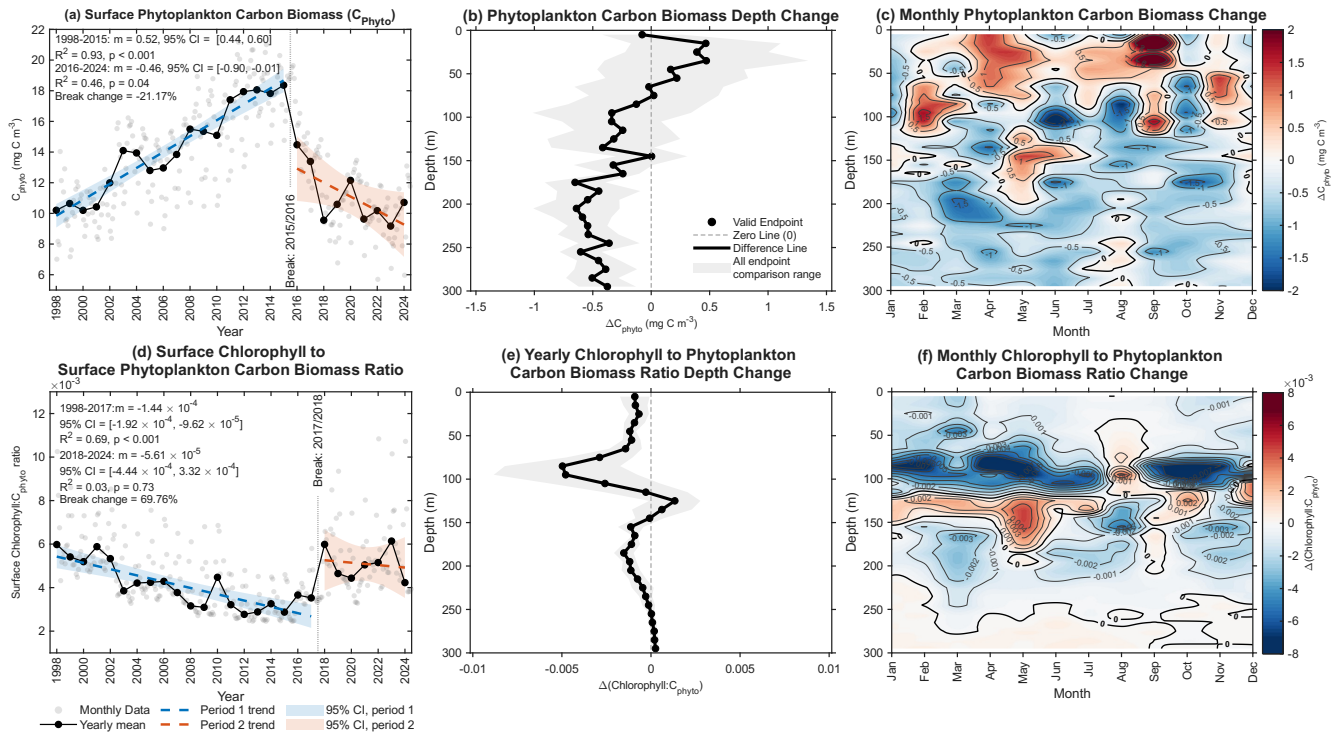


Figure 2. Changes in phytoplankton carbon biomass and chlorophyll-to-phytoplankton carbon ratio in the North Pacific Sub-tropical Gyre (NPSG). (a, d) Surface phytoplankton carbon biomass (C_{phyto}) and surface chlorophyll-to-phytoplankton carbon ratio (chlorophyll: C_{phyto}), respectively, from 1998 to 2024. Grey points show monthly observations, and black circles show annual means calculated after removing within-year outliers using a median absolute deviation (MAD)-based criterion with a threshold factor of 3. Breakpoints were identified using a global one-break minimum-sum-of-squared-errors (SSE) search and evaluated using a Bai-Perron-style bootstrap supremum- F (sup- F) test, continuous segmented regression, a Davies-type bootstrap maximum slope-change test, and model comparison using the Akaike information criterion (AIC), corrected Akaike information criterion (AICc), and Bayesian information criterion (BIC), where breakpoint uncertainty was estimated using residual bootstrap resampling. Dashed blue and orange lines show the linear trends during Period 1 (before the selected breakpoint) and Period 2 (after the selected breakpoint), respectively, with corresponding blue and orange shading indicating their 95% confidence intervals (CI). Trend slopes (m), 95% CI, coefficient of determination (R^2), probability value (p -value), and percentage change across the breakpoint are reported in each panel. (b, e) Vertical changes in C_{phyto} and chlorophyll: C_{phyto} , respectively, between the recent (2023-2024) and early (2016-2017) periods. Solid black lines show the recent-minus-early mean differences, and vertical dashed lines denote zero change. Grey shading shows the range across the four endpoint comparisons (2023-2016, 2023-2017, 2024-2016, and 2024-2017), providing a visual consistency check across endpoint pairs. Filled circles identify depth bins for which all four comparisons have the same sign, indicating a consistent direction of change across all endpoint combinations. (c, f) Hovmöller plots showing the monthly depth and time distribution of changes in C_{phyto} and chlorophyll: C_{phyto} , respectively, between the recent (2023-2024) and early (2016-2017) periods, calculated on a common month and depth grid. Red shading indicates higher and blue shading lower values during the recent period, with contours showing the magnitude and zero crossing of the differences.



240 We then examined independent physical observations, which showed that upper-ocean reorganisation was already underway before the biological breakpoint. Physical Argo observations showed marked changes in MLD (Fig. 3d) and subsurface OHC (Fig. 4d) around 2013-2014 (Table S6.a & b), broadly coincident with the development of the North Pacific marine heatwave (the “Blob”) from late 2013 and preceding the strong 2015-2016 El Niño (Bond et al., 2015; Chen et al., 2021; Shi et al., 2022). These events were associated with substantial warming and changes in upper-ocean stratification across the North Pacific, conditions that can alter nutrient supply and phytoplankton dynamics. The timing of these physical changes, followed by the transitions in C_{phyto} in 2015-2016 and chlorophyll: C_{phyto} in 2017-2018, suggests that the surface biological changes occurred within a broader period of upper-ocean reorganisation. Although this sequence is consistent with a biological response to changing physical conditions, it does not establish that the climate anomalies caused the observed transitions.

We further assessed vertical biological reorganisation to place the surface patterns in context. BGC-Argo observations showed that recent changes in C_{phyto} and chlorophyll: C_{phyto} were vertically distinct (Fig. 2b & e; Table S4). Relative to the 2016-2017 mean, mean C_{phyto} during 2023-2024 was higher between 15 and 55 m, whereas reductions dominated below approximately 175 m (Fig. 2b; Table S4). A small increase was also observed at 145 m, although its magnitude was minimal ($< 0.001 \text{ mg C m}^{-3}$). In contrast, chlorophyll: C_{phyto} increased only between approximately 125 and 135 m when comparing the 2023-224 and 2016-2017 means, while changes at the remaining depths were negative (Fig. 2e; Table S4).

255 The monthly patterns showed a similar vertical separation. C_{phyto} generally increased within the upper 15-100 m during most months, with the main exceptions occurring in December and January (Fig. 2c). In contrast, increases in chlorophyll: C_{phyto} were concentrated deeper in the water column, primarily between 125 and 150 m during most months. August differed from this pattern, with positive changes extending upward from approximately 50 to 125 m (Fig. 2f).

These results show that C_{phyto} and chlorophyll: C_{phyto} exhibited contrasting changes both at the surface and throughout the water column. Surface C_{phyto} shifted from a strong increase before the 2015-2016 breakpoint to a decline thereafter, whereas chlorophyll: C_{phyto} declined until the 2017-2018 breakpoint and showed no significant trend subsequently. At depth, recent increases in C_{phyto} were more persistent within the upper 100 m (Figs. 2b & c), while increases in chlorophyll relative to carbon were concentrated predominantly below 100 m (Figs. 2e & f).

3.3 Surface Warming and Mixed-Layer Changes

265 SST increased throughout the NPSG ROI between 1998 and 2024 (Figs. 3a & b). The regional annual mean SST increased at approximately $1.88 \times 10^{-2} \text{ }^{\circ}\text{C yr}^{-1}$ ($R^2 = 0.59$; $p = 2.65 \times 10^{-6}$), corresponding to an overall warming of approximately $0.5 \text{ }^{\circ}\text{C}$ across the 27-year record (Fig. 3b). Spatially, positive SST trends occurred across most of the mapped North Pacific domain, including throughout the ROI, although the magnitude of warming varied spatially (Fig. 3a).

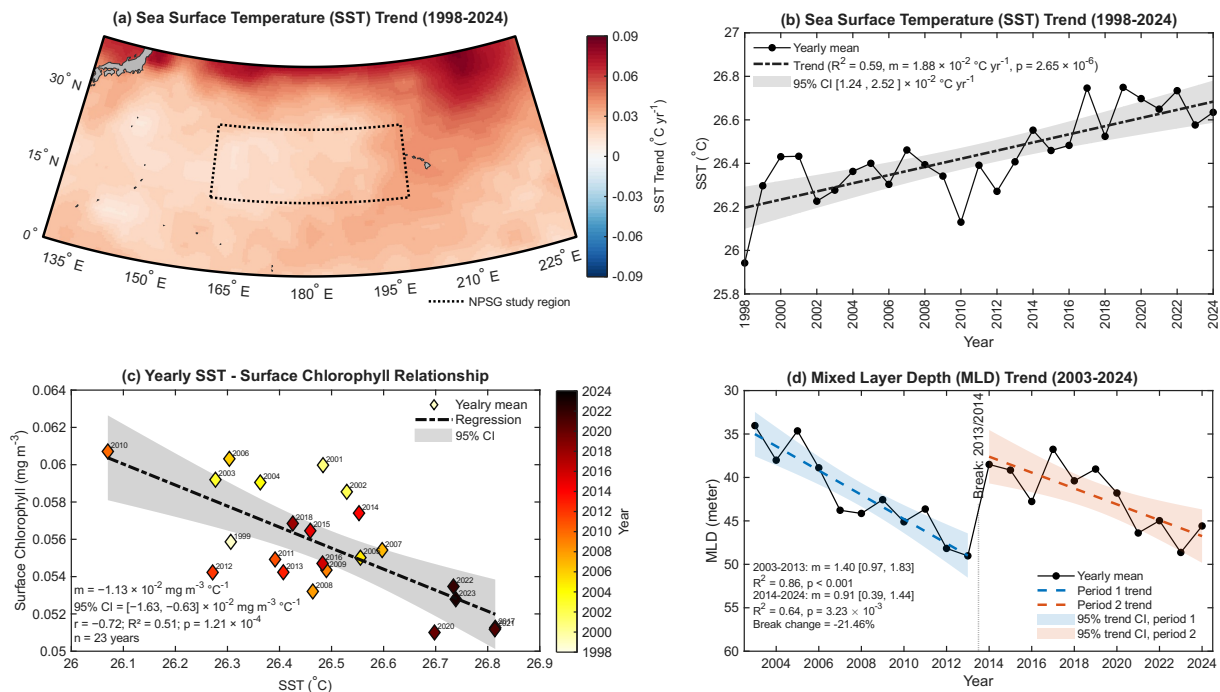


Figure 3. Long-term changes in sea surface temperature (SST), its relationship with surface chlorophyll, and mixed-layer depth (MLD) in the North Pacific Subtropical Gyre (NPSG). (a) SST trends during January 1998-December 2024 from the Extended Reconstructed Sea Surface Temperature version 6 (ERSSTv6) dataset (Huang et al., 2025a, b). Ordinary least-squares trends were calculated on the original grid and interpolated to 0.5° for visualization only. Red and blue indicate warming and cooling, respectively. The dashed box marks the study region ($14\text{--}28^\circ\text{N}$, $160\text{--}200^\circ\text{E}$). (b) Annual mean SST calculated using cosine-of-latitude weighting after calendar-month-specific outlier removal. Black circles and connecting lines show annual means, the dashed line and grey shading show the linear trend and its 95% confidence interval (CI). (c) Annual mean SST versus surface chlorophyll. Diamonds represent individual years, progressing from light to dark for earlier to more recent years. The dashed line and grey shading show the regression and its 95% CI. (d) Annual mean MLD during 2003-2024 after outlier removal. Breakpoints were selected by a global one-break minimum-SSE search and assessed using bootstrap tests, segmented regression, and information criteria; uncertainty was estimated by residual bootstrapping. Dashed blue and orange lines show trends before and after the selected breakpoint, respectively, with matching shading showing their 95% CI. Regression slopes (m), 95% CI, R^2 , and p -values are reported in (b-d); Pearson's r and the number of years (n) in (c); and the percentage change across the breakpoint in (d).



Annual SST and surface chlorophyll were negatively associated (Fig. 3c). Across the 23 years with at least 10 matched
270 monthly observations, surface chlorophyll decreased by $1.13 \times 10^{-2} \text{ mg m}^{-3}$ for each 1°C increase in SST. The relationship
was moderately strong ($r = -0.72$, $R^2 = 0.51$) and statistically significant ($p = 1.21 \times 10^{-4}$), with warmer years generally
associated with lower annual mean surface chlorophyll (Fig. 3c).

MLD also changed substantially between 2003 and 2024 (Fig. 3d). From 2003 to 2013, MLD deepened significantly at
1.40 m yr^{-1} ($R^2 = 0.86$; $p < 0.001$). A marked transition occurred between 2013 and 2014, when annual MLD shoaled by
275 approximately 21.5% (Fig. 3d; Table S6). From 2014 to 2024, MLD again deepened, but at a lower rate of 0.91 m yr^{-1}
($R^2 = 0.64$; $p = 0.003$).

As mentioned in Section 3.2, the timing of the MLD breakpoint coincided with the development the “Blob”. Prior to the
breakpoint, MLD in the NPSG deepened to approximately 50 m before shoaling to about 38 m in 2014 (fig. 3d; Table S6).
Bond et al. (2015) showed that winter 2013-2014 was characterized by exceptionally weak winds, reduced ocean heat loss, and
280 unusually weak seasonal mixed-layer deepening, while Shi et al. (2022) demonstrated that relatively shallow MLD can enhance
the sensitivity of upper-ocean temperature to surface heat input and favour warm-blob development. Chen et al. (2021) further
showed that the prolonged 2013-2016 Blob evolved through interacting atmospheric and oceanic processes, with surface heat-
flux anomalies dominating its initial wintertime development and vertical ocean processes becoming more important during
subsequent phases. The observed MLD shoaling in our record therefore coincided with a broader reorganisation of North
285 Pacific upper-ocean conditions during the onset of the 2013-2016 Blob.

3.4 Vertical Thermal, Density, and Optical Reorganization

The increase in SST was accompanied by strong depth-dependent changes in OHC between 2003 and 2024 (Fig. 4). Mean
OHC was highest in the upper water column and declined with depth (Fig. 4a), while the anomaly field showed a transition
from negative anomalies early in the record to positive anomalies, particularly between approximately 50 and 200 m during
290 2011-2014 (Fig. 4b). Layer-specific analyses showed that the strongest changes occurred below the mixed layer (Fig. 4c-e).
OHC between the MLD and Z_{eu} increased from 2003 to 2013 at $8.05 \times 10^{-4} \text{ GJ m}^{-3} \text{ yr}^{-1}$ ($p = 3.17 \times 10^{-4}$), followed by
a 1.41% decrease between 2013 and 2014 and no significant trend thereafter (Fig. 4d; Table S6.a). Similarly, OHC from Z_{eu}
to 300 m increased at $5.93 \times 10^{-4} \text{ GJ m}^{-3} \text{ yr}^{-1}$ ($p = 2.28 \times 10^{-4}$), followed by a approximately 4% decrease across 2013-
2014 and a flat post-breakpoint trend (Fig. 4e; Table S6.a). In contrast, OHC between the surface and MLD showed an earlier
295 breakpoint between 2007 and 2008 and only weak pre-breakpoint change ($7.35 \times 10^{-4} \text{ GJ m}^{-3} \text{ yr}^{-1}$, $p = 0.069$), with no
significant trend thereafter (Fig. 4c; Table S6).

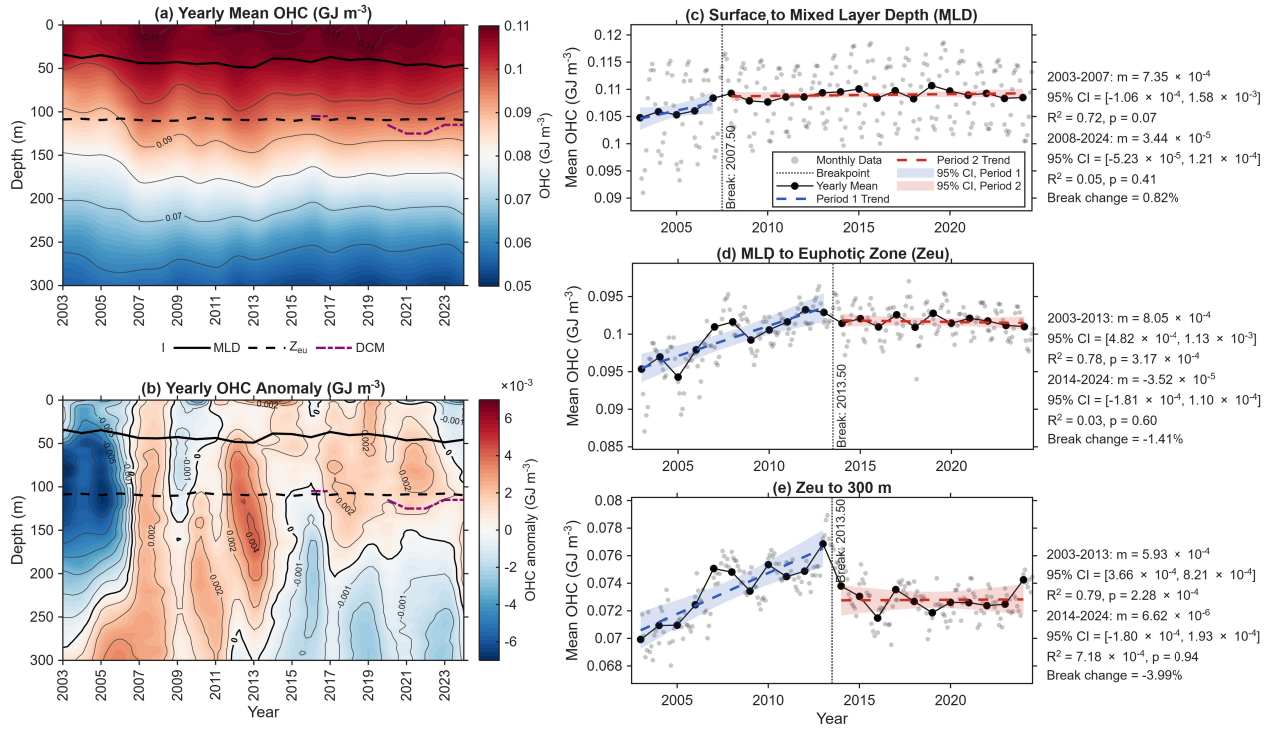


Figure 4. Vertical redistribution and layer-specific changes in ocean heat content (OHC) in the North Pacific Subtropical Gyre (NPSG), 2003-2024. (a) Annual mean volumetric OHC (GJ m^{-3}) in the upper 300 m, calculated from Argo Conservative Temperature using a reference density of 1025 kg m^{-3} and specific heat capacity of $3985 \text{ J kg}^{-1} \text{ K}^{-1}$. Profiles were aggregated using monthly platform medians, equal-month annual platform means, and equal-platform yearly means. (b) OHC anomalies relative to the long-term mean at each depth, with the zero contour separating positive and negative anomalies. In (a, b), red and blue indicate higher and lower values, respectively. Fields were interpolated to a 2 m by 0.25-year grid using modified Akima interpolation and lightly smoothed for display only; gaps exceeding two years were left unfilled, and no extrapolation was applied. Solid black, dashed black, and magenta dash-dotted lines mark mixed-layer depth (MLD), euphotic-zone depth (Z_{eu}), and deep chlorophyll maximum (DCM) depth, respectively. (c-e) Vertically integrated OHC for (c) surface to MLD, (d) MLD to Z_{eu} , and (e) Z_{eu} to 300 m. Grey points show monthly values, black circles and connecting lines show annual means after outlier removal. Breakpoints were selected by a global one-break minimum-SSE search and assessed using bootstrap tests, segmented regression, and information criteria; breakpoint uncertainty was estimated by residual bootstrapping. Dashed blue and orange lines show trends before and after the selected breakpoint, respectively, with matching shading indicating 95% confidence intervals (CI). Slopes (m), 95% CI, R^2 , p -values, and percentage changes across breakpoints are reported in each panel.

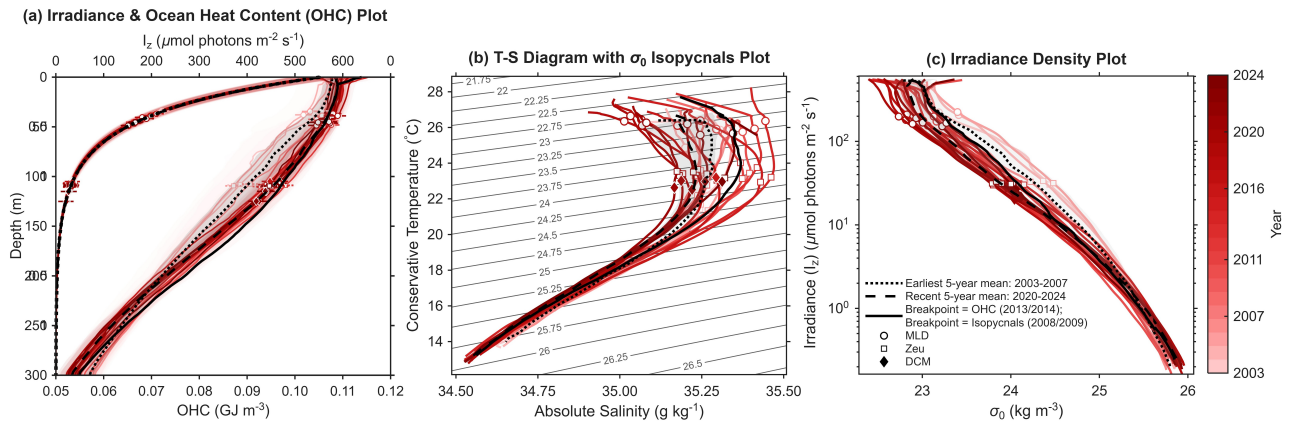


Figure 5. Coupled changes in ocean heat content (OHC), hydrographic structure, potential density isopycnals (σ_0), and underwater irradiance (I_z) in the North Pacific Subtropical Gyre (NPSG). (a) Annual depth profiles of OHC (lower x-axis) and mean I_z at depth (upper x-axis) from 2003 to 2024. Physical Argo profiles were aggregated using monthly platform medians, equal-month annual platform means, and equal-platform yearly means. Monthly I_z profiles were calculated using the Beer-Lambert relationship, $I_z = \text{PAR}_{\text{surf}} \exp(-K_{\text{PAR}} z)$, with K_{PAR} approximated from the diffuse attenuation coefficient at 490 nm (K_{d490}), and annual profiles were obtained from the monthly values after median-based outlier removal. (b) Temperature-salinity (T-S) diagram constructed from annual Absolute Salinity and Conservative Temperature profiles. Grey contours show σ_0 calculated using the Thermodynamic Equation of Seawater 2010 (TEOS-10). For visualization only, profiles were smoothed along depth and interpolated onto a 0.1-m grid using modified Akima (MAKIMA) interpolation without altering the underlying annual hydrographic values. (c) Relationship between σ_0 and I_z through the water column. Each annual trajectory pairs σ_0 and I_z values at the same depth, illustrating changes in the underwater light environment across the density structure. Here I_z shown on a logarithmic scale. For panels (a-c), profiles progress from light to dark red for earlier to more recent years. Dotted and dashed black curves show the earliest (2003-2007) and recent (2020-2024) five-year means, respectively. Open circles, open squares, and filled diamonds denote mixed-layer depth (MLD), euphotic-zone depth (Z_{eu}), and deep chlorophyll maximum (DCM), respectively.



These OHC changes were accompanied by substantial changes in upper-water-column temperature, salinity, and density structure. CT, SA, and σ_0 were therefore examined within the same three dynamically defined layers: surface-to-MLD, MLD-to- Z_{eu} , and Z_{eu} -300 m (Figs. 5, S4, & S5; Table S6).

300 The layer-resolved CT analysis showed strongly depth-dependent thermal evolution (Figs. S5a, d, & g; Table S6). Within the surface-to-MLD layer, CT showed a selected breakpoint between 2007 and 2008, corresponding to a 0.82% increase, although the bootstrap confidence interval extended to later years, indicating uncertainty in the exact timing of this transition. The pre-breakpoint trend was positive but not statistically significant, and no significant trend was detected thereafter (Fig. S5.a). In contrast, significant warming persisted below the mixed layer until the selected 2013-2014 breakpoints. CT between the
305 MLD and Z_{eu} increased from 2003 to 2013 at $0.20\text{ }^{\circ}\text{C yr}^{-1}$ ($R^2 = 0.78$, $p = 3.17 \times 10^{-4}$), followed by a 1.41% decrease across the breakpoint and no significant trend thereafter (Fig. S5.d; Table S6.a). The breakpoint timing in this layer was less precisely constrained than in the deeper layer. CT from Z_{eu} to 300 m increased at $0.15\text{ }^{\circ}\text{C yr}^{-1}$ from 2003 to 2013 ($R^2 = 0.79$, $p = 2.28 \times 10^{-4}$), followed by a 4% decrease across the tightly constrained 2013-2014 breakpoint and no significant post-breakpoint trend (Fig. S5.g; Table S6.a). Thus, the thermal evolution of the upper water column was vertically asynchronous,
310 with an earlier surface-layer transition and a more consistently resolved subsurface transition around 2013-2014.

SA exhibited a later and likewise depth-dependent response (Figs. S5b, e, & h; Table S6). Within the surface-to-MLD layer, SA showed essentially no trend from 2003 to 2016, followed by a tightly constrained breakpoint between 2016 and 2017 associated with a 0.28% decrease (Table S6a). After this breakpoint, SA increased significantly at $0.05\text{ g kg}^{-1}\text{ yr}^{-1}$ ($R^2 = 0.82$, $p = 0.0019$; Fig. S5.b; Table S6.b). Below the mixed layer, the selected salinity transitions occurred earlier, between 2015 and
315 2016. SA between the MLD and Z_{eu} increased from 2003 to 2015 at $0.013\text{ g kg}^{-1}\text{ yr}^{-1}$ ($R^2 = 0.56$, $p = 0.0033$), followed by a 0.33% decrease across a tightly constrained 2015-2016 breakpoint and no significant trend thereafter (Fig. S5.e; Table S6.a). Likewise, SA from Z_{eu} to 300 m increased at $0.007\text{ g kg}^{-1}\text{ yr}^{-1}$ from 2003 to 2015 ($R^2 = 0.66$, $p = 7.90 \times 10^{-4}$), followed by a 0.14% decrease across the selected 2015-2016 breakpoint and no significant post-breakpoint trend (Fig. S5.h; Table S6.a). However, the bootstrap interval for this deeper salinity transition extended back to 2012, indicating greater uncertainty in its
320 exact timing (Table S6.b). Overall, the dominant salinity changes occurred later than the thermal transitions, with the most clearly resolved changes below the mixed layer centred on 2015-2016 and the surface mixed-layer response occurring around 2016-2017 (Table S6.a).

σ_0 , which reflects the combined thermal and haline state of seawater, also exhibited strong depth dependence. The T-S diagram illustrates this combined control, with decreasing CT at a given SA shifting water toward higher- σ_0 isopycnals, whereas decreasing SA at a given CT shifts water toward lower- σ_0 isopycnals (Fig. 5b). Consequently, simultaneous changes
325 in CT and SA can reinforce or partially compensate one another, explaining why the density trajectories did not necessarily follow either variable independently.

The layer-resolved analysis revealed markedly different density responses among the three depth intervals (Figs. S5.c, f, & i; Table S6). Within the surface-to-MLD layer, mean σ_0 decreased from 2003 to 2018 at $-0.03\text{ kg m}^{-3}\text{ yr}^{-1}$ ($R^2 = 0.68$,
330 $p = 8.92 \times 10^{-5}$), followed by a selected breakpoint between 2018 and 2019 associated with a 0.79% decrease (Fig. S5.c; Table S6). The bootstrap interval extended from 2015.5 to 2019.5, indicating some uncertainty in the precise timing of this



transition (Table S6.a). Density then increased at $0.082 \text{ kg m}^{-3} \text{ yr}^{-1}$ ($R^2 = 0.98$, $p = 8.57 \times 10^{-5}$). This later density increase followed the 2016-2017 transition in surface SA and its subsequent positive trend, indicating an increasing haline contribution to recent surface-density evolution. Within the MLD-to- Z_{eu} layer, σ_0 showed a selected breakpoint between 2008 and 2009, corresponding to a 1% increase (Table S6). Density decreased from 2003 to 2008 at $-0.11 \text{ kg m}^{-3} \text{ yr}^{-1}$ ($R^2 = 0.70$, $p = 0.037$), followed by a weaker and non-significant decline thereafter ($p = 0.062$; Fig. S5.f). However, the bootstrap confidence interval for the breakpoint extended from 2007.5 to 2016.5 (Table S6.a), and the ΔBIC (Table S6.b) support was comparatively modest, indicating that the exact timing of this intermediate-layer density transition is poorly constrained. The clearest density transition occurred in the Z_{eu} -300 m layer. Mean σ_0 decreased from 2003 to 2013 at $-0.03 \text{ kg m}^{-3} \text{ yr}^{-1}$ ($R^2 = 0.75$, $p = 5.95 \times 10^{-4}$), followed by a 0.67% increase across the tightly constrained 2013-2014 breakpoint and no significant trend thereafter (Fig. S5.i; Table S6.a). This density transition coincided with the 4% decrease in CT in the same layer, whereas the selected SA breakpoint occurred later, in 2015-2016. The timing therefore indicates that the 2013-2014 increase in deeper σ_0 was more closely associated with the thermal transition, with subsequent salinity changes further modifying the density structure (Fig. 5b; Table S6.a). Overall, the T-S relationships in Fig. 5b and the asynchronous CT and SA transitions show that upper-ocean density evolved through changing thermal and haline contributions that differed with both depth and time.

The optical structure changed differently from the physical structure (Figs. 5a & c). Annual mean Z_{eu} remained comparatively stable at approximately 107-111 m and showed no statistically supported breakpoint, with irradiance at Z_{eu} remaining near $30\text{-}33 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (Fig. 5a). In contrast, irradiance at the MLD varied substantially as the MLD changed depth, ranging from approximately 151 to $224 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$. The separation between MLD and Z_{eu} decreased from approximately 74 m early in the record to 60 m in 2013, before increasing to approximately 79 m in 2014. This 2013-2014 transition coincided with the principal breakpoints in subsurface OHC (Figs. 5a & c).

Where BGC Argo chlorophyll observations were available, the DCM generally occurred near or slightly below Z_{eu} (Fig. 5). Irradiance at the DCM declined from approximately $34\text{-}35 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ in 2016-2017 to approximately $26 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ in 2023-2024, with even lower values during 2021-2022. Thus, the more recent DCM occurred under lower-light conditions than during the earliest BGC Argo observations.

These vertical thermal, density and optical pattern show that the physical reorganization of the NPSG involved coordinated but depth-dependent changes in heat storage, temperature, salinity, density, and mixed-layer structure, while Z_{eu} remained comparatively stable. The clearest transition occurred around 2013-2014, when subsurface OHC and the separation between the MLD and Z_{eu} changed, altering the vertical relationship among physical, optical, and biological boundaries.

3.5 Subsurface Apparent Oxygen Utilisation

AOU showed a consistent vertical structure in 2020, 2023, and 2024 (Fig. 6; Table S7). Values were close to zero or slightly negative above the Z_{eu} , whereas positive AOU increased below approximately 100-120 m and continued to increase toward 300 m. The annual mean MLD was 40-44 m, considerably shallower than Z_{eu} (108-109 m) and the DCM (115 m) (Table S7.a).

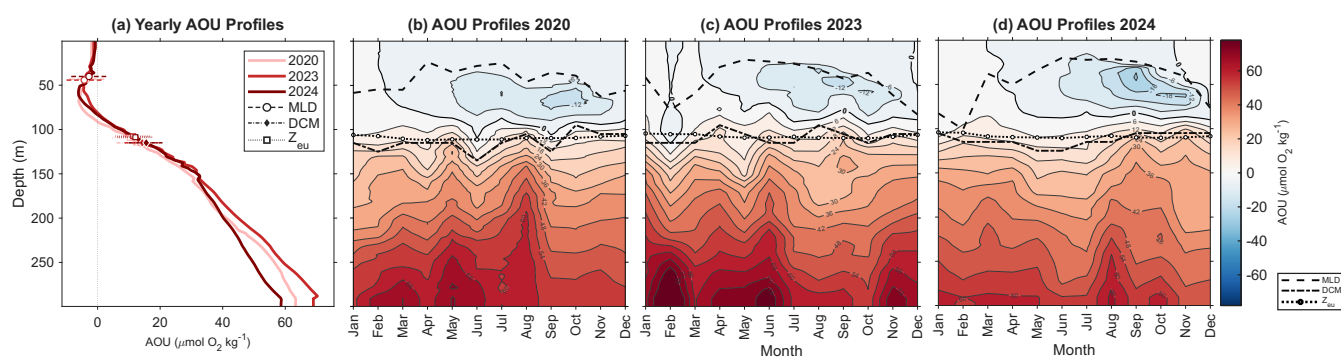


Figure 6. Annual and monthly apparent oxygen utilization (AOU) structure in the North Pacific Subtropical Gyre (NPSG) for 2020, 2023, and 2024. (a) Annual AOU depth profiles for 2020, 2023, and 2024. AOU was calculated as oxygen saturation minus observed dissolved oxygen, with oxygen saturation derived using the Thermodynamic Equation of Seawater 2010 (TEOS-10) from Absolute Salinity, Conservative Temperature, depth, latitude, and longitude. Valid profiles were linearly interpolated onto a common 1-m depth grid from 0 to 300 m. Monthly AOU was calculated as the median for each platform and then averaged equally across platforms after median-based outlier removal. Annual profiles were obtained from observed monthly values only, requiring at least three valid months at each depth, and a three-point moving mean was applied for display. Profiles progress from light to dark red for 2020, 2023, and 2024, respectively. (b-d) Monthly depth distributions of AOU for (b) 2020, (c) 2023, and (d) 2024. Monthly fields were derived from equal-platform AOU profiles on the common 1-m depth grid. Short internal gaps of up to three consecutive months were linearly interpolated for Hovmöller visualization only, while longer or unsupported gaps remained missing; no temporal or vertical smoothing was applied. Red shading indicates positive AOU, blue shading indicates negative AOU, and the black zero contour separates positive and negative values, with contour intervals of $6 \mu\text{mol O}_2 \text{ kg}^{-1}$. For panels (a-d), dashed lines with open circles indicate mixed-layer depth (MLD), dash-dotted lines with filled diamonds indicate deep chlorophyll maximum (DCM), and dotted lines with open squares indicate euphotic-zone depth (Z_{eu}).



Mean AOU from surface to MLD and MLD to Z_{eu} remained slightly negative in all three years, ranging from -1.98 to $-0.86 \mu\text{mol O}_2 \text{ kg}^{-1}$ and from -1.62 to $-0.22 \mu\text{mol O}_2 \text{ kg}^{-1}$, respectively (Fig. 6a; Table S4.a). In contrast, mean AOU below Z_{eu} was strongly positive, reaching 42.62 , 45.57 , and $40.72 \mu\text{mol O}_2 \text{ kg}^{-1}$ in 2020, 2023, and 2024, respectively (Figs. 6a-c; Table S4.a). Around the DCM, mean AOU was lower compare to below Z_{eu} but remained positive, ranging from 11.19 to $14.75 \mu\text{mol O}_2 \text{ kg}^{-1}$ (Table S4.a).

The annual AOU inventory tendencies also differed among layers and years (Table S4.b). Negative tendencies dominated in 2020, particularly between the MLD and Z_{eu} (-28.90) and below Z_{eu} (-30.56). By 2023 and 2024, tendencies in the upper layers were close to zero or slightly positive, whereas the Z_{eu} -300 m layer remained negative (-7.09 and -6.97 , respectively). Overall, the main AOU transition remained near the Z_{eu} -DCM region, while the magnitude of both AOU and its annual inventory tendency varied among years.

4 Discussion

4.1 Physical Reorganization and the Subsequent Biological Response

The biological changes in the NPSG occurred after major physical changes had already developed at different depths in the upper ocean. Although SST increased throughout 1998-2024, the Argo observations showed that thermal, haline, and density changes occurred at different times and depths layer rather than as a uniform warming of the upper water column (Figs. 3-5 & S5; Table S6). The surface thermal response occurred first, whereas warming persisted below the mixed layer until 2013-2014. This later subsurface transition was evident in both CT and OHC within the MLD- Z_{eu} and Z_{eu} -300 m layers (figs. 4d & S5.c), indicating that changes in the deeper upper-ocean thermal structure continued after the surface layer had already changed regime.

The 2013-2014 transition was also accompanied by clear evidence of stronger vertical density stratification. MLD shoaled by approximately 21.5%, while Z_{eu} and the irradiance at Z_{eu} remained comparatively stable, increasing the separation between the base of the mixed layer and the lower boundary of the Z_{eu} (Figs. 3d & 5a). Independent density metrics showed the same breakpoint timing, with $\Delta\sigma_0$ between 10 m and Z_{eu} increasing by approximately 34% and the mean vertical density gradient increasing by approximately 35% (Table S6). These changes demonstrate that the density contrast across the upper Z_{eu} column strengthened substantially around 2013-2014. Because Z_{eu} itself showed no structural breakpoint, this reorganization primarily reflected changes in mixed-layer and density structure rather than a major change in the depth of light penetration (Fig. 5).

The T-S structure shows why the density response differed among layers and did not simply track either CT or SA (Fig. 5b). On surface level, temperature changed earlier, whereas the principal salinity transitions occurred mainly during 2015-2017 (Table S6.a). In the Z_{eu} -300 m layer, the increase in σ_0 across 2013-2014 coincided with a marked decrease in CT, while the corresponding SA breakpoint occurred later. This timing indicates a stronger thermal contribution to the deeper density transition. In contrast, the later increase in surface SA preceded the reversal toward increasing surface σ_0 after 2018-2019, suggesting a progressively greater haline contribution to recent mixed-layer density changes. The T-S relationships in Fig. 5b illustrate this balance where cooling shifts water toward denser isopycnals, whereas freshening shifts it toward lighter



isopycnals, so thermal and haline effects may reinforce or partially compensate one another. The asynchronous CT, SA, and σ_0 transitions therefore indicate a progressive hydrographic reorganization rather than a single synchronous water-mass shift.

Viewed chronologically, the physical changes indicate a progressive reorganization of the upper ocean. An earlier thermal adjustment was detected in the surface-to-MLD layer around 2007-2008, although its breakpoint timing was relatively uncertain. Changes in density within the MLD- Z_{eu} layer were also detected around 2008-2009, but with broad breakpoint uncertainty (Table S6). The strongest and most consistently resolved physical transition occurred around 2013-2014, when MLD shoaled, the MLD- Z_{eu} interval expanded, subsurface CT and OHC changed markedly, σ_0 increased in the Z_{eu} -300 m layer, and the vertical density contrast strengthened. This timing coincided with the onset of the 2013–2016 northeast Pacific “Blob” (Bond et al., 2015; Chen et al., 2021; Shi et al., 2022). Salinity changes followed mainly during 2015-2017, with breakpoints in the two subsurface layers around 2015-2016 and in the surface-to-MLD layer around 2016-2017, overlapping with the strong 2015-2016 El Niño (L’Heureux et al., 2017; Santoso et al., 2017). The mixed-layer density response changed later, with a selected breakpoint around 2018-2019. These timing suggests that upper-ocean reorganization developed progressively across several years spanning the Blob and subsequent 2015-2016 El Niño, rather than through a single instantaneous transition.

The principal biological transitions occurred after this major physical reorganization. Surface C_{phyto} changed between 2015 and 2016 (Fig. 2a), followed by the surface chlorophyll: C_{phyto} transition between 2017 and 2018 (fig. 2d), whereas surface chlorophyll itself showed no structural breakpoint (Fig. 1b). The exact timing and magnitude of the merged C_{phyto} transition remain uncertain because the same breakpoint was not independently reproduced by the single-sensor records (Table S6). Nevertheless, its occurrence after the independently observed changes in MLD, subsurface thermal structure, and density stratification places the biological transition within an already altered physical environment (Figs. 3d, 4d, & S5; Table S6). We therefore interpret the sequence as evidence that the physical and biological changes occurred successively, rather than as proof of direct causation.

The vertical chlorophyll observations provide further evidence of biological adjustment within this reorganized water column. BGC-Argo showed that the strongest recent chlorophyll decreases occurred between approximately 75 and 105 m, while positive differences appeared intermittently at greater depths, particularly near 125-135 m (Fig 1d; Table S4). At the same time, the DCM occurred repeatedly in deeper bins after 2016-2017, although its exact depth varied among years (Fig. S2.a). This interannual variability is important, but the overall tendency toward a deeper DCM is independently supported by the long-term HOT record at fixed Station ALOHA, where the five-year mean DCM deepened from approximately 75 m in 1998-2002 to approximately 100 m in 2020-2024 (Fig. S3). The agreement between the regional BGC-Argo observations and the fixed-station HOT record therefore strengthens the evidence for a long-term downward shift in the vertical position of chlorophyll accumulation despite substantial year-to-year variability. The chlorophyll reduction at approximately 75-105 m is consistent with this vertical redistribution. This depth range corresponds to the shallower portion of the earlier DCM environment, whereas some of the recent positive chlorophyll differences occurred deeper in the water column. The pattern therefore suggests a redistribution of chlorophyll accumulation toward greater depth rather than a uniform decline throughout the subsurface water column.

Importantly, the deeper DCM developed while Z_{eu} remained comparatively stable. The DCM therefore did not simply follow a downward displacement of the Z_{eu} boundary. Instead, chlorophyll accumulation shifted deeper within a broadly



similar optical depth range and occurred under lower irradiance during the more recent BGC-Argo period. This is consistent with DCM position reflecting the depth-dependent balance among irradiance, nutrient availability, phytoplankton biomass, and photoacclimation rather than simply tracking Z_{eu} (Letelier et al., 2004; Rii et al., 2016b; Letelier et al., 2017).

435 The stronger density stratification and larger MLD- Z_{eu} separation provide a plausible physical context for this deeper DCM. Stratification is controlled jointly by temperature, salinity, and density, and stronger stratification limits vertical mixing and exchange between surface and subsurface waters (Cheng et al., 2025). The MLD- Z_{eu} layer separates the high-light, nutrient-depleted surface mixed layer from deeper waters where nutrient concentrations generally increase. A greater physical separation between these environments could therefore alter their vertical coupling and shift the depth at which the balance between
440 light availability and nutrient access favours chlorophyll accumulation (Karl and Church, 2017; Letelier et al., 2017; Cheng et al., 2025). However, because our observations do not directly quantify turbulent diffusivity, entrainment, or vertical nutrient flux, the stronger stratification should not be interpreted as direct evidence of a specific reduction in nutrient supply.

4.2 Biological Reorganization was not a Uniform Decline in Phytoplankton Biomass

After establishing that the chlorophyll decline was not uniform through the water column, we assessed whether it reflected a
445 corresponding change in phytoplankton biomass. The contrasting behaviour of C_{phyto} and chlorophyll: C_{phyto} shows that the surface chlorophyll decline was not simply proportional to biomass loss (Fig. 2). C_{phyto} provides a proxy for phytoplankton carbon biomass, whereas chlorophyll: C_{phyto} reflects pigmentation relative to carbon (Behrenfeld et al., 2005). Their different temporal behaviour therefore indicates that changes in biomass were accompanied by changes in cellular pigmentation, rather than chlorophyll varying solely as a biomass signal (Behrenfeld and Boss, 2014; Letelier et al., 2004; Rii et al., 2016b).

450 This interpretation is also similar with the surface community structure observed at Station ALOHA. In the upper water column, recent C_{phyto} was higher while chlorophyll declined (Fig. 2b & e), and *Prochlorococcus* showed more positive tendencies whereas *Synechococcus* and picoeukaryotes generally tended to decline (Fig. S3). Although most of these annual community trends did not remain significant after FDR correction, their directions are consistent with an increasing relative contribution of *Prochlorococcus* to the surface picophytoplankton assemblage. This is consistent with the established ecology of the NPSG,
455 where *Prochlorococcus* is numerically dominant in the warm, oligotrophic waters of Station ALOHA and is particularly well adapted to low-nutrient subtropical environments (Partensky and Garczarek, 2010; van den Engh et al., 2017; Thompson et al., 2021). More broadly, high *Prochlorococcus* abundance is characteristic of warm oligotrophic waters, including subtropical gyres, reflecting both efficient nutrient utilization and the thermal niches of different ecotypes (van den Engh et al., 2017). Because phytoplankton groups differ in pigment content and carbon-to-chlorophyll characteristics, a greater contribution of
460 *Prochlorococcus* could lower chlorophyll concentration relative to carbon without requiring an equivalent reduction in total phytoplankton carbon (Rii et al., 2016b; Thompson et al., 2021; Sasai et al., 2022; Beckett et al., 2024; Winter et al., 2025).

The response around the DCM was different. Recent increases in chlorophyll: C_{phyto} were concentrated deeper in the Z_{eu} , whereas corresponding changes in C_{phyto} were weaker, indicating that enhanced subsurface chlorophyll did not necessarily represent a proportional increase in carbon biomass (Fig. 2b & e). Because phytoplankton can increase cellular chlorophyll relative to carbon under lower irradiance through photoacclimation (Letelier et al., 2004; Rii et al., 2016b; Letelier et al., 2017),
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the deeper recent DCM does not necessarily represent a deeper maximum in phytoplankton carbon. The HOT community structure also varied with depth. Below approximately 100 m, *Prochlorococcus* generally declined, whereas picoeukaryotes increased between approximately 100 and 150 m (Fig. S3). This shift points to a greater contribution of phytoplankton groups associated with lower-irradiance conditions in the deeper part of the euphotic zone (Rii et al., 2016a, 2022). This depth range overlaps the deeper recent DCM and the region where chlorophyll: C_{phyto} increased, suggesting that greater pigment investment under lower irradiance and a changing contribution of deeper-occurring phytoplankton groups may both have enhanced subsurface chlorophyll.

The deeper DCM therefore appears to reflect more than a simple downward displacement of a fixed biomass maximum. Because Z_{eu} remained comparatively stable while the DCM deepened, recent chlorophyll accumulation occurred under lower irradiance and within a different biological environment. The combined patterns are most consistent with vertical redistribution of biomass, increased chlorophyll investment per unit carbon through photoacclimation, and depth-dependent changes in community composition. Together, these processes help explain why chlorophyll, chlorophyll: C_{phyto} , and C_{phyto} did not vary in parallel and why the long-term surface chlorophyll decline should not be interpreted as a uniform decline in phytoplankton biomass.

4.3 Recent Vertical Reorganization and Biogeochemical Implications

The recent BGC-Argo observations indicate that the ecological reorganization of the NPSG also coincided with a distinct subsurface oxygen-utilisation structure. During 2020, 2023, and 2024, AOU remained near zero or slightly negative above Z_{eu} , but increased rapidly below approximately 100-120 m, close to the Z_{eu} and DCM (Fig. 6; Table S4). This places the recent DCM near the transition between relatively well-ventilated upper waters and deeper waters with progressively greater accumulated oxygen utilisation. Negative AOU in the upper water column indicates oxygen supersaturation and can reflect photosynthetic production, recent ventilation, and air-sea gas exchange, whereas increasing positive AOU at depth reflects the combined effects of respiration, ventilation history, and water-mass transport (Sarmiento and Gruber, 2006; Emerson and Bushinsky, 2014).

The position of this AOU transition is relevant because the recent DCM was deeper and occurred under lower irradiance than during the earliest BGC-Argo observations (Figs. 1 & 5). At the same time, chlorophyll: C_{phyto} changed strongly around the upper DCM, while C_{phyto} reductions became more pronounced deeper in the water column (Fig. 2; Table S2). The recent biological structure therefore intersected gradients in light, biomass, pigmentation, and oxygen utilisation rather than simply shifting downward as an unchanged chlorophyll maximum. This vertical organization is consistent with a changing environment for phytoplankton production and subsequent organic-matter processing.

The AOU observations nevertheless should not be interpreted as a direct measure of contemporary carbon export. AOU integrates biological oxygen consumption together with ventilation, circulation, and water-mass residence time, so elevated values below Z_{eu} indicate accumulated respiratory processing rather than an instantaneous export flux (Sarmiento and Gruber, 2006; Emerson and Bushinsky, 2014). The interannual differences also support this interpretation, where mean AOU below



Z_{eu} was highest in 2023, whereas AOU around the DCM was highest in 2024 (Fig. 6; Table S4), indicating that deeper oxygen
 500 utilisation did not vary synchronously with conditions at the DCM.

These observations therefore point to a changing biogeochemical setting rather than a quantified change in biological carbon export. The deeper DCM, altered chlorophyll: C_{phyto} , depth-dependent changes in C_{phyto} , and shifts in phytoplankton community composition all have the potential to modify where organic carbon is produced and processed in the water column (Figs. 1, 2, 5, & S3). However, determining whether the biological carbon pump has strengthened or weakened would require
 505 direct estimates of production and export. Here, AOU is therefore interpreted as biogeochemical context for the recent vertical reorganization, not as a quantitative estimate of carbon sequestration.

5 Conclusions

This study shows that the long-term decline in surface chlorophyll across the NPSG occurred within a progressively warming and reorganizing upper ocean. SST increased throughout 1998-2024, while Argo observations revealed depth-dependent
 510 changes in CT, OHC, salinity, and density structure. The clearest physical transition occurred around 2013-2014, when the MLD shoaled, subsurface CT and OHC changed, and the vertical density contrast across the upper euphotic zone strengthened. Because Z_{eu} and irradiance at its lower boundary remained comparatively stable, these changes primarily reflected a reorganization of the physical structure of the upper ocean rather than a major change in light penetration.

The biological response developed after these physical changes and was not expressed simply as a decline in phytoplankton
 515 biomass. Surface chlorophyll declined, but C_{phyto} and chlorophyll: C_{phyto} followed different trajectories, showing that chlorophyll and phytoplankton carbon biomass were partly decoupled. In the upper water column, recent C_{phyto} increased even as chlorophyll declined, indicating that lower chlorophyll did not necessarily represent biomass loss. The HOT observations suggest that changes in community composition may have contributed to this decoupling, with a greater relative contribution of *Prochlorococcus* in surface waters. Together with changes in cellular pigmentation, such community shifts can alter
 520 chlorophyll concentration without producing an equivalent change in total phytoplankton carbon.

The biological reorganization was also strongly depth-dependent. Chlorophyll accumulation shifted downward and the DCM deepened, while C_{phyto} and chlorophyll: C_{phyto} changed differently with depth. Around the deeper DCM, increases in chlorophyll relative to carbon were not accompanied by equivalent increases in C_{phyto} , indicating that the deeper chlorophyll maximum did not simply represent a deeper biomass maximum. Instead, the downward displacement of the DCM appears to reflect
 525 a combination of vertical redistribution of biomass, increased chlorophyll investment per unit carbon under lower irradiance, and changes in community composition, including a greater contribution of picoeukaryotes in the deeper Z_{eu} .

The deeper DCM developed within a relatively stable Z_{eu} but at lower irradiance, indicating that the vertical biological response was driven by changes within the Z_{eu} rather than by a simple deepening of the optical boundary itself. The stronger density stratification and greater separation between the mixed layer and deeper euphotic waters provide a plausible physical
 530 setting for this redistribution by altering the vertical coupling between surface and subsurface environments.



Finally, the recent AOU structure shows that this reorganized phytoplankton community occupied a vertically distinct biogeochemical environment, with low or slightly negative AOU in the upper Z_{eu} and substantially higher AOU below Z_{eu} . These observations indicate changes in where organic matter may be produced and processed in the water column, although they do not provide a direct measure of carbon export.

535 Our results show that declining surface chlorophyll in the NPSG represents only one component of a broader physical and biological reorganization. Understanding ecosystem responses to continued warming in oligotrophic subtropical gyres therefore requires distinguishing chlorophyll from phytoplankton carbon biomass and considering changes in upper-ocean structure, cellular pigmentation, community composition, and vertical habitat together.

Code and data availability. All data supporting the findings of this study are publicly available from open-access repositories:

- 540 – **Satellite ocean-colour and optical data:** European Space Agency Ocean Colour Climate Change Initiative (ESA OC-CCI, <https://www.oceancolour.org>) (Sathyendranath et al., 2019) and Copernicus Marine Environment Monitoring Service (CMEMS, <https://data.marine.copernicus.eu>) (European Union-Copernicus Marine Service (2022)) .
- **Sea-surface temperature:** NOAA Extended Reconstructed Sea Surface Temperature (ERSST v6, <https://www.ncei.noaa.gov/products/extended-reconstructed-sst>) (Huang et al., 2025a, b).
- 545 – **In situ physical and biogeochemical profiles:** Core physical Argo temperature and salinity profiles were obtained from the International Argo program (<https://argo.ucsd.edu>), while chlorophyll, particulate backscattering at 700 nm, and dissolved oxygen were obtained from the Biogeochemical-Argo program (<https://biogeochemical-argo.org>).
- **Station ALOHA observations:** Long-term chlorophyll and phytoplankton community observations from the Hawaii Ocean Time-series (HOT) program were obtained through the HOT Data Organization and Graphical System (HOT-DOGS, <http://hahana.soest.hawaii.edu/hot/hot-dogs/>).
- 550

The dataset assembled for this study is archived at <https://doi.org/10.5281/zenodo.23004516> (Adroli, 2026a). Code for data processing and statistical analyses is archived as software version v1.0.0 at <https://doi.org/10.5281/zenodo.23004976> (Adroli, 2026b).

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