

Lagrangian Eddy Trapping Fosters Chlorophyll Hot Spots in the North Pacific Subtropical Gyre

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Key Points:

- Mesoscale eddy trapping of chlorophyll is quantified using Lagrangian coherency metrics over feature lifetimes, from genesis to decay.
- Sea level anomaly eddies mix laterally with outside waters, resulting in weaker chlorophyll anomalies than within coherent eddies.
- The chlorophyll signature of eddy trapping differs regionally within a gyre, seasonally, by eddy age, and between cyclones and anticyclones.

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Abstract

Vertical motions associated with mesoscale ocean eddies modulate the light and nutrient environment, stimulating phytoplankton biomass and chlorophyll anomalies. Populations within eddies may be trapped by the horizontal circulation or laterally diluted by mixing with surrounding waters. Conventionally, eddy boundaries are determined using Eulerian methods from daily satellite sea level anomaly fields. However, Eulerian methods do not delineate the bounds of trapped water masses, which is important to consider when interpreting eddy-induced changes in chlorophyll concentration. Integrated Lagrangian particle tracking methods, on the other hand, more accurately identify coherent structure boundaries that trap fluid masses for time scales relevant to phytoplankton bloom evolution. From two decades of remote sensing observations in the North Pacific Subtropical Gyre, we compared coincident Eulerian and Lagrangian eddy atlases to assess the impact of eddy trapping on chlorophyll concentration. We found more positive chlorophyll anomalies within Lagrangian coherent vortices than in Eulerian eddy boundaries and outside-eddy waters. Yet, there are striking differences seasonally and regionally within the gyre. Chlorophyll is most enriched within coherent boundaries of the Hawaiian Lee eddies and in the region southeast of the Islands in fall and winter. Our results suggest that typical Eulerian analyses underestimate the role of mesoscale eddies in enhancing chlorophyll by not accounting for lateral mixing. Consequently, quantifying the contribution of mesoscale eddies toward open ocean primary production is more complex than previously assumed.

Plain Language Summary

Mesoscale eddies are rotating ocean currents up to hundreds of kilometers in diameter. While some eddies continuously mix with their surroundings, referred to as leaky or dispersive, others are coherent and trap their constituents. Phytoplankton are free-floating microbes and their local concentrations are affected by the motions of these currents. The pigment chlorophyll enables phytoplankton to photosynthesize, which changes the ocean color and can be measured from space. We used satellite datasets and simulations of currents in the North Pacific to examine the effect of eddy coherency on phytoplankton concentration. We found coherent eddies trap phytoplankton, harboring greener waters than leaky eddies. In dispersive eddies, anomalous chlorophyll concentrations are diluted by mixing with surrounding waters. Thus, studies that do not quantify eddy trapping may underestimate the role of eddies in stimulating phytoplankton growth, which has implications for the global carbon budget. We also show that the chlorophyll signature of eddy trapping can vary regionally, seasonally, and as a function of eddy age. Most significantly, to the south of the Hawaiian Islands, we observed greener waters in coherent eddies than in their leaky counterparts in the fall and winter, signatures that are sustained over feature lifetimes.

1 Introduction

The North Pacific Subtropical Gyre (NPSG) maintains low phytoplankton biomass but is subject to high ecosystem variability (Karl & Church, 2017). Mesoscale eddies contribute to this variability, bringing nutrient-rich deep waters into the sunlit surface and stimulating phytoplankton growth in a temporary, quasi-isolated, altered environment. Eddies in the NPSG, including at Station ALOHA and the Hawaiian Lee Eddies, are the focus of seminal works describing biophysical interactions. For example, observations show that eddies affect biogeochemical cycling by enhancing primary production (Falkowski et al., 1991; Allen et al., 1996; Seki et al., 2001; Chen et al., 2008; Landry et al., 2008; McAndrew et al., 2008; Nicholson et al., 2008), modifying phytoplankton community structure (Olaizola et al., 1993; Vaillancourt et al., 2003; Brown et al., 2008; Fong et al., 2008; Barone et al., 2019; Harke et al., 2021), and intensifying carbon export (Bidigare et al.,

2003; Benitez-Nelson et al., 2007; Rii et al., 2008; Zhou et al., 2021; Barone et al., 2022). The NPSG, and analogous gyres in other basins, represent ecosystems of globally important scale, so the integrated effects of mesoscale biophysical interactions therein may play a significant role in Earth’s carbon cycle.

1.1 Satellite Chlorophyll Signature of Eddies

Continuous satellite remote sensing of the Sea Level Anomaly (SLA) and chlorophyll-*a* (chl-*a*; a proxy for phytoplankton biomass) reveals significant relationships between ocean color anomalies and mesoscale eddies in global subtropical waters (Gaube et al., 2014; Dufois et al., 2016; He et al., 2016; Huang et al., 2017; Xu et al., 2019; Travis & Qiu, 2020). Yet, these relationships are complex; they differ regionally, seasonally, and between cyclonic and anticyclonic eddy polarities (see review by McGillicuddy Jr. (2016) and references therein). Cyclonic eddies in the Northern Hemisphere rotate counter-clockwise, depress the sea level, and shallow density surfaces. Eddy pumping in cyclones vertically displaces nutrient-rich deep waters into the euphotic zone, increasing phytoplankton biomass and surface chl-*a*. On the other hand, eddy-induced Ekman pumping can drive downwelling in the center of cyclones and decrease chl-*a*.

In contrast to cyclones, anticyclones in the Northern Hemisphere rotate clockwise, locally increase the sea level, and deepen isopycnals, which can reduce nutrient availability and decrease biomass. Other processes elevate biomass in subtropical anticyclones, including Ekman suction and winter convective mixing that vertically displaces nutrients into the mixed layer (Dufois et al., 2016). The vertical displacements of density surfaces in mesoscale eddies of either polarity can also cause phytoplankton cells to adjust their pigment content to adapt to differing light levels, further altering chlorophyll concentrations (Cornec et al., 2021; He et al., 2021; Strutton et al., 2023). These various mechanisms can result in anomalous concentrations of chl-*a* in subtropical gyre anticyclones and cyclones compared to outside-eddy waters.

1.2 Eddy Trapping

The horizontal circulation of mesoscale eddies can “trap” the signature of vertically-driven perturbations to phytoplankton biomass, acting to localize blooms (Gower et al., 1980; Provenzale, 1999; Fennel, 2001; Condie & Condie, 2016; He et al., 2022) and even preserve them as features transit across ocean basins (Lehahn et al., 2011; Villar et al., 2015). Eddy trapping is anticipated to garner monopoles of anomalous chl-*a* in eddy centers. However, it is still a challenge to disentangle from space-based observations whether mesoscale anomalies are signatures of actively changing biomass due to vertical processes or an advected, preserved plankton patch (Gaube et al., 2014).

Eddy trapping has major ecological implications. For example, coherent eddies formed near the Hawaiian coastline affect larval recruitment by trapping and transporting waters offshore (Vaz et al., 2013). Lateral trapping can also modulate trophic interactions (d’Ovidio et al., 2013; Lehahn et al., 2017) and alter phytoplankton community diversity by separating populations and sheltering them from competition (Bracco et al., 2000; Bastine & Feudel, 2010; Perruche et al., 2011; Clayton et al., 2013; Lévy et al., 2014; Hernández-Carrasco et al., 2023). So, coherent eddies may foster fluid dynamical niches (d’Ovidio et al., 2010; Lévy et al., 2015; Vortmeyer-Kley et al., 2019).

Individual eddies have varying trapping strengths, but censuses of the satellite chl-*a* response to eddies have not directly addressed the effects of this variability. The boundaries of mesoscale eddies are commonly detected using Eulerian metrics, for example from the SLA by assuming geostrophic balance (Chelton et al., 2011), and are often presumed to trap water masses. However, studies consistently find that Eulerian-detected boundaries are not necessarily materially coherent (Beron-Vera et al., 2013; Haller & Beron-

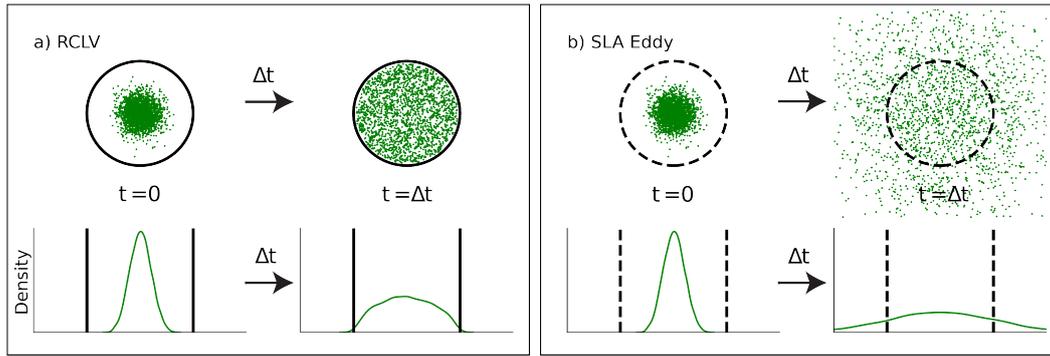


Figure 1. Schematic of the fates of phytoplankton blooms in coherent and leaky eddies. **(a)**, **(b)** At $t = 0$, identical blooms are induced by the eddies. **(c)** At $t = \Delta t$, phytoplankton cells in the coherent eddy are distributed within the boundaries, but in-eddy waters do not mix with surrounding waters. **(d)** At $t = \Delta t$, the bloom in the leaky eddy is diluted via mixing with outside-eddy waters. This resulted in a lower biomass concentration than in the coherent eddy, despite the initial generation of an equivalent bloom.

113 Vera, 2013; Y. Wang et al., 2015; Beron-Vera et al., 2019; T. Liu et al., 2019; Andrade-
 114 Canto et al., 2020; Katsanoulis et al., 2020; T. Liu et al., 2022; Denes et al., 2022). In
 115 fact, only 54% of SLA eddies in the NPSG contain a coherent structure of substantial
 116 size that persists for at least a month (Jones-Kellett & Follows, 2024). This suggests that
 117 waters along SLA eddy boundaries mix with surrounding waters, and for many, the entire
 118 eddy structure is dispersive.

119 By delineating between coherent and “leaky” eddies, we can better understand the
 120 magnitudes and fates of eddy-driven biogeochemical perturbations. Figure 1 schemat-
 121 ically demonstrates the outcome of equivalent phytoplankton blooms generated in a (a)
 122 coherent and (b) leaky eddy. After the initial blooms are diluted for time Δt , the coher-
 123 ent eddy maintains a more highly concentrated population than the leaky eddy because
 124 the cells cannot escape the bounds. We anticipate that such eddy-driven anomalies will
 125 dissipate as eddies age due to lateral dilution (although this process is slowed in a co-
 126 herent eddy), vertical dilution, or ecological dynamics such as grazing or the reduction
 127 of nutrient availability.

128 Here we address two hypotheses: (i) Coherent eddies are more likely to contain “hot
 129 spots” of chlorophyll relative to the climatological mean field by suppressing lateral di-
 130 lution of eddy-driven anomalies. (ii) Eddy chlorophyll anomalies, relative to their im-
 131 mediate surroundings, will decline with eddy age even in the most coherent features.

132 1.3 Overview

133 Lagrangian methods accurately measure eddy coherency in a time-varying flow (Haller,
 134 2015). Interpreting biophysical interactions in a Lagrangian sense follows naturally, since
 135 phytoplankton experience a moving reference frame (Woods & Onken, 1982; Lehahn et
 136 al., 2018). To test the hypothesis that Lagrangian coherent vortices contain elevated chl-
 137 *a* concentrations compared to leaky, Eulerian eddies, we analyzed two decades of satel-
 138 lite observations and the development of eddy boundaries in the NPSG. We compared
 139 an SLA eddy atlas with a complementary Lagrangian coherent eddy atlas built for bio-
 140 geochemical applications in Section 2.1. Section 3.1 evaluates an overall elevation of sur-
 141 face chl-*a* due to eddy trapping in the gyre. Key seasonal and sub-regional differences

142 in the biological response to eddy trapping are revealed in Section 3.2. Lastly, Section
 143 3.3 examines the evolution of chl-*a* anomalies in vortices that maintain coherency for five
 144 or more months. Our results suggest that perturbations in biomass triggered by eddies
 145 may be underestimated when lateral mixing and dilution are not accounted for.

146 2 Materials and Methods

147 The study domain extends from 2000 to 2019 and the region 15-30°N, 180-230°E
 148 (see the box in Fig. 2a). We selected these spatial bounds to reduce the degrees of free-
 149 dom associated with large-scale environmental variability from the ultra-oligotrophic west-
 150 ern NPSG, Transition Zone Chlorophyll Front (Glover et al., 1994), California Current
 151 System, and equatorial currents. Focusing on this area of the gyre enabled us to com-
 152 prehensively evaluate sub-regional and seasonal patterns in the chlorophyll signatures
 153 of eddy trapping. We used the Copernicus Marine Service (CMEMS) 1/4° daily satel-
 154 lite geostrophic current and SLA gridded fields for Eulerian and Lagrangian eddy iden-
 155 tification (CMEMS, 2020). We obtained the 8-day averaged satellite chl-*a* Ocean Color
 156 Climate Change Initiative (OC-CCI) product with a spatial resolution of 4km at the equa-
 157 tor (Sathyendranath et al., 2019).

158 2.1 Eddy Atlases

159 2.1.1 Eulerian Eddy Atlas

160 We used the OceanEddies algorithm to generate an Eulerian eddy atlas from the
 161 satellite SLA (Faghmous et al., 2015). The flexible software allowed us to set param-
 162 eters aligned as closely as possible to the Lagrangian eddy atlas, described in Section 2.1.2.
 163 OceanEddies identifies an eddy boundary as the outermost closed contour containing a
 164 single SLA extremum and tracks the movement of feature over time. We required ed-
 165 dies to have a minimum detectable lifespan of 32 days and boundaries to contain twelve
 166 or more 1/4° grid cells. The smallest SLA eddy from this criteria has an area of 8,048km²
 167 with a radius of approximately 50km, consistent with the Rossby radius of deformation
 168 in the domain (Chelton et al., 1998). We set the eddy disappearance parameter to 3 days,
 169 which accounts for noise in the gridded SLA satellite product that could cause a prema-
 170 ture termination to eddy tracking. We reduced the temporal resolution of the SLA at-
 171 las to an 8-day frequency, synchronized with the OC-CCI chl-*a* product, for the ensu-
 172 ing analysis. From two decades of data, we tracked 6,846 unique SLA eddies (or 52,553
 173 observations resolved every 8 days), including 3,322 anticyclones characterized by SLA
 174 maxima and 3,524 cyclones characterized by SLA minima.

175 2.1.2 Lagrangian Eddy Atlas

176 We expanded upon the Lagrangian eddy atlas developed by Jones-Kellett and Fol-
 177 lows (2024) to identify and track coherent vortices. Eddy boundaries were derived from
 178 the Lagrangian Averaged Vorticity Deviation (LAVD), a measure of the integrated vorticity
 179 experienced by a Lagrangian particle over a timescale of interest (Haller et al., 2016).
 180 First, the LAVD for Lagrangian particles is mapped to their gridded initialization loca-
 181 tions. Closed contours surrounding a local maximum in the resulting LAVD field are as-
 182 summed to be fluid sets in rigid-body rotation, referred to as Rotationally Coherent La-
 183 grangian Vortices (RCLVs) (Haller et al., 2016; Tarshish et al., 2018). Then, RCLVs that
 184 maintained coherency for at least 32 days were tracked through time and space at an 8-
 185 day resolution using backward-in-time particle simulations synchronized with the OC-
 186 CCI 8-day chl-*a* product (Fig. S1).

187 Young, developing eddies can harbor large biological anomalies (Gaube et al., 2013).
 188 So to holistically evaluate how eddy trapping alters chl-*a* concentration, it was impor-
 189 tant to resolve RCLV genesis. The RCLV atlas presented by Jones-Kellett and Follows

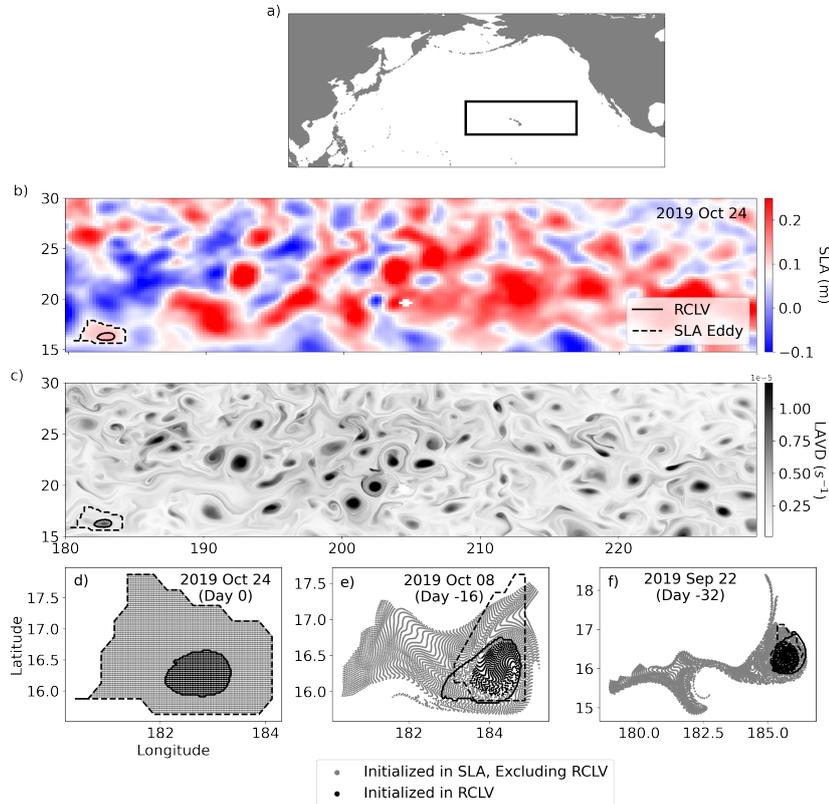


Figure 2. (a) The North Pacific Ocean, where the black box outlines the bounds of the sub-tropical gyre domain that is the focus of this study. (b) The SLA field on 24 October 2019, with the boundaries of one eddy overlaid. The black dotted contour represents the SLA eddy boundary, and the black solid contour is the Rotationally Coherent Lagrangian Vortex (RCLV) boundary. (c) The Lagrangian Average Vorticity Deviation (LAVD) field on 24 October 2019, with the same eddy boundaries as in (b) overlaid. (d-f) The advection of Lagrangian particles, moving backward-in-time from left to right. (d) Lagrangian particles were initialized inside the SLA (gray and black) and RCLV (black) boundaries on 24 October 2019. The gray particles are categorized as “SLA excluding RCLV”. (e) The particle locations on 8 October 2019, or 16 days backward-in-time from the initialization date, and (f) on 22 September 2019, or 32 days backward-in-time. The evolving SLA (dotted contour) and RCLV (solid contour) eddy boundaries are overlaid for each corresponding date.

190 (2024) (Jones-Kellett, 2023a) included features that were above a size threshold and co-
 191 herent for at least 32 days. In other words, the youngest eddies captured in Version 1
 192 are already 32 days old. Here, we initialized Lagrangian particles in each 32-day-old RCLV
 193 and tracked them backward in time with the OceanParcels software (Delandmeter & van
 194 Sebille, 2019) to 8 days of age. Following the existing atlas resolution, at 8-day timesteps
 195 (ages 24, 16, and 8), we drew closed contours to encompass the particle set (Fig. S2).
 196 The quality control steps conducted for the extended RCLV atlas are detailed in the de-
 197 cision tree in Fig. S3. This new version of the RCLV atlas (Jones-Kellett, 2024) contains
 198 11,855 unique RCLVs (or 75,445 polygons resolved every 8 days), including 5,592 anti-
 199 cyclones characterized by a negative sign of relative vorticity and 6,263 cyclones char-
 200 acterized by a positive sign of relative vorticity.

201 The animation supplement shows the space-time evolution of (a) RCLVs overlaid
 202 on the LAVD fields that they were derived from and (b) SLA eddies overlaid on the SLA
 203 for the year 2010. Panel (c) shows the boundaries of both eddy types overlaid on the cli-
 204 matological chl-*a* anomaly (Eq. 1).

205 2.2 Eddy Categorization

206 When comparing RCLVs and SLA eddies from concurrent atlases, it is notable that
 207 some features are observed with only one method whereas many are detected with both
 208 (T. Liu et al., 2019). However, when eddies are identified in both datasets, the bound-
 209 aries can differ considerably. “Overlapping” RCLVs tend to be nested within a larger SLA
 210 eddy boundary, so waters associated with SLA eddies or RCLVs are not necessarily mu-
 211 tually exclusive (Jones-Kellett & Follows, 2024).

212 We categorized each pixel from the satellite chl-*a* fields as background (i.e., outside-
 213 eddy) or inside an eddy. In-eddy pixels can be within an SLA eddy, RCLV, or both. Pix-
 214 els inside an SLA eddy boundary but not an RCLV are referred to as “SLA excluding
 215 RCLV”. This includes the dispersive regions of overlapping eddies (i.e., the gray parti-
 216 cles in Fig. 2d) and the entirety of SLA eddies that do not contain a coherent structure.
 217 The “SLA eddy” category includes all pixels within an eddy boundary irrespective of whether
 218 it contains an RCLV (i.e., the gray *plus* the black particles in Fig. 2d). This classifica-
 219 tion is directly comparable to studies that invoke Eulerian eddy identification methods.
 220 Figure 2d-f demonstrates the considerable difference in the trapping nature of the re-
 221 spective eddy identification methods. The black particles initialized in the RCLV remain
 222 inside the eddy after advection backward through time, whereas many gray particles ini-
 223 tialized in the SLA eddy are not associated with the feature only 16 days prior.

224 2.3 Chlorophyll Anomaly Definitions

225 The climatological chl-*a* anomaly is a temporal, Eulerian metric defined

$$226 \delta c_{clim}(x, y, t) = c(x, y, t) - \frac{1}{M} \sum_{t'=0}^M c(x, y, t') \quad (1)$$

227 where $c(x, y, t)$ is the chl-*a* at location (x, y) and time t . The second term describes the
 228 2000 to 2019 average chl-*a* in the month corresponding to the date t (i.e., the monthly
 229 climatology shown in Fig. S4), such that M is the number of data points available for
 230 that month. A positive δc_{clim} indicates that chl-*a* is higher than the average at that lo-
 231 cation in the given month. We used δc_{clim} to isolate the mesoscale-driven changes in chl-
 232 *a* that are distinct from the seasonal cycle.

233 We define the relative difference in the eddy and background probability density
 234 distributions of δc_{clim} as

$$235 f(\delta c_{clim}) = \frac{p_E(\delta c_{clim}) - p_B(\delta c_{clim})}{p_B(\delta c_{clim})}. \quad (2)$$

236 $p_E(\delta c_{clim})$ is the density distribution of the climatological chl-*a* anomalies in an eddy
 237 type and $p_B(\delta c_{clim})$ is the density distribution of anomalies in the background ocean.
 238 $f(\delta c_{clim})$ is the likelihood of observing a given chlorophyll anomaly in waters sampled
 239 in the eddy type versus the background. For example, $f(\delta c_{clim}) > 0$ indicates the given
 240 value of δc_{clim} is more likely to be observed in an eddy than outside.

241 The local, eddy-associated chl-*a* anomaly is defined

$$242 \quad \delta c_{loc} = \underbrace{\frac{1}{A_{in}} \oint_I c(x, y) dI}_{\text{Inside Eddy}} - \underbrace{\frac{1}{A_{out}} \oint_O c(x, y) dO}_{\text{Outside Eddy}} \quad (3)$$

243 where I is the eddy polygon with area A_{in} , and O is the annulus from the eddy bound-
 244 ary to double the eddy radius with area A_{out} . The first term of Eq. 3 is the average chl-
 245 *a* inside the eddy and the second is the average in the immediate surroundings. A pos-
 246 itive δc_{loc} indicates that the mean chl-*a* concentration is higher within the eddy than out-
 247 side. Since this metric follows an eddy through time and space, it can be considered a
 248 Lagrangian chl-*a* anomaly.

249 3 Results

250 3.1 Chlorophyll Signatures of Eddy Trapping

251 To isolate eddy-driven changes in chl-*a*, we removed the seasonality at each grid
 252 cell in the satellite chl-*a* fields (Eq. 1), yielding climatological chl-*a* anomaly fields from
 253 2000 to 2019. We binned the climatological chl-*a* data by the categorizations described
 254 in Section 2.2: Anticyclonic RCLV, Anticyclonic SLA eddy, Anticyclonic SLA exclud-
 255 ing RCLV, Cyclonic RCLV, Cyclonic SLA eddy, Cyclonic SLA excluding RCLV, or back-
 256 ground. Background chlorophyll observations are outside of all eddy types.

257 3.1.1 Anticyclonic Eddies

258 Anticyclonic eddies alter chlorophyll concentrations in the NPSG. Figure 3a shows
 259 the probability density distributions of the chl-*a* anomaly relative to the seasonal clima-
 260 tology (δc_{clim}) for anticyclones (in red) and the background ocean (in gray). The quan-
 261 tiles of the distributions (indicated by the dots in Fig. 3a) consistently shift toward higher
 262 δc_{clim} in RCLVs compared to SLA eddies. The distribution of δc_{clim} in RCLVs is also
 263 shifted more positively relative to the background ocean except at the 99% quantile. These
 264 results suggest that anticyclonic eddy trapping elevates chl-*a* in the NPSG.

265 To further disentangle how the eddies alter surface chlorophyll, we plotted $f(\delta c_{clim})$
 266 in Fig. 3b. This metric quantifies whether a given δc_{clim} is more likely to be observed
 267 in randomly sampled waters of the background ocean or an eddy. Each quadrant of the
 268 figure can be interpreted as follows:

- 269 • **Q1: Positive** anomalies are **more likely** to be observed in an eddy than in the
 270 background ($f(+\delta c_{clim}) > 0$).
- 271 • **Q2: Negative** anomalies are **more likely** to be observed in an eddy than in the
 272 background ($f(-\delta c_{clim}) > 0$).
- 273 • **Q3: Negative** anomalies are **less likely** to be observed in an eddy than in the
 274 background ($f(-\delta c_{clim}) < 0$).
- 275 • **Q4: Positive** anomalies are **less likely** to be observed in an eddy than in the back-
 276 ground ($f(+\delta c_{clim}) < 0$).

277 Negative values of δc_{clim} are less likely to occur within all anticyclonic eddy types
 278 than in the background (Fig. 3b: Q3). Positive chl-*a* anomalies are more common in all
 279 anticyclonic eddy types compared to outside eddies (Fig. 3b: Q1), except at extremely

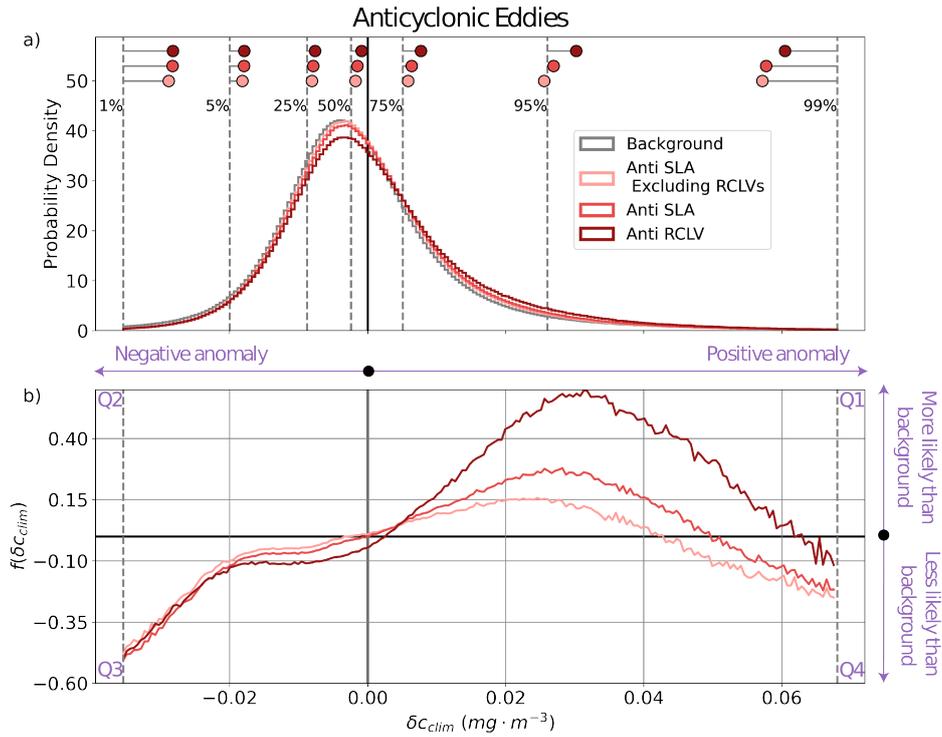


Figure 3. (a) The histograms depict the probability density distributions of the climatological chl-*a* anomalies (δc_{clim} ; Eq. 1) in anticyclones from the 1 – 99% quantiles. The vertical, dotted gray lines depict the quantiles of the background distribution. The dots show the equivalent quantiles for each eddy category, demonstrating the shifts in the distributions from the background. (b) The relative difference in the anticyclonic eddy density distribution from the background density distribution ($f(\delta c_{clim})$; Eq. 2) plotted from the 1 to 99% quantiles (i.e., the gray dotted lines). A positive $f(\delta c_{clim})$ indicates that the given δc_{clim} is more likely to be observed when sampling an in-eddy water parcel than when sampling the background.

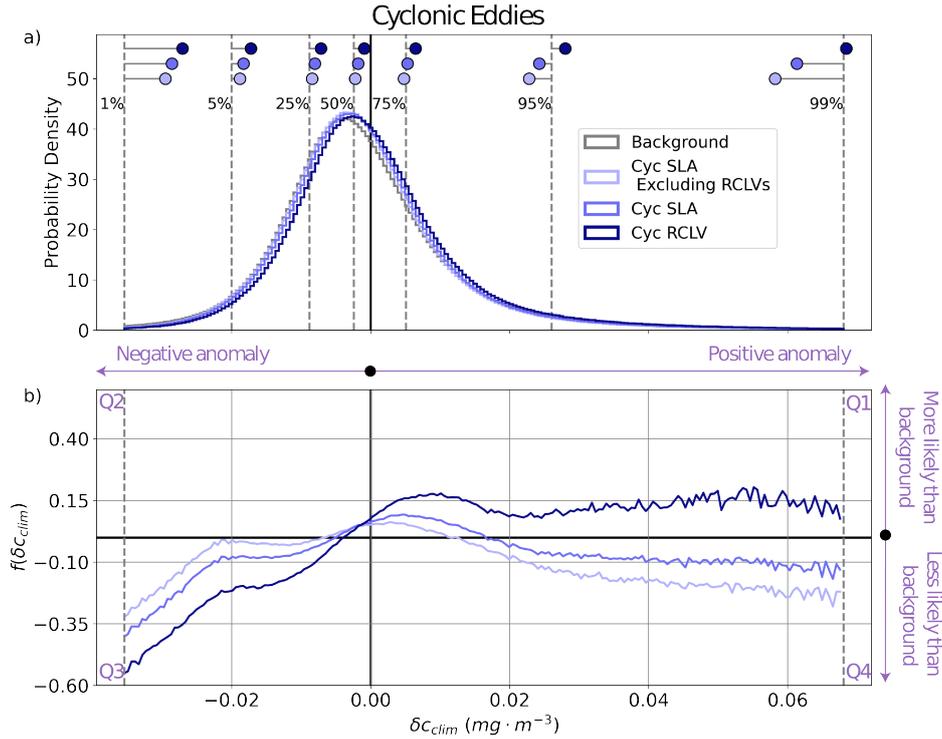


Figure 4. Same as Figure 3, but for cyclonic eddies. **(a)** The histograms depict the probability density distributions of the climatological chl-*a* anomalies ($\delta_{c_{clim}}$; Eq. 1) in cyclones from the 1 – 99% quantiles. The vertical, dotted gray lines depict the quantiles of the background distribution. The dots show the equivalent quantiles for each eddy category, demonstrating the shifts in the distributions from the background. **(b)** The relative difference in the cyclonic eddy density distribution from the background density distribution ($f(\delta_{c_{clim}})$; Eq. 2) plotted from the 1 to 99% quantiles (i.e., the gray dotted lines). A positive $f(\delta_{c_{clim}})$ indicates that the given $\delta_{c_{clim}}$ is more likely to be observed when sampling an in-eddy water parcel than when sampling the background.

280 high values (Fig. 3b: Q4). More specifically, anomalies over $0.0504 \text{ mg}\cdot\text{m}^{-3}$ occurring
 281 in SLA eddies and $0.0631 \text{ mg}\cdot\text{m}^{-3}$ in RCLVs are rarer than in the background. There-
 282 fore, anticyclones elevate chl-*a* up to a certain threshold.

283 21% of satellite pixels co-located within anticyclonic SLA eddies are also contained
 284 within an RCLV (Table S2). In other words, only a fifth of the aggregate SLA eddy area
 285 is coherent timescales on the order of months. The leaky zones of SLA eddies, or SLA
 286 excluding RCLVs, are more likely than the background to contain positive $\delta_{c_{clim}}$, but
 287 only up to $0.0424 \text{ mg}\cdot\text{m}^{-3}$. This threshold is lower than for RCLVs and the all-inclusive
 288 SLA eddy categories, indicating that the highest chl-*a* anomalies associated with SLA
 289 eddies are largely contained within nested Lagrangian coherent structures.

290 3.1.2 Cyclonic Eddies

291 Cyclonic eddies alter surface chlorophyll in the NPSG compared to outside-eddy
 292 waters with signatures that differ in some ways from anticyclones. Negative climatolog-
 293 ical anomalies are less likely to occur in all cyclonic eddy types than in the background
 294 ocean and least likely in RCLVs (Fig. 4b: Q3), as was the case for anticyclones. Cyclonic

295 RCLVs are likelier to have positive chl-*a* anomalies than the background ocean (Fig. 4b:
 296 Q1). However, unlike anticyclonic RCLVs, cyclonic coherent structures elevate chl-*a* to,
 297 or maintain chl-*a*, even at very high values. Yet, moderately positive δC_{clim} are less likely
 298 to occur in cyclones (Fig. 4b: Q1) compared to anticyclones (Fig. 3b: Q1). Other than
 299 for very modest values ($< 0.016 \text{ mg} \cdot \text{m}^{-3}$), SLA cyclones are less likely to have posi-
 300 tive chl-*a* anomalies than the background (Fig. 4b: Q1, Q4). 23% of satellite pixels in
 301 cyclonic SLA eddies are also contained within an RCLV (Table S3) and are not included
 302 in the ‘‘SLA eddies excluding RCLVs’’ category. The leakiest components of SLA eddies
 303 are less likely than the background to contain a positive chlorophyll anomaly greater than
 304 $0.0117 \text{ mg} \cdot \text{m}^{-3}$. Hence, in both cyclones and anticyclones, coherent structures within
 305 SLA eddies are more often associated with positive chl-*a* anomalies than the background
 306 ($\delta C_{clim} > 0$).

307 In summary, RCLVs of both polarities are less likely to have negative chl-*a* anoma-
 308 lies and more likely to have positive anomalies compared to the background and SLA
 309 eddies. Fewer positive chl-*a* anomalies are attributed to SLA eddies when excluding nested
 310 RCLVs than to all-encompassing SLA eddies. This supports the hypothesis that phy-
 311 topkton blooms are rapidly diluted via lateral mixing when coherent structures do
 312 not trap and preserve the eddy-driven biological perturbations.

313 3.2 Regional and Seasonal Subdomains

314 Further examination reveals significant regional and seasonal variations in the role
 315 of eddy trapping toward altering chl-*a* concentrations in the NPSG. Subdomains of con-
 316 trasting mesoscale eddy character can be defined using the eddy polarity probability (P)
 317 (Chaigneau et al., 2009), defined

$$318 P(x, y) = \frac{F_A(x, y) - F_C(x, y)}{F_A(x, y) + F_C(x, y)}. \quad (4)$$

319 $F_A(x, y)$ ($F_C(x, y)$) is the number of times the pixel at location (x, y) was inside an an-
 320 ticyclone (cyclone) from 2000 to 2019. Anticyclonic eddy polarity is more frequent than
 321 cyclonic when $P > 0$. Figure 5a depicts the geographic distribution of P for RCLVs,
 322 revealing more anticyclonic activity north of 23°N , cyclonic domination to the southeast
 323 of Hawai‘i, and signatures of the Lee eddies to the west of the islands. We found distinct
 324 and sometimes dramatic differences in the chl-*a* responses between anticyclonic and cy-
 325 clonic eddies of the north, southeast, and Hawaiian Lee provinces. The monthly chl-*a*
 326 climatologies vary moderately by region (Fig. S5).

327 3.2.1 Northern Eddies

328 In the winter and spring (Fig. 5b, d) there are no substantial disparities in chl-*a*
 329 anomalies between northern RCLVs and SLA eddies. However, some differences emerge
 330 in the summer and fall (Fig. 5f, h), indicating an influence of eddy trapping on chloro-
 331 phyll patchiness in the surface ocean. Although Section 3.1 documents an overall increase
 332 in positive chl-*a* anomalies within RCLVs compared to SLA eddies, there are exceptions
 333 to this pattern in the north province. This emphasizes the need for focused regional and
 334 seasonal analyses and illustrates the complexity of biogeochemical response to mesoscale
 335 eddies.

336 Occurrences of positive δC_{clim} are more common in all types of anticyclones (rep-
 337 resented by the red curves in Fig. 5) than in the background during the northern fall and
 338 winter, up to approximately $0.0555 \text{ mg} \cdot \text{m}^{-3}$ in the winter and $0.0394 \text{ mg} \cdot \text{m}^{-3}$ in the
 339 fall. This aligns with global observations of elevated surface chl-*a* in wintertime anticy-
 340 clonic eddies in subtropical gyres (Dufois et al., 2016). During the summer and fall, an-
 341 ticyclonic RCLVs, but not SLA eddies, are likelier to have a negative chl-*a* anomaly than
 342 the background. This suggests that, in some cases, limited dilution in RCLVs yields a

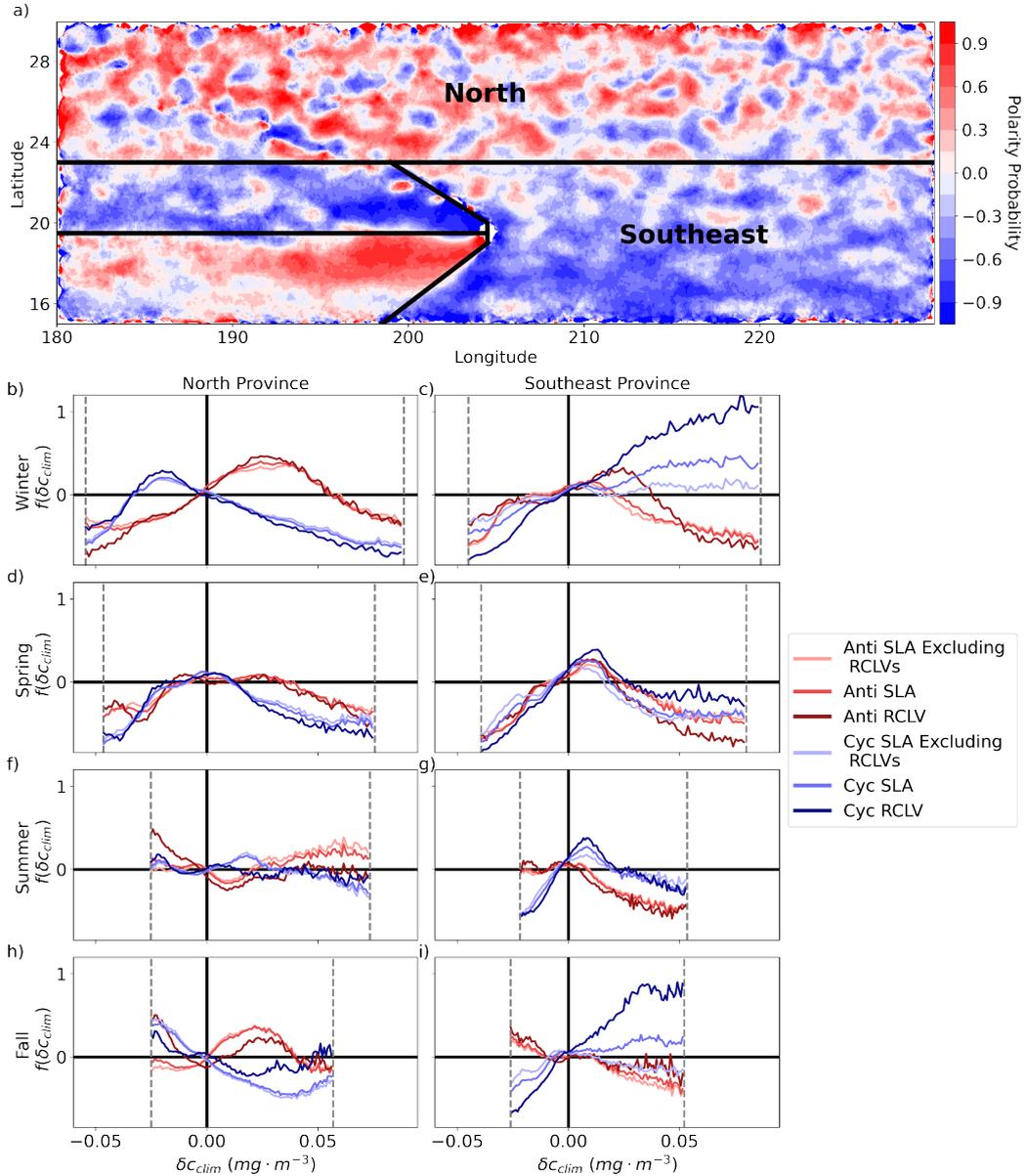


Figure 5. (a) RCLV polarity probability (Eq. 4). Red (blue) indicates that anticyclones (cyclones) are more common at the location. The black lines delineate mesoscale-driven provinces as defined in this study. (b-i) The relative difference in the probability density distribution of the climatological chl-*a* anomaly (δc_{clim}) from the background ($f(\delta c_{clim})$) for each eddy type. Each row corresponds with a season such that winter includes December through February. The dotted gray lines show the 1-99% quantiles of the background ocean for the season and region. These are the cutoff boundaries of the curves so that there is sufficient data underlying the calculations of $f(\delta c_{clim})$. Figures S6 and S7 show the corresponding probability density distributions.

343 local depletion of chl-*a*. On the other hand, SLA anticyclones have $f(\delta c_{clim}) > 0$ for
 344 more positive values of δc_{clim} than RCLVs in the summer and fall, indicating that eddy
 345 edge processes are responsible for enhancing chl-*a* concentrations within SLA-derived
 346 boundaries during these seasons.

347 Northern cyclonic eddies (represented by the blue curves in Fig. 5) generally ex-
 348 hibit fewer positive chl-*a* anomalies than the background across all seasons except the
 349 summer, where the distributions resemble the background ocean. Moreover, cyclonic RCLVs
 350 are less prone to have positive anomalies than SLA eddies in all seasons except for the
 351 fall, indicating that eddy trapping does not typically heighten chlorophyll levels in cy-
 352 clonic features of the northern province. In the winter and fall, northern cyclones of all
 353 types are likelier to display negative δc_{clim} values than the background.

354 3.2.2 Southeastern Eddies

355 The probability density distributions of δc_{clim} exhibit substantial disparities be-
 356 tween RCLVs and SLA eddies within the southeast province, especially in cyclones, for
 357 all seasons (Fig. 5c, e, i) except for the summer (Fig. 5g). Notably, anticyclones are much
 358 less prevalent than cyclones in the southeast province, so observations of anticyclones
 359 in this region play a small role in their overall effects in the gyre shown in Fig. 3. Con-
 360 versely, the high frequency of cyclones in the southeast contributes largely to the data
 361 in Fig. 4.

362 Southeastern anticyclonic eddies have distinct relationships with chl-*a* compared
 363 to their northern counterparts. In winter, anticyclonic RCLVs are more likely to exhibit
 364 positive δc_{clim} values but up to a lower threshold ($0.0374 \text{ mg}\cdot\text{m}^{-3}$) than in the north-
 365 east ($0.0542 \text{ mg}\cdot\text{m}^{-3}$). Unlike in the northeast, wintertime SLA anticyclones have dis-
 366 tributions more akin to the background. During spring, all anticyclonic eddy types are
 367 likelier than the background to have small positive δc_{clim} , up to $0.02 \text{ mg}\cdot\text{m}^{-3}$. How-
 368 ever, positive chl-*a* anomalies in southeastern anticyclones are unlikely in summer and
 369 fall, with all types in the fall showing a propensity for negative anomalies. This differs
 370 from the northern fall where positive δc_{clim} values are found in anticyclonic eddies and
 371 only RCLVs are likely to have negative anomalies.

372 Cyclonic δc_{clim} distributions in the southeast province differ greatly from the north.
 373 All cyclone types exhibit $f(\delta c_{clim}) < 0$ for negative δc_{clim} throughout the year, sug-
 374 gesting that cyclones consistently enhance chl-*a* in this region. During fall and winter,
 375 cyclonic RCLVs are much likelier than the background and SLA eddies to have positive
 376 δc_{clim} , especially at high values. Because the chl-*a* signatures of cyclonic SLA eddies ex-
 377 cluding RCLVs are similar to the background, positive anomalies in the SLA eddies can
 378 be largely attributed to RCLVs nested within their bounds. Thus, eddy trapping plays
 379 a prominent role in elevating local chl-*a* anomalies in cyclones of the southeast province.
 380 During spring and summer, southeastern cyclones are more likely to have positive anoma-
 381 lies of δc_{clim} within certain thresholds. This cutoff is $0.0182 \text{ mg}\cdot\text{m}^{-3}$ for cyclonic SLA
 382 eddies in the spring and $0.0263 \text{ mg}\cdot\text{m}^{-3}$ for RCLVs. In summer, it is $0.0192 \text{ mg}\cdot\text{m}^{-3}$
 383 for SLA eddies and $0.0246 \text{ mg}\cdot\text{m}^{-3}$ for RCLVs.

384 3.2.3 Hawaiian Lee Eddies

385 The ‘‘Hawaiian Lee Eddies’’ are large, long-lived features that consistently form in
 386 the Lee of the Hawaiian Islands (Fig. 6a). Anticyclones are generated by the shear in-
 387 stability between the eastward-flowing Hawaiian Lee Countercurrent and the westward-
 388 flowing North Equatorial Current (Calil et al., 2008; Yoshida et al., 2010; Y. Liu et al.,
 389 2012). Lee cyclones are produced from wind stress curl anomalies due to trade wind block-
 390 ing by the islands (Lumpkin, 1998; Dickey et al., 2008; Yoshida et al., 2010). The Hawai-
 391 ian Lee Countercurrent to the south and the westward-flowing Hawaiian Lee Current to

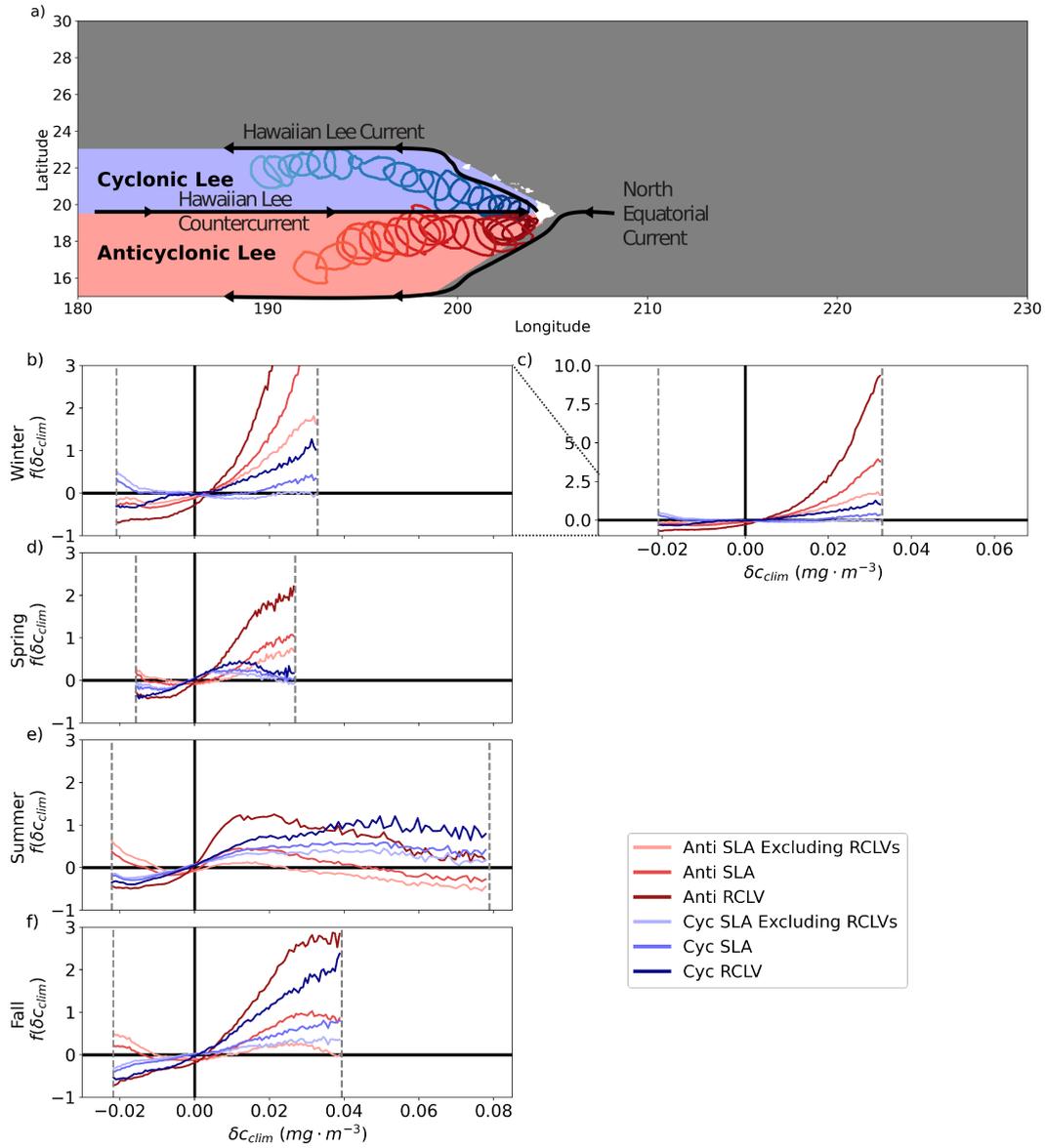


Figure 6. (a) Schematic of the currents that sustain the Hawaiian Lee Eddies. The region dominated by cyclones (anticyclones) is blue (red). The boundaries of two RCLVs are plotted every 16 days to show the common propagation pathways westward from the islands, where the darker contours represent young eddies and the lighter represent old eddies. (b-f) The relative difference in probability density distributions of the climatological chl-*a* (δc_{clim}) anomaly from the background ($f(\delta c_{clim})$). The dotted gray lines show the 1-99% quantiles of the background ocean for the season and region. These are the cutoff boundaries of the curves so that there is sufficient data underlying the calculations of $f(\delta c_{clim})$. Figure S8 shows the corresponding probability density distributions. Note that the y-axis differs from Figs. 3, 4, and 5 to accommodate larger values of $f(\delta c_{clim})$. Panel (c) includes the same information as (b) with a different y-axis to expose the entirety of the curves.

392 the north sustain the cyclonic vorticity, evident from bands in the sign of polarity prob-
 393 ability to the west of the Islands (Fig. 5a).

394 RCLVs and SLA Lee Eddies of both polarities drive more positive chlorophyll anom-
 395 alies than the background throughout the entire annual cycle (Fig. 6b-f), distinguishing
 396 them from features examined in Sections 3.2.1 and 3.2.2. RCLVs of both polarities have
 397 more positive chl-*a* anomalies than their corresponding SLA eddies and the background
 398 across all seasons. SLA eddies excluding RCLVs more closely resemble the background,
 399 highlighting the importance of trapping for locally enhancing the chl-*a* signature of the
 400 Hawaiian Lee Eddies.

401 Although the chl-*a* anomalies of the Lee Eddies are consistently positive, the mag-
 402 nitudes vary seasonally. In summer and fall, δc_{clim} distributions are similar between cy-
 403 clones and anticyclones, whereas, during the winter and spring, anticyclones are much
 404 more prone to positive anomalies. Even the leakiest anticyclonic features host positive
 405 δc_{clim} on par with cyclonic RCLVs during these seasons. Wintertime anticyclonic RCLVs
 406 host the most extreme positive δc_{clim} compared to all other eddies in the domain. Sum-
 407 mer and fall witness more negative anomalies of chl-*a* in anticyclonic SLA eddies than
 408 in the background, suggesting that chl-*a* can also be depleted in these features. This is
 409 only the case for cyclonic SLA eddies in the winter.

410 To summarize the regional variations, the response to anticyclones and cyclones
 411 is different in the north, but there is less contrast between SLA and RCLV features, sug-
 412 gesting a weak role for trapping there. In the southeast, there are differences between
 413 chl-*a* anomalies in SLA and RCLV features, suggesting a stronger role for trapping. In
 414 the Lee of the Hawaiian Islands, cyclones and anticyclones elevate chl-*a* and there is a
 415 strong signature of trapping in the contrast between SLA and RCLV features.

416 3.3 Evolution of Long-lived Coherent Eddies

417 The RCLV atlas enables the examination of chl-*a* patches as they evolve through
 418 time as quasi-isolated systems. Accordingly, we analyzed the in-eddy anomaly compared
 419 to the immediate surroundings, δc_{loc} (Eq. 3), as a function of age for the 245 RCLVs (109
 420 anticyclones, 136 cyclones) that maintained coherency for 150 or more days. Figure S9
 421 illustrates the consistent westward propagation of these features.

422 Figure 7 shows the magnitude of the local, Lagrangian chlorophyll anomalies with
 423 age, separated by season and province. The results reject the initial hypothesis that anoma-
 424 lies would decline over eddy lifetimes, although this is sometimes true. There is not a
 425 single, consistent pattern of change in δc_{loc} with age, rather it depends on the region,
 426 season, and polarity, complimenting the results of Section 3.2. For example, RCLVs in
 427 the north have minimally altered chl-*a* compared to their immediate surroundings ex-
 428 cept in wintertime anticyclones, which show some elevation relative to their surround-
 429 ings early in their lifetimes. Southeastern cyclonic RCLVs foster heightened chl-*a* re-
 430 lative to their surroundings in the winter and fall, and these anomalies do decline with
 431 eddy age, consistent with the initial hypothesis. Hawaiian Lee RCLVs, both cyclones and
 432 anti-cyclones, have dramatically enhanced chl-*a* relative to their surroundings through-
 433 out their lifetimes. Interestingly, δc_{loc} monotonically and substantially increases with eddy
 434 age in winter-time Lee Eddy anticyclones.

435 4 Discussion

436 Harnessing the temporal and spatial coverage of satellite observations, we measured
 437 the effects of mesoscale eddy trapping on chl-*a* in the NPSG over two decades. We com-
 438 pared Lagrangian (RCLV) and Eulerian (SLA) eddy atlases to differentiate the biolog-
 439 ical signatures of coherent eddies, dispersive eddies, and the background ocean. As hy-

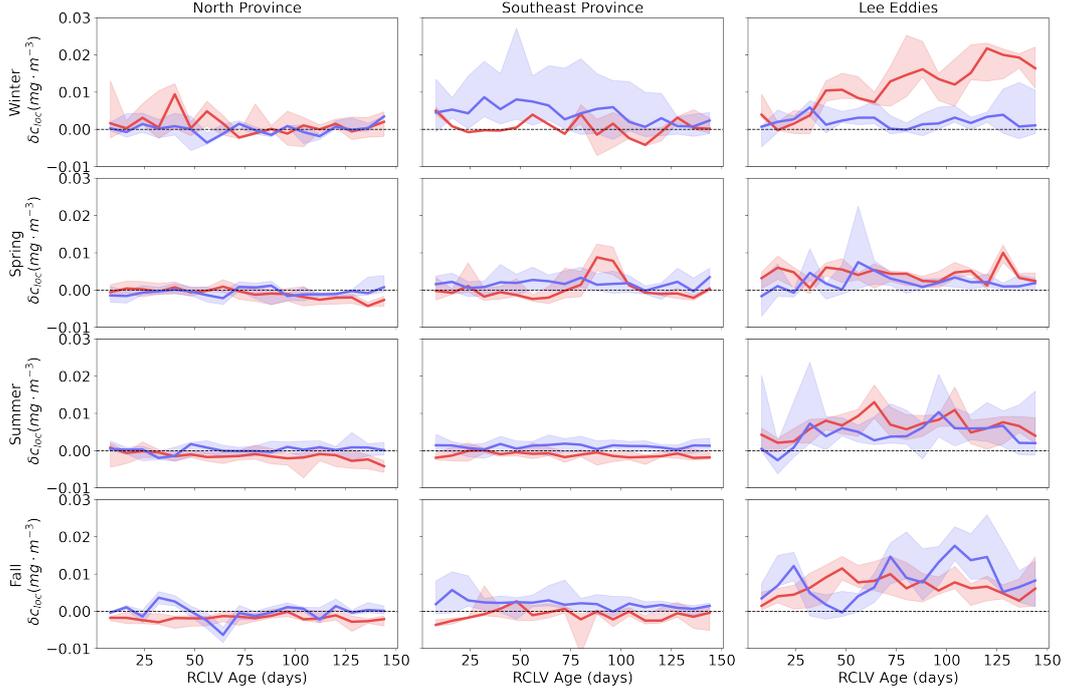


Figure 7. Local chl-*a* anomalies (δc_{loc}) in RCLVs with lifespans of 150+ days. Each column corresponds to a mesoscale-driven province and each row with the season. Cyclonic (anticyclonic) eddies are in blue (red). The solid lines show the median δc_{loc} by RCLV age, and the shaded areas are the ranges of the 25 to 75% quantiles.

440 pothesized, more positive climatological chl-*a* anomalies are observed in RCLVs than in
 441 SLA eddies or outside-eddy waters (Figs. 3, 4).

442 We find systematic regional and seasonal variations in surface chl-*a* anomalies in
 443 response to Lagrangian eddy trapping within the gyre (Figs. 5, 6). Notably, the mod-
 444 ulation of chl-*a* differs between cyclones and anticyclones in the northern NPSG province,
 445 though the impact of trapping is weakest there. Chl-*a* is strongly altered by trapping
 446 in the southeastern region, particularly in the Hawaiian Lee Eddies.

447 We did not find a consistent, overall pattern in the chlorophyll anomalies of coherent
 448 features as a function of age (Fig. 7). In the southeast province, winter-time cyclonic
 449 RCLVs have elevated chlorophyll relative to their surroundings- a signature that declines
 450 with age. In the Lee Eddy region, cyclones and anticyclones have strong positive chl-*a*
 451 anomalies relative to their surroundings, mostly independent of age, except in winter-
 452 time anticyclones for which the intensity of the anomaly grows significantly throughout
 453 eddy lifetimes.

454 4.1 Interpretation of Results with an Idealized Model

455 To interpret the comparisons of chl-*a* anomalies in SLA eddies and RCLVs, we con-
 456 sider the following idealized model that describes the biological and lateral mixing in-
 457 fluences on the surface chl-*a* concentration in an eddy (B_{in}):

$$458 \frac{dB_{in}}{dt} = \mu B_{in} - \Psi(B_{in} - B_{out}). \quad (5)$$

459 B_{out} is the outside-eddy concentration, μ is the net biological rate of change (e.g., growth,
460 mortality, photoacclimation) that may be driven by vertical processes, and Ψ is the lateral
461 fluid exchange rate at the eddy boundary.

462 A coherent eddy minimizes Ψ , whereas a leaky eddy has a higher lateral fluid ex-
463 change rate with outside-eddy waters. In the simple case where trapping and leaky ed-
464 dies have an equivalent net positive biological rate of change (μ) and a constant outside-
465 eddy concentration (B_{out}), the coherent eddy will have a more positive $\frac{dB_{in}}{dt}$, promot-
466 ing higher in-eddy concentrations (B_{in}). Indeed, the pattern generally observed across
467 the NPSG domain is more positive chl-*a* anomalies in RCLVs (Figs. 3, 4).

468 In the northern province, the chl-*a* anomalies in RCLVs do not differ substantially
469 from SLA eddies. When chl-*a* anomalies appear similar to the background for both types,
470 such as in the spring (Fig. 5d), this indicates that broadly, eddies are not perturbing the
471 nutrient environment in an influential way. When anomalies are positive in anticyclones
472 in the winter (Fig. 5b), Eq. 5 suggests that the net population growth rate (μ) must be
473 higher in SLA eddies than in coherent structures to maintain the same B_{in} . For exam-
474 ple, lateral dilution in northern wintertime SLA anticyclones may drive higher growth
475 rates or reduce the grazing pressure (Lehahn et al., 2017; Ser-Giacomi et al., 2023). When
476 SLA eddies contain more positive anomalies than RCLVs, such as anticyclones in the north-
477 ern summer and fall (Fig. 5f, h), potential mechanisms include increased vertical mix-
478 ing associated with submesoscale filaments on eddy edges (Calil & Richards, 2010; Pe-
479 terson et al., 2011; Mahadevan, 2016; F. Liu et al., 2017; L. Wang et al., 2018; Guo et
480 al., 2019), eddy-eddy interactions (Guidi et al., 2012), wind interactions, or horizontal
481 advection of chlorophyll-rich waters into the peripheries (Xu et al., 2019).

482 Some RCLVs have more negative chl-*a* anomalies than the background including
483 both polarities in the northern fall (Fig. 5h), wintertime cyclones in the north (Fig. 5b),
484 anticyclones in the northern summer (Fig. 5f), and southeastern anticyclones in the fall
485 (Fig. 5i). According to Eq. 5, a decrease in chl-*a* concentration within an eddy (B_{in}) oc-
486 curs when $\mu B_{in} < \Psi(B_{in} - B_{out})$. In a coherent eddy where Ψ is minimized, an anoma-
487 lously low μ will result in lower chl-*a*. Low nutrient supply rates due to deeper density
488 surfaces in anticyclones or high mortality may cause this. Alternatively, phytoplankton
489 cells may decrease their chlorophyll-to-carbon ratio if light availability increases (Geider,
490 1987; MacIntyre et al., 2000) from shoaling isopycnals in the interior of cyclones. RCLVs
491 may continue to harbor negative anomalies longer than SLA eddies because the chl-*a* deficit
492 is shielded from mixing with surrounding waters.

493 Negative anomalies are more likely to occur in SLA eddy boundaries than their RCLV
494 counterparts in some seasons in the Hawaiian Lee Eddy province (Fig. 6) and in cyclones
495 in the northern fall (Fig. 5h). This could occur if the grazing pressure is higher on eddy
496 edges than in the center, as found in some observations (Froneman & Perissinotto, 1996;
497 Goldthwait & Steinberg, 2008; Gødo et al., 2012; Schmid et al., 2020).

498 4.2 Implications of Regional and Seasonal Variability

499 The overall influence of trapping in the gyre (Figs. 3, 4) is obscured because the
500 differences in chl-*a* between RCLVs and SLA eddies are minimized in the north but max-
501 imized in the south. Furthermore, the magnitude and sign of satellite chl-*a* anomalies
502 differ regionally and seasonally. This study highlights the NPSG, but Gaube et al. (2014)
503 showed that the cross-correlation of sea surface height with chl-*a* anomalies is inconsis-
504 tent across the global ocean. Similarly, we expect that the relative impacts of Lagrangian
505 trapping on phytoplankton vary by location.

506 The Hawaiian Lee Eddies consistently form close to land, making them more ac-
507 cessible, and accordingly, have been heavily sampled. They have been presented as “rep-
508 resentative” features of the open ocean (Falkowski et al., 1991; Olaizola et al., 1993; Bidi-

509 gare et al., 2003; Benitez-Nelson et al., 2007), but our results demonstrate that the chl-
 510 *a* signatures of the Lee Eddies differ considerably from eddies in the surrounding gyre.
 511 Hawaiian Lee Eddies of all types elevate chl-*a* more than any other subdomain, notably
 512 in wintertime anticyclones, with trapping further enhancing local hot spots of chl-*a*. There-
 513 fore the underlying mechanisms for the biological response to eddies in the north, south-
 514 east, and Hawaiian Lee regions of the NPSG may not be equivalent.

515 4.3 Interpretation of the Response to Eddy Age

516 We hypothesized that perturbations to surface chl-*a* would dilute as eddies age. How-
 517 ever, we found a markedly varied pattern in the chl-*a* anomaly as a function of age for
 518 long-lived RCLVs that depends on the season and province. We again invoke a simple
 519 model to interpret these results, expanding upon Eq. 5.

520 The local anomaly (δc_{loc} ; Eq. 3) compares the chl-*a* concentration inside an eddy
 521 (B_{in}) relative to the concentration in the eddy's immediate surroundings (B_{out}). The
 522 change in chl-*a* concentration outside of the eddy is

$$523 \frac{dB_{out}}{dt} = \mu B_{out} + \Psi \left(\frac{A_{in}}{A_{out}} \right) (B_{in} - B_{out}), \quad (6)$$

524 where A_{in} is the area of the eddy and A_{out} is the area of the annulus from the eddy bound-
 525 ary to double the radius. In this simplified case, we neglect the influences of mixing with
 526 waters beyond the annulus, vertical processes, and acclimation of pigments.

527 The rate of change in δc_{loc} is

$$528 \frac{d}{dt}(\delta c_{loc}) = \frac{dB_{in}}{dt} - \frac{dB_{out}}{dt}. \quad (7)$$

529 Now consider the case where μ is equivalent inside and outside an eddy. This is more
 530 likely to occur toward the end of an eddy's life when perturbations due to eddy pump-
 531 ing and eddy-wind interactions are dampened (Huang et al., 2017). By assuming the fea-
 532 ture is circular ($A_{in} = \pi r^2$), we substitute Eqs. 5 and 6 into Eq. 7:

$$533 \frac{d}{dt}(\delta c_{loc}) = \left(\mu - \frac{4}{3}\Psi \right) (B_{in} - B_{out}). \quad (8)$$

534 Intuitively, Eq. 8 indicates that a larger Ψ (i.e., a leakier boundary) will cause chl-*a* anoma-
 535 lies in eddies to dilute more rapidly (Fig. S10). A positive $\frac{d}{dt}(\delta c_{loc})$ is sustained when
 536 $\mu > \frac{4\Psi}{3}$ and $B_{in} > B_{out}$. Since chl-*a* is anomalously high in Hawaiian Lee RCLVs, these
 537 features are most likely to meet both conditions, consistent with the results of Fig. 7.
 538 In most cases, however, an eddy-associated chl-*a* anomaly will decay via lateral dilution
 539 without sustained net positive growth. In light of this, we suggest that the biological rate
 540 of change in the most isolated eddy environments tends to be on par or smaller than the
 541 dilution rate; anomalies stimulated in dispersive SLA eddies are diluted even faster.

542 4.4 Limitations and Future Investigation

543 Satellite-observed changes in chl-*a* at the mesoscale remain enigmatic concerning
 544 the underlying ecological dynamics because chlorophyll is not a direct measurement of
 545 phytoplankton biomass. For example, it is unknown whether elevated chl-*a* in winter-
 546 time subtropical gyre anticyclones is due to increased productivity (Dufois et al., 2016)
 547 or changes in the cellular chlorophyll-to-carbon ratio due to photoacclimation (Corne-
 548 et al., 2021; He et al., 2021; Strutton et al., 2023). While both can be true (Su et al., 2021),
 549 higher fish catch occurs in anticyclones compared to cyclones around the Hawaiian Is-
 550 lands (Arostegui et al., 2022) potentially suggesting that increased phytoplankton pro-
 551 ductivity supports higher trophic levels.

552 Changes in chl-*a* may also indicate a change in community structure. Waga et al.
 553 (2019) used a size structure ocean color algorithm to infer that anticyclones in subtrop-
 554 ical gyres support larger phytoplankton cells than cyclonic eddies. Hernández-Carrasco
 555 et al. (2023) found that Lagrangian coherence promoted diatom blooms in the Mediter-
 556 ranean Sea, but to what extent phytoplankton community structure may differ in RCLVs
 557 and SLA eddies remains an open question. Further, a succession of phytoplankton types,
 558 as found in a model simulation of Hawaiian Lee Eddies (Friedrich et al., 2021), may un-
 559 derlie observed chl-*a* concentrations. Retrospective analysis of existing observations from
 560 eddies and targeted in situ campaigns would provide valuable insight into the relation-
 561 ship between eddy trapping and phytoplankton functional types.

562 Although satellites are the only ocean observing systems that obtain nearly full spa-
 563 tial coverage within days, a fundamental limitation is the restriction to the surface. Ed-
 564 dyes affect subsurface chl-*a* in the NPSG by altering the depth of the deep chlorophyll
 565 maximum (Gaube et al., 2019; Xiu & Chai, 2020) and the vertical community structure
 566 (Olaizola et al., 1993; Brown et al., 2008; Fong et al., 2008; Barone et al., 2019). There-
 567 fore, the biological response to eddies at depth may differ from the surface signature (Huang
 568 & Xu, 2018; Zhao et al., 2021). The size of Lagrangian coherent boundaries may also
 569 change with depth (Nencioli et al., 2008; Ntaganou et al., 2023). Another limitation of
 570 satellite chl-*a* observations is missing data from cloud coverage including during storms,
 571 which can stimulate phytoplankton blooms in eddies (X. Liu et al., 2009; Shang et al.,
 572 2015; Villar et al., 2015; Chacko, 2017; Mikaelyan et al., 2020). Co-locating the bounds
 573 of RCLVs with autonomous vehicles and shipboard observations are promising avenues
 574 of future exploration to circumnavigate satellite limitations.

575 **5 Conclusion**

576 By co-locating satellite chl-*a* observations with two decades of Eulerian and La-
 577 grangian coherent eddies in the NPSG, we show more positive chl-*a* anomalies are found
 578 within the bounds of RCLVs compared to SLA eddies. This is consistent with the hy-
 579 pothesis that lateral processes dilute local, recent changes to biomass in dispersive ed-
 580 dies. However, there are significant regional and seasonal differences within the NPSG,
 581 and trends in chl-*a* anomalies as a function of eddy age differ even in the most coher-
 582 ent features. Based on these results, we expect that the response to eddy trapping is vari-
 583 able across the global ocean due to the complexity of mesoscale biophysical interactions.
 584 Finally, we argue that the effects of lateral dilution and the diversity of trapping behav-
 585 iors must be considered when evaluating biogeochemical states in eddies to accurately
 586 determine the contribution of mesoscale processes to global primary production.

587 **Open Research Section**

588 This study used CMEMS Level 4, 1/4° SLA and geostrophic velocity gridded global
 589 ocean dataset, Version 008_047 (CMEMS, 2020). The 8-day average chl-*a* product is pro-
 590 duced by OC-CCI (Version 6.0) and distributed by the European Space Agency (Sathyendranath
 591 et al., 2019). We used the OceanEddies MATLAB software to detect and track Eulerian
 592 SLA eddy contours. The software was obtained from [https://github.com/ifrenger/
 593 OceanEddies](https://github.com/ifrenger/OceanEddies) (last access: 13 October 2021). The OceanParcels v2.0 Python package was
 594 used to run Lagrangian particle simulations (Delandmeter & van Sebille, 2019). The fig-
 595 ures were created with Matplotlib 3.3.4 (Caswell et al., 2021; Hunter, 2007).

596 The Python software developed for this study is available on GitHub and Zenodo
 597 (Jones-Kellett, 2023b). The NPSG RCLV dataset is publicly available, distributed by
 598 Simons CMAP at https://simonscmf.com/catalog/datasets/RCLV_atlas_version2
 599 (Jones-Kellett, 2024).

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604 **Acronyms**

605 **Chl-*a*** Chlorophyll-*a*
 606 **CMEMS** Copernicus Marine Service
 607 **LAVD** Lagrangian Averaged Vorticity Deviation
 608 **NPSG** North Pacific Subtropical Gyre
 609 **OC-CCI** Ocean Color Climate Change Initiative
 610 **RCLV** Rotationally Coherent Lagrangian Vortex
 611 **SLA** Sea Level Anomaly

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