

1 **Nitrogen biogeochemistry of adjacent mesoscale eddies in the North Pacific**  
2 **Subtropical Gyre**

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9 **Key Points**

- 10 • Subsurface nutrients along isopycnals were higher at the edges of a cyclonic eddy than  
11 surroundings, indicating shallow remineralization.
- 12 • Nitrate isotope ratios evidenced nitrate partial assimilation below the euphotic zone,  
13 coincident with negative preformed nutrients.
- 14 • Biological N<sub>2</sub> fixation couldn't be inferred from <sup>15</sup>N/<sup>14</sup>N of sinking particles compared to  
15 subsurface nitrate due to eddies' non-steady state.

16 **Key words:** mesoscale eddies, N stable isotope, N<sub>2</sub> fixation

17 **Abstract**

18 We examined the nitrogen (N) biogeochemistry of adjacent cyclonic and anticyclonic eddies  
19 near Hawai'i in the North Pacific Subtropical Gyre (NPSG) and explored mechanisms that may  
20 sustain productivity in the cyclone after the initial intensification stage. The top of the nutricline  
21 was uplifted into the euphotic zone in the cyclone and depressed in the anticyclone. Subsurface  
22 nutrient concentrations and apparent oxygen utilization at the cyclone's inner periphery were  
23 higher than expected from isopycnal displacement, suggesting that shallow remineralization of  
24 organic material generated excess nutrients in the subsurface. The excess nutrients may  
25 provide a supply of subsurface nutrients to sustain productivity in maturing eddies. The shallow  
26 remineralization also raises questions regarding the extent to which cyclonic eddies promote  
27 deep carbon sequestration in subtropical gyres such as the NPSG. An upward increase in nitrate  
28  $^{15}\text{N}/^{14}\text{N}$  isotope ratios below the euphotic zone, indicative of partial nitrate assimilation,  
29 coincided with negative preformed nutrients – potentially signaling heterotrophic bacterial  
30 consumption of carbon-rich (nitrogen-poor) organic material. The  $^{15}\text{N}/^{14}\text{N}$  of material collected  
31 in shallow sediment traps was significantly higher in the cyclone than the anticyclone and  
32 showed correspondence to the  $^{15}\text{N}/^{14}\text{N}$  ratio of the nitrate supply, which is acutely sensitive to  
33 sea level anomaly in the region. A number of approaches were applied to estimate the  
34 contribution of  $\text{N}_2$  fixation to export production; results among approaches were inconsistent,  
35 which we attribute to non-steady state conditions during our observation period.

36 **Plain Language Summary**

37 Mesoscale eddies are ubiquitous physical manifestations of “swirling water” throughout the  
38 ocean, equated with the “weather” of the ocean. They have distinct properties compared to  
39 surroundings, transporting heat, salt and nutrients horizontally and vertically. Their influence  
40 on ocean ecosystems is difficult to study due to their ephemeral nature. We examined the  
41 nitrogen (N) biogeochemistry of adjacent cyclonic (counter-clockwise in the northern  
42 hemisphere) and anticyclonic (clockwise in the northern hemisphere) eddies in the North  
43 Pacific Subtropical Gyre. Nitrogen, in the form of nitrate, is an essential nutrient that promotes  
44 phytoplankton growth in the sun-lit surface. Nutrients were higher than surroundings directly

45 below the sun-lit surface of the cyclonic eddy, signaling the relatively shallow decomposition of  
46 sinking organic matter. This shallow nutrient reservoir at the subsurface may fertilize the  
47 surface of mature and decaying cyclonic eddies from mixing. Nitrate N isotope ratio signaled  
48 nitrate consumption below the sun-lit surface, potentially by non-photosynthetic microbes  
49 assimilating carbon-rich material. We had hoped to exploit depth profiles of nitrate N isotopes  
50 ratios to assess the contributions of a specific microbial metabolism (“di-nitrogen fixation”) to  
51 the rain of particles out of the surface, however the disparate timing of these processes within  
52 these eddies made this exercise uncertain.

### 53 **1 Introduction**

54 Mesoscale eddies are ubiquitous features in the ocean (Chelton et al., 2011), facilitating the  
55 lateral and vertical transport of heat, salt, and nutrients (Conway et al., 2018; Dong et al., 2014;  
56 Gupta et al., 2022; Spingys et al., 2021; Zhang et al., 2014). They can trap water and  
57 biogeochemical signatures in their interior as they propagate (Chelton et al., 2011; D’Ovidio et  
58 al., 2013; Early et al., 2011). The vertical motions of density surfaces in eddies influence their  
59 biogeochemistry by modulating the depth of the nutricline relative to euphotic zone. Doming  
60 isopycnals in cyclonic eddies increase the nutrient supply to the euphotic zone, whereas  
61 deepening isopycnals in anticyclonic eddies lower the nutrient supply (Falkowski et al., 1991;  
62 Gaube et al., 2014; McGillicuddy & Robinson, 1997; McGillicuddy, 2016; McGillicuddy et al.,  
63 1998; Siegel et al., 1999). The nutrient flux induced by mesoscale eddies is cited to account for  
64 as much as 50 % of new production in the subtropical ocean (McGillicuddy et al., 1998).

65 The North Pacific Subtropical Gyre (NPSG) is characterized by low surface nutrients and low  
66 biomass (Karl et al., 1997; Karl, 1999; Karl & Church, 2017). Persistent thermal stratification of  
67 the upper ocean isolates the nutricline from the influence of wind mixing, impeding the delivery  
68 of nutrients into euphotic zone (Dore et al., 2008; Letelier et al., 2004). Near Ocean Station  
69 ALOHA (A Long-term Oligotrophic Habitat Assessment, located at 22°45’ N and 158° W) in the  
70 NPSG, mesoscale eddies occur during 30 % of the time, driving changes in nutrient delivery and  
71 plankton community structure in the deep euphotic zone (Barone et al., 2019; Benitez-Nelson  
72 et al., 2007; Bidigare et al., 2003; Johnson et al., 2010; Letelier et al., 2000; Nicholson et al.,  
73 2008; Rii et al., 2008; Seki et al., 2001). Cyclonic eddies can stimulate primary productivity

74 relative to surroundings from the initial “eddy pumping” of nutrients via the shoaling of  
75 isopycnals (e.g., Falkowski et al., 1991; Siegel et al., 1999). Increased subsurface productivity  
76 persists throughout the mature and decaying stages of cyclonic eddies, ostensibly maintained  
77 by the diapycnal mixing of nutrients into the euphotic zone (Barone et al., 2022; Benitez-Nelson  
78 et al., 2007; Siegel et al., 1999).

79 Cyclonic eddies are also thought to promote the export of carbon to depths where CO<sub>2</sub> is  
80 effectively sequestered from the atmosphere, although observations corroborating this notion  
81 in subtropical gyres remain scant. In this regard, Bidigare et al. (2003) described enhanced  
82 <sup>234</sup>Th-derived carbon export in a cyclonic eddy in the lee of Hawai’i. However, a number of  
83 studies reported no increase in particulate organic material export in subtropical cyclonic  
84 eddies, but otherwise recorded enhanced silica and particulate inorganic carbon export relative  
85 to background (Barone et al., 2022; Benitez-Nelson et al., 2007; Buesseler et al., 2008; Maiti et  
86 al., 2008; Rii et al., 2008).

87 The stoichiometry of new and export production may also be influenced by mesoscale  
88 eddies. A characteristic feature of the NPSG (and the Sargasso Sea) is the surface drawdown of  
89 dissolved inorganic carbon that occurs in the conspicuous absence of nutrients. The subsurface  
90 drawdown of dissolved oxygen, in turn, occurs in the absence of stoichiometrically proportional  
91 nutrient production (Abell et al., 2005; Johnson et al., 2010). While these features are not  
92 definitively explained (e.g., Barone et al., 2022; Johnson et al., 2010; Letscher & Villareal, 2018),  
93 they may portend of the surface production and shallow remineralization of carbon-rich organic  
94 material (Abell et al., 2005; Emerson & Hayward, 1995; Fawcett et al., 2018). Mesoscale eddies  
95 may modulate these stoichiometric features, potentially offering insights into their origins.

96 Finally, mesoscale eddies in subtropical gyres are cited to influence the magnitude of  
97 marine dinitrogen (N<sub>2</sub>) fixation as well as the community composition of N<sub>2</sub> fixing organisms  
98 (Dugenne et al., 2023). The biomass of diazotrophic cyanobacteria and N<sub>2</sub> fixation rates are  
99 generally higher in anticyclonic eddies compared to surroundings (Davis & McGillicuddy, 2006;  
100 Liu et al., 2020; Löscher et al., 2016), including at Station ALOHA (Dugenne et al., 2023; Fong et  
101 al., 2008). Conversely, enhanced N<sub>2</sub> fixation was observed in cyclonic eddies in the Northwest  
102 Subtropical Pacific, a dynamic ascribed to excess surface phosphate and an elevated iron supply

103 from depth (Yuan et al., 2023). N<sub>2</sub> fixation reportedly fuels a substantive fraction of new and  
104 export production in the NPSG (Barone et al., 2022; Böttjer et al., 2017; Church et al., 2009;  
105 Karl et al., 1997). Hence, if mesoscale eddies enhance N<sub>2</sub> fixation they may also enhance export  
106 production.

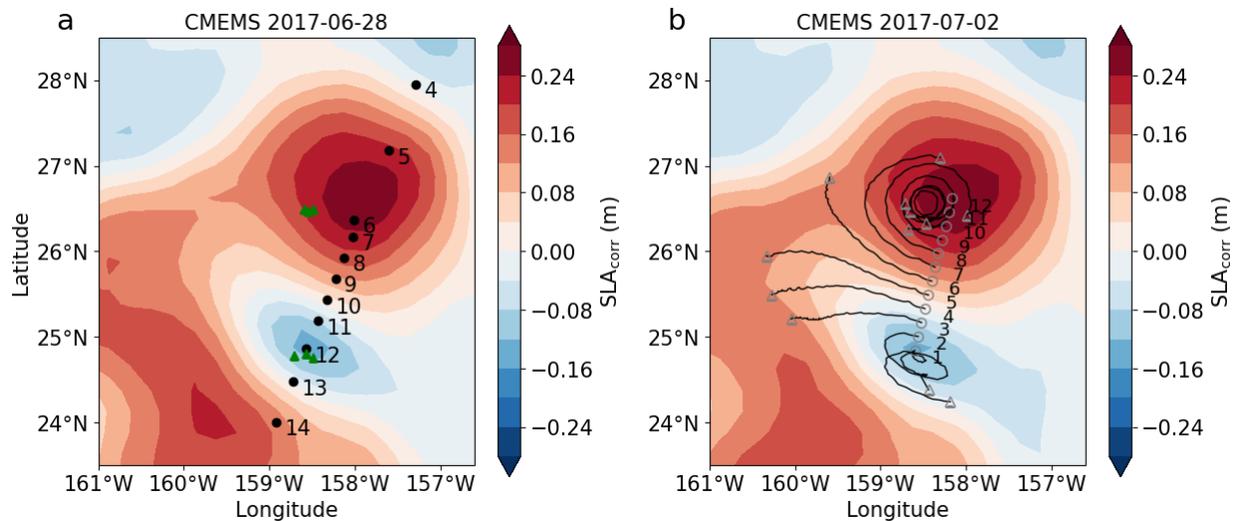
107 Adjacent mesoscale eddies of opposite polarity were sampled as part of the MESO-SCOPE  
108 (Microbial Ecology of the Surface Ocean-Simons Collaboration on Ocean Processes and Ecology)  
109 expedition in June – July of 2017 (Barone et al., 2022). Both eddies were generated in the  
110 central NPSG away from the continental margins and drifted westward (Barone et al., 2022).  
111 The cyclone and anticyclone were extreme mesoscale events relative to historical Eulerian  
112 observations at Station ALOHA (Barone et al., 2022). At the time of sampling, the cyclone was in  
113 a weakening phase, while the anticyclone was in a stable phase (Dugenne et al., 2023). The  
114 cyclone sustained higher rates of primary production in the deep euphotic zone than both the  
115 anticyclone and mean conditions at Station ALOHA (Hawco et al., 2021). The center of the  
116 cyclonic eddy hosted a more abundant community of eukaryotic phytoplankton at the deep  
117 chlorophyll maximum that resulted in larger chlorophyll concentrations, which was sustained  
118 by the increased diapycnal nutrient flux (Barone et al., 2022). Nitrate and O<sub>2</sub> had an anomalous  
119 stoichiometry in both of the mesoscale features (Barone et al., 2022). High depth-integrated  
120 rates of N<sub>2</sub> fixation (670 μmol N m<sup>-2</sup> d<sup>-1</sup>) were observed in the anticyclone, concurrent with the  
121 onset of a *Crocospaera* bloom (Dugenne et al., 2023).

122 We obtained opportunistic samples from the campaign to characterize the stable N isotope  
123 ratios (<sup>15</sup>N/<sup>14</sup>N) of nitrate, which we interpret in the context of corresponding hydrography and  
124 biogeochemical properties. Nutrient distributions provide evidence of shallow remineralization,  
125 with implications for the mechanisms sustaining productivity in cyclonic eddies. Nitrate isotope  
126 ratios at the top of the nutricline suggest that deviations from canonical nutrient  
127 remineralization stoichiometry may derive from heterotrophic nitrate assimilation. An attempt  
128 to infer the contribution of biological N<sub>2</sub> fixation to the export flux from a nitrogen isotope mass  
129 balance of particles collected in shallow sediment traps relative to nitrate upwelled to the  
130 euphotic zone illustrates inherent limitations of this approach in a system that violates steady  
131 state assumptions.

## 132 2 Materials and Methods

133 Two eddies of opposite polarity in the north of Hawai'i islands were surveyed during the  
134 MESO-SCOPE expedition from June 26 to July 15, 2017, near station ALOHA. A comprehensive  
135 description of the survey is detailed in Barone et al. (2022). Briefly, the eddies were identified  
136 from sea level anomaly (SLA) based on the satellite altimetry product distributed by Copernicus  
137 Marine Environment Monitoring Service (CMEMS). SLA was corrected for interannual trend and  
138 seasonal cycle, termed  $SLA_{corr}$  (Barone et al., 2019). The corrected sea level anomaly values  
139 differed by more than two standard deviations from mean values recorded at Station ALOHA  
140 between 1993 and 2018 (Barone et al., 2022). Eddies were tracked with the Mesoscale Eddy  
141 Trajectories Atlas (META3.2 delayed time all satellite version) distributed by AVISO+ (Archiving,  
142 Validation and Interpretation of Satellite Ocean data), as well as with a simplified regional  
143 tracking algorithm detailed in Barone et al. (2022).

144 An initial survey was conducted along a transect bisecting both eddy centers to  
145 characterize surface hydrography, which included underway conductivity, temperature, and  
146 depth measured with an underway CTD (Teledyne). Current speed and direction were  
147 measured with a hull-mounted acoustic doppler current profiler (ADCP, Workhorse 300 kHz,  
148 Teledyne). Twelve (12) water column Photosynthetically Active Radiation (PAR) profiles (Fig. 1a)  
149 were measured (near local noon) near the center of the cyclone and anticyclone between July 4  
150 and 11, 2017, using a free-falling optical profiler with data binned to 1-m intervals (Satlantic  
151 HyperPro, Sea-Bird Scientific, Bellevue, WA, USA). After the initial survey, the upper ocean  
152 biogeochemistry was characterized at 11 stations along the transect (Fig. 1a) using a rosette  
153 mounted with 10 L Niskin® bottles, and profiling instruments including a CTD (Sea-Bird 911  
154 plus), a chlorophyll fluorometer (Seapoint SCF), a polarographic  $O_2$  sensor (SBE 43, Sea-Bird)  
155 and a transmissometer (c-star, Sea-Bird). The chlorophyll fluorometer was calibrated with  
156 chloropigment concentrations and the  $O_2$  sensor with determinations obtained by Winkler  
157 titrations, consistent with protocols adopted by HOT (Carpenter, 1965; Tupas et al., 1997).  
158 Water samples for nutrient and nitrate isotope analyses were collected at ~25 m intervals from  
159 5 m to 500 m with higher vertical resolution (~5 m intervals) near the deep chlorophyll  
160 maximum (DCM). Samples were frozen (-20°C) after collection pending analysis.



161

162 **Figure 1. (a) Hydrographic stations along the transect. Contours are corrected sea level**  
 163 **anomaly ( $SLA_{corr}$ ) during the MESO-SCOPE sampling (June 28, 2017). Green triangles are**  
 164 **locations of PAR profiles. (b) Sediment trap deployment (open circles) and recovery**  
 165 **(triangles) positions, with lines denoting trajectories. Contours are  $SLA_{corr}$  at the time of**  
 166 **sediment trap deployment (July 2, 2017).**

167 Twelve (12) free-drifting surface-tethered sediment traps were deployed at 150 m across  
 168 the eddy centers at  $\sim 18$  km spacing to collect sinking particles. Traps were retrieved after 10 –  
 169 13 days (Fig. 1b). The surface-tethered array included 12 individual particle interceptor trap  
 170 collector tubes (Knauer et al., 1979) processed following the HOT (Hawaii Ocean Time-series)  
 171 program methods (Karl & Lukas, 1996).

172 The concentrations of nitrate plus nitrite (N+N) and soluble reactive phosphorus (herein  
 173 termed phosphate,  $PO_4^{3-}$ ) were analyzed using a SEAL Autoanalyzer III using standard  
 174 colorimetric protocols (Dore et al., 1996; Foreman et al., 2016). Samples with N+N  
 175 concentrations less than  $100 \text{ nmol L}^{-1}$  were analyzed using a chemiluminescent method  
 176 (Foreman et al., 2016).

177 The N isotope ratios of nitrate ( $^{15}\text{N}/^{14}\text{N}$ ) in water samples from station 4 to 13 were  
 178 measured with the denitrifier method (Casciotti et al., 2002; Sigman et al., 2001) for  
 179 concentrations exceeding  $0.5 \text{ } \mu\text{mol L}^{-1}$ . Nitrate was converted to nitrous oxide ( $\text{N}_2\text{O}$ ) by cell  
 180 concentrates of the denitrifying bacterial strain *Pseudomonas chlororaphis* (ATCC 43928,  
 181 Manassas, VA, USA), which lacks the terminal  $\text{N}_2\text{O}$  reductase. The  $\text{N}_2\text{O}$  gas was extracted and

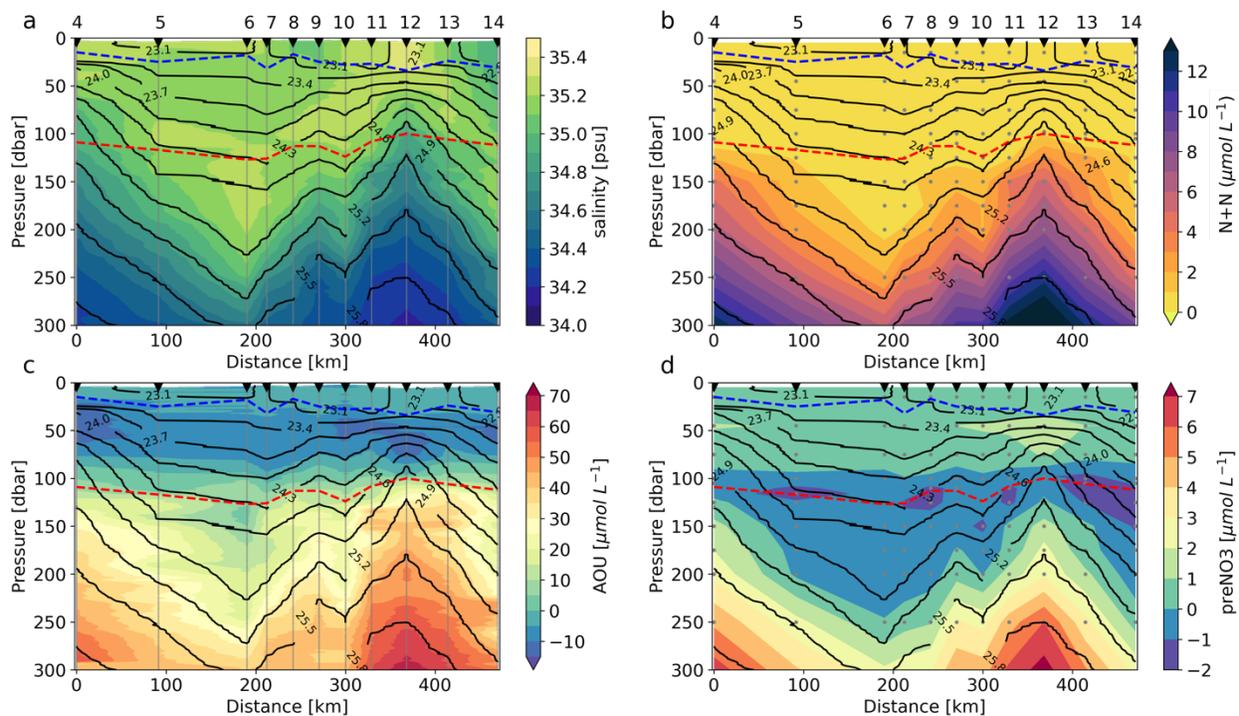
182 purified using a custom-modified Thermo Fisher Scientific Gas Bench II fronted by dual cold  
 183 traps and a GC Pal autosampler, and analyzed with a Thermo Delta V Advantage continuous  
 184 flow gas chromatograph isotope ratio mass spectrometer (Casciotti et al., 2002; McIlvin &  
 185 Casciotti, 2011). The N isotope ratios are expressed in delta ( $\delta$ ) notation in units of per mil (‰)  
 186 vs. a standard material (N<sub>2</sub> gas in the air):  $\delta^{15}\text{N}_{\text{sample}} = [({}^{15}\text{N}/{}^{14}\text{N})_{\text{sample}}/({}^{15}\text{N}/{}^{14}\text{N})_{\text{standard}} - 1] \times$   
 187 1000. Nitrate isotopic analyses were calibrated to internationally recognized nitrate reference  
 188 materials IAEA-NO3 (International Atomic Energy Agency, Vienna, Austria) and USGS-34  
 189 (National Institute of Standards and Technology, Gaithersburg, MD, USA), with reported  $\delta^{15}\text{N}$   
 190 values of 4.7 ‰ and -1.8 ‰ (vs. air). Working solutions were diluted from primary stocks into  
 191 nutrient-free seawater to concentrations bracketing sample concentrations to account for  
 192 potential matrix effects (Weigand et al., 2016; Zhou et al., 2022). Individual samples were  
 193 measured 3 – 9 times to achieve an analytical uncertainty to  $\leq 0.3$  ‰. The oxygen isotope  
 194 ratios of nitrate ( $\delta^{18}\text{O}_{\text{NO}_3}$ ) were not measured concurrently as we did not secure sufficient  
 195 sample volumes to estimate these reliably (*see* Zhou et al., 2022).

196 We define the mixed layer depth as the first depth where the density was  $0.03 \text{ kg m}^{-3}$   
 197 greater than the near-surface value at 10 m (de Boyer Montégut, 2004). Because PAR profiles  
 198 were limited to locations near the center of the cyclone and anticyclone, we equate the DCM to  
 199 the base of the euphotic zone. We note that this approximation is not entirely accurate as the  
 200 average depth of the euphotic zone (defined as the depth with 1% of the surface downwelling  
 201 PAR irradiance) was  $103 \pm 4$  m in the cyclone and  $108 \pm 1$  m in the anticyclone, whereas that of  
 202 DCM was  $106 \pm 5$  m in the cyclone, and  $119 \pm 6$  m in the anticyclone. From the dissolved oxygen  
 203 measurements, we derive the Apparent Oxygen Utilization (AOU) to discern the extent of  
 204 remineralization, defined as the difference between the O<sub>2</sub> concentration at saturation and the  
 205 observed O<sub>2</sub> ( $\text{AOU} (\mu\text{mol L}^{-1}) = O_{2 \text{ saturation}} - O_{2 \text{ observed}}$ ). We also derive the concentration  
 206 of preformed nitrate ( $\text{preNO}_3^-$ ), which is the difference between the observed [N+N] and that  
 207 expected from remineralization, such that  $\text{preNO}_3^- = [\text{N} + \text{N}]_{\text{observed}} - \text{AOU}/R_{\text{O}_2/\text{N}}$ , where  
 208  $R_{\text{O}_2/\text{N}} = 10.5$ , the stoichiometric ratio of O<sub>2</sub> consumption to nitrate regeneration during  
 209 remineralization (Anderson, 1995).

### 210 **3 Results**

### 211 3.1 Physical characteristics of the eddies

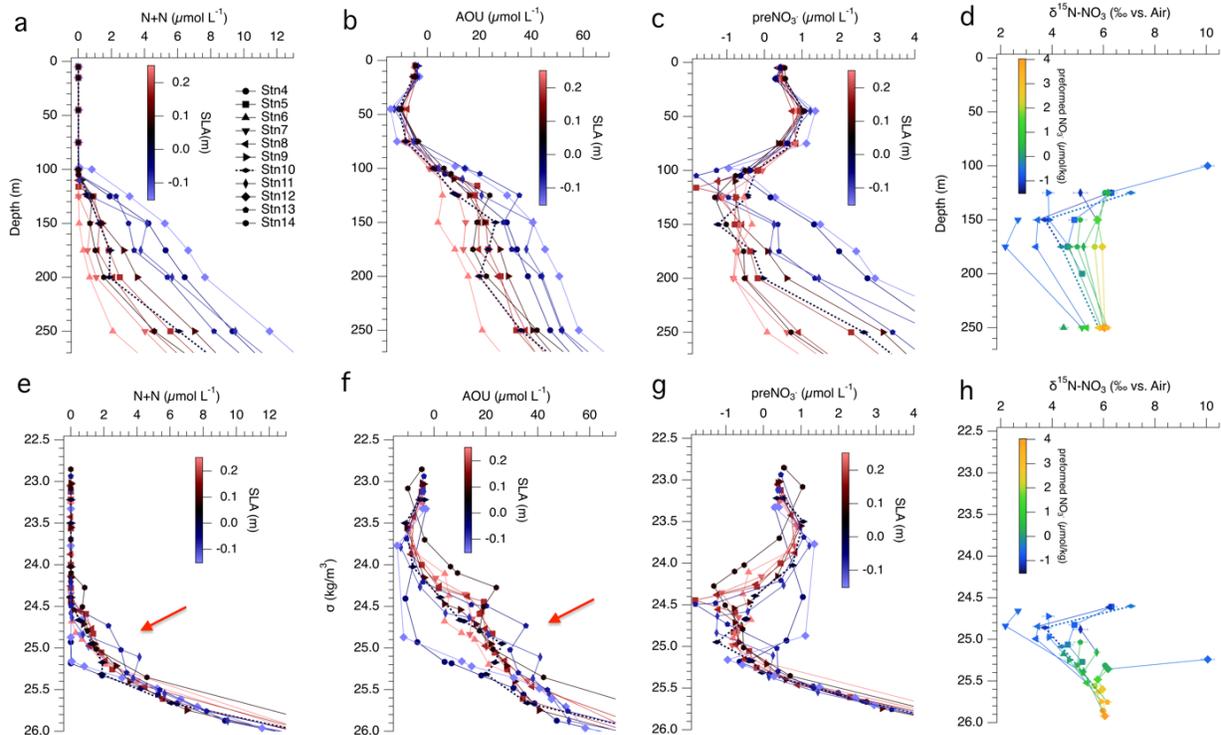
212 The adjacent cyclone and anticyclone were characterized by respective shoaling vs.  
 213 deepening of isohalines and isopycnals (Fig. 2a). The surface mixed layer depth varied from 15  
 214 to 34 m, similar in the center of the anticyclone (station 6; 18 m) and cyclone (station 12; 34 m).  
 215 Both cyclone and anticyclone were nonlinear, characterized by a ratio of rotational fluid speed  
 216 ( $U$ ) to translation speed ( $c$ ) larger than 1,  $U/c > 1$ , in the upper 600 m (Supporting Information  
 217 Text S1; Fig. S1). In the upper 200 m, the value of  $U/c$  was  $> 4$ , suggesting that the eddies  
 218 trapped water within their interiors as they propagated (Fig. S1; Chelton et al., 2011; Flierl,  
 219 1981). At the time of sampling, the cyclone was 134-day old and the anticyclone was 48-day old  
 220 based on the AVISO+ META3.2 Delayed Time all satellites version. The regional algorithm of  
 221 Barone et al. (2022) characterizes the cyclone as 240-day old and the anticyclone was 78-day  
 222 old.



223  
 224 **Figure 2.** Depth sections along the hydrographic transect of (a) salinity, (b) N+N  
 225 concentration, (c) AOU and (d) preformed nitrate ( $\text{preNO}_3^-$ ). The contours are potential  
 226 density surfaces. The red and blue dashed lines denote the depth of the chlorophyll  
 227 maximum and the depth of the mixed layer, respectively.

### 228 3.2 Biogeochemical characteristics of the eddies

229 The DCM, situated between 100 – 127 m among stations, was assumed to mark the base of  
230 the euphotic zone, with the shallowest DCM in the center of the cyclone and the deepest in the  
231 anticyclone (Fig. 2). N+N at all stations was  $< 0.01 \mu\text{mol L}^{-1}$  in the surface mixed layer. N+N at  
232 the DCM at the center of the cyclone (100 m) was  $0.8 \mu\text{mol L}^{-1}$ , compared to  $< 0.01 \mu\text{M}$  at the  
233 DCM at the center of the anticyclone (127 m) – consistent with isopycnal displacement (Fig. 2b;  
234 Fig. 3a). Along the isopycnals delineated by potential density anomalies of  $24.3$  to  $25.3 \text{ kg m}^{-3}$ ,  
235 [N+N] and coincident  $[\text{PO}_4^{3-}]$  were notably higher at the subsurface of the cyclonic eddy's inner  
236 edges (station 11 at 150 m and station 13 at 125 – 150 m) – and at the southern outer edge of  
237 the cyclone (station 14 at 125 m) – than at corresponding density horizons below the euphotic  
238 zone outside the cyclone (Fig. 2b; Fig. 3a; Fig. S2). This density horizon was otherwise uplifted  
239 above the euphotic zone at the center of the cyclone, thus depleted in [N+N] (Fig. 3e). Station  
240 10 was selected as the reference station to estimate the excess and deficit in [N+N] along the  
241  $\sigma_\theta = 24.3$  to  $25.3 \text{ kg m}^{-3}$  isopycnal surface given its near zero  $\text{SLA}_{\text{corr}}$ . At stations 11, 13 and 14,  
242 the depth-integrated excess [N+N] was  $0.03$  –  $0.1 \text{ moles N m}^{-2}$  relative to station 10, while the  
243 depth-integrated deficit of [N+N] at the center of the cyclone (station 12) and station 4 was  
244  $0.08$  –  $0.1 \text{ moles N m}^{-2}$ .



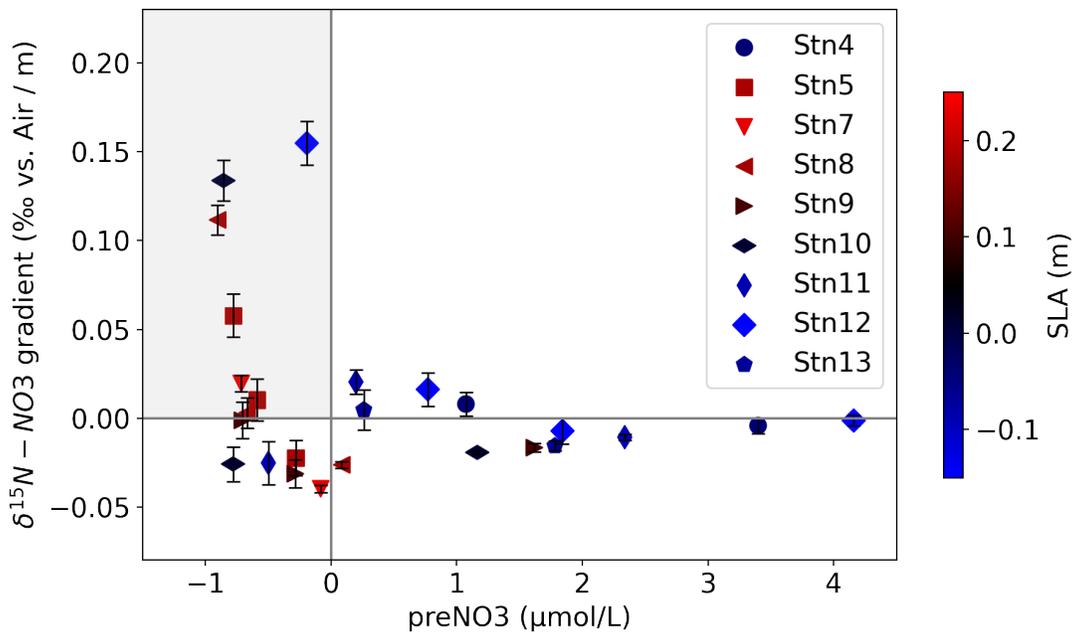
245  
 246 **Figure 3.** Shallow depth profiles at stations along the hydrographic transect of (a) N+N  
 247 concentration, (b) AOU, (c)  $\text{preNO}_3^-$  and (d)  $\delta^{15}\text{N}_{\text{NO}_3}$ . Corresponding potential density profiles  
 248 of (e) N+N concentration, (f) AOU, (g)  $\text{preNO}_3^-$  and (h)  $\delta^{15}\text{N}_{\text{NO}_3}$ . Colors represent corrected sea  
 249 level anomaly in (a-c, e-g) and preformed  $\text{NO}_3^-$  concentration in (d, h). The red arrows in (e, f)  
 250 point to the blobs of excess nutrients along isopycnal at the edges of the cyclone. Station 10  
 251 is shown in the dotted line.

252 AOU values were negative throughout the euphotic zone due to net photosynthesis,  
 253 reaching minima between 28 – 62 m depth at all stations (*i.e.*,  $\text{O}_2$  maxima), with the lowest AOU  
 254 value of  $-17.5 \mu\text{mol L}^{-1}$  observed in the cyclone center (Fig. 2c; Fig. 3b). AOU increased from  
 255 negative values throughout the euphotic zone (*i.e.*,  $\text{O}_2$  excess above saturation), to positive  
 256 values below the euphotic zone (Fig. 2c; Fig. 3b). The highest subsurface AOU was at the center  
 257 of the cyclone, and the lowest in the center of the anticyclone – consistent with isopycnal  
 258 displacement. As with  $[\text{N+N}]$ , AOU values along the  $\sigma_\theta = 24.3$  to  $25.3 \text{ kg m}^{-3}$  isopycnal were  
 259 higher at the subsurface of the cyclone’s inner edges (stations 11 and 13) and at its southern  
 260 outer edge (station 14) than below the DCM at outer stations. At stations where these density  
 261 horizons were otherwise uplifted into the euphotic zone, AOU along isopycnal decreased to

262 prominent minima at the center of the cyclone (station 12) and at station (station 4) due to  
263 incident net primary production (Fig. 3f). Compared to outer station 10, excess AOU along the  
264  $\sigma_\theta = 24.3$  to  $25.3 \text{ kg m}^{-3}$  isopycnals at was  $0.4 - 1.1 \text{ moles O}_2 \text{ m}^{-2}$  (at stations 11, 13 and 14). The  
265 excess subsurface AOU at the cyclone's inner edges showed stoichiometric correspondence to  
266 excess [N+N] (Anderson, 1995), with  $\text{AOU}_{\text{excess}}:\text{N}_{\text{excess}} = 10.9 \pm 6.3$ .

267 The  $\text{preNO}_3^-$  showed characteristic negative values at the base of the euphotic zone ( $-1.9$  to  
268  $-0.4 \text{ }\mu\text{M}$  in the cyclone and  $-1.8$  to  $0 \text{ }\mu\text{M}$  in the anticyclone; Fig. 2d). Negative values at the  
269 subsurface occupied broader depth and isopycnal intervals in the anticyclone, from the base of  
270 the euphotic zone to  $\sim 200 \text{ m}$  ( $\sigma_\theta = 24.0 - 25.2 \text{ kg m}^{-3}$ ), compared to  $\sim 125 \text{ m}$  ( $\sigma_\theta = 24.9 - 25.2$   
271  $\text{kg m}^{-3}$ ) in the cyclone. Values of  $\text{preNO}_3^-$  increased with depth to positive values below the  $\sigma_\theta =$   
272  $25.2 \text{ kg m}^{-3}$  isopycnal.

273 Depth profiles of  $\delta^{15}\text{N}_{\text{NO}_3}$  along transect revealed lower values at the subsurface of the  
274 anticyclone ( $2.5 - 5\text{‰}$ ) and higher values at the subsurface cyclone ( $5 - 10\text{‰}$ ; Fig. 3d). This  
275 difference derives from a steep increase in  $\delta^{15}\text{N}_{\text{NO}_3}$  with potential density, as  $\delta^{15}\text{N}_{\text{NO}_3}$  values  
276 increased with depth, converging along density intervals (Fig. 3h). Nevertheless, although  
277 subsurface values were generally lower in the anticyclone, the  $\delta^{15}\text{N}_{\text{NO}_3}$  values directly at the  
278 base of the euphotic zone at all stations were higher than at the subsequent depth interval –  
279 and differed among stations along isopycnals – signaling local fractionation due to partial  
280 nitrate assimilation. This assimilation signal was notably coincident with the minima in  $\text{preNO}_3^-$   
281 (*i.e.*, negative  $\text{preNO}_3^-$ ), where corresponding AOU values were positive (Fig. 4).



282  
 283 **Figure 4.** Gradients of  $\delta^{15}\text{N}_{\text{NO}_3}$  over depth plotted against  $\text{preNO}_3$ , with markers denoting  
 284 different stations and colors corrected sea level anomaly. Positive  $\delta^{15}\text{N}_{\text{NO}_3}$  gradients represent  
 285 upward increase of  $\delta^{15}\text{N}_{\text{NO}_3}$  ( $\delta^{15}\text{N}_{\text{NO}_3}$  increases towards shallower depths). The shaded area is  
 286 where the upward increase of  $\delta^{15}\text{N}_{\text{NO}_3}$  coincides negative  $\text{preNO}_3$ .

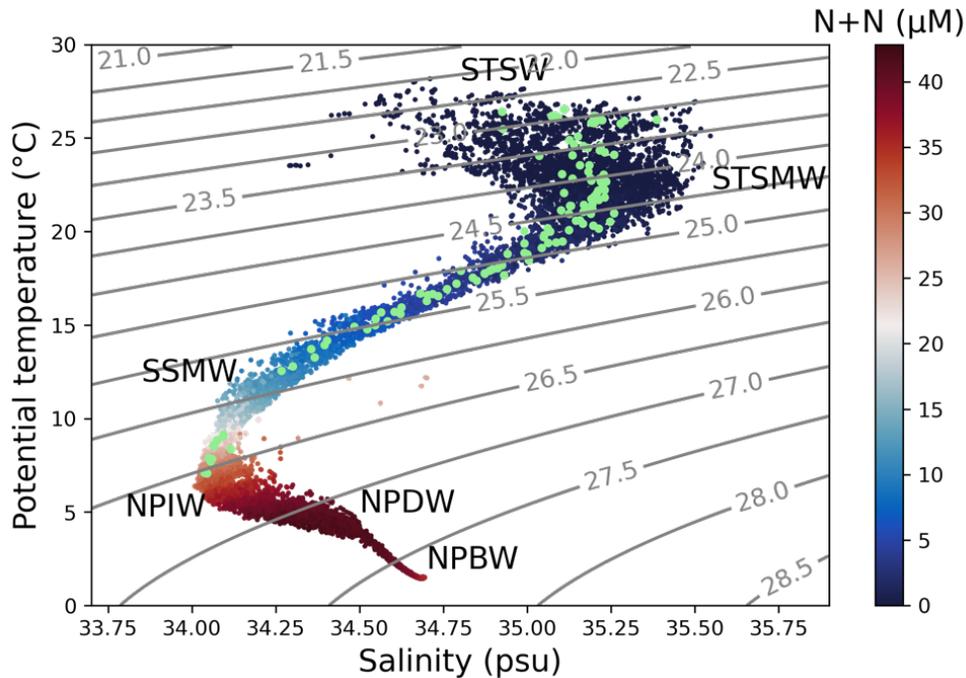
## 287 4 Discussion

### 288 4.1 Origin of subsurface nutrients

289 The physical and biogeochemical properties of the cyclone and anticyclone showed  
 290 characteristics shared by regional eddies (Ascani et al., 2013; Barone et al., 2022; Church et al.,  
 291 2009; Gaube et al., 2013; Seki et al., 2001; Xiu & Chai, 2020). The DCM was shallower in the  
 292 cyclone and had higher fluorescence and chlorophyll-a concentrations. Primary productivity in  
 293 the deep euphotic zone was coherently higher in the cyclone (Hawco et al., 2021). Depth-  
 294 integrated  $\text{O}_2$  concentrations in the euphotic zone were higher in the cyclone than in the  
 295 anticyclone.

296 The enhanced primary production observed in the lower euphotic zone of the cyclone  
 297 center was ostensibly sustained by a greater vertical nutrient supply from diapycnal mixing; the  
 298 vertical displacement of isopycnals associated with the mesoscale features resulted in higher  
 299 nutrient concentrations directly below the euphotic zone of the cyclone compared to the

300 anticyclone, borne of a steep gradient in nutrient concentrations with density (Barone et al.,  
301 2022). The gradient of the regional nutricline is explained by the incidence of Subtropical  
302 Salinity Maximum Water (STSMW;  $\sigma_{\theta} = 24.2 \text{ kg m}^{-3}$ ) at the base of the euphotic zone (Fig. 5),  
303 which is depleted of nutrients at its origin near the subtropical front (25° to 30°N; Casciotti et  
304 al., 2008; Sabine et al., 1995; Tsuchiya, 1968). Nutrients therein derive in part from diapycnal  
305 mixing with underlying Shallow Salinity Minimum Water (SSMW;  $\sigma_{\theta} = 25.8 \text{ kg/m}^3$ ) formed in the  
306 northeastern subtropical gyre, which overlies North Pacific Intermediate Water (NPIW;  $\sigma_{\theta} = 26.8$   
307  $\text{kg m}^{-3}$ ; Talley, 1985, 1993). The low  $\delta^{15}\text{N}_{\text{NO}_3}$  in STSMW (as low as  $2.2 \pm 0.1 \text{ ‰}$  in the anticyclone)  
308 relative to deeper waters suggests that nitrate therein also originated from the remineralization  
309 of newly fixed N (Casciotti et al., 2008). The  $\delta^{15}\text{N}_{\text{NO}_3}$  in NPIW at intermediate depths is ca.  $7.1 \text{ ‰}$   
310 (Casciotti et al., 2008; Lehmann et al., 2018; Sigman et al., 2009). The  $\delta^{15}\text{N}_{\text{NO}_3}$  in SSMW above is  
311  $5.6 \text{ ‰}$ , intermediate between NPIW and STSMW. The upward decrease in  $\delta^{15}\text{N}_{\text{NO}_3}$  is consistent  
312 with the addition of newly fixed N from the remineralization of organic material with a nominal  
313  $\delta^{15}\text{N}$  value of  $-2 - 0 \text{ ‰}$  (Carpenter et al., 1997; Delwiche et al., 1979; Hoering & Ford, 1960;  
314 Minagawa & Wada, 1986), integrated over the residence time of the water mass since it was  
315 ventilated (Casciotti et al., 2008; Liu et al., 1996). The low subsurface  $\delta^{15}\text{N}_{\text{NO}_3}$  could additionally  
316 result from isotope fractionation during remineralization, as bacteria preferentially degrade  
317  $^{14}\text{N}$ , leading to a relatively low  $\delta^{15}\text{N}_{\text{NO}_3}$  of the remineralized nitrate (Altabet, 1988; Casciotti et  
318 al., 2008) – a notion to which we return in a later section. Directly at the base of the euphotic  
319 zone, the sharp increases in  $\delta^{15}\text{N}_{\text{NO}_3}$  compared to corresponding values along isopycnals are  
320 consistent with isotope fractionation due to the partial assimilation of nitrate.



321  
 322 **Figure 5. Potential temperature vs. salinity from bottle data spanning the 30-year time series**  
 323 **at Station ALOHA, with contours of potential density and colors of N+N concentrations.**  
 324 **Observations of the two eddies in this study are in green. Labeled water masses include**  
 325 **Subtropical Surface Water (STSW), Subtropical Salinity Maximum Water (STSMW), Shallow**  
 326 **Salinity Minimum Water (SSMW), North Pacific Intermediate Water (NPIW), North Pacific**  
 327 **Deep Water (NPDW) and North Pacific Bottom Water (NPBW). The data are from The Hawaii**  
 328 **Ocean Time-series observations (<http://hahana.soest.hawaii.edu/hot/hot-dogs/>).**

329 Away from the center at peripheral stations inside the cyclone, nutrient concentrations  
 330 were even higher than along corresponding density horizons outside of the eddy (and higher  
 331 than the mean conditions at  $\sigma_\theta \approx 25.0 \text{ kg m}^{-3}$  from the Station ALOHA climatology; Fig. S3),  
 332 suggesting shallow remineralization within the cyclone. A related feature was observed by  
 333 Buesseler et al. (2008) in a cyclonic eddy in the North Atlantic Subtropical Gyre, wherein excess  
 334 thorium-234 was focused directly below the DCM. The excess [N+N] along isopycnals in the  
 335 cyclone was associated with a corresponding stoichiometric excess in AOU, suggesting that that  
 336 these signals derived proximately from shallow remineralization within the eddy.

337 The excess [N+N] along isopycnals could result from the shallow remineralization of the  
 338 vertical flux of sinking particles generated in lighter density horizons that were uplifted into the

339 euphotic zone directly above. Alternatively, the correspondence of excess subsurface nutrients  
340 at the cyclone's inner edges with the isopycnal uplifted into the euphotic zone in the center of  
341 the cyclone leads us to postulate that the excess remineralized nutrients could have arisen from  
342 particles exported along isopycnals (Boyd et al., 2019) – thus adding to the incident nutrient  
343 reservoir. Small sinking particles from the euphotic zone may attain neutral buoyancy at  
344 fringing isopycnals, preventing export to further depths (McCave, 1975; Omand et al., 2020;  
345 Washburn et al., 1989). We observed no evidence of shallow suspended particles from beam  
346 transmission and attenuation coefficients (data not shown), although shallow remineralization  
347 could have occurred primarily before the occupation. Otherwise, particles generated in the  
348 uplifted isopycnal in the cyclone center may have been advected tangentially toward the edges  
349 of the eddy (Gaube et al., 2013; Zhou et al., 2020), then exported gravitationally. Particles may  
350 also be subducted to the subsurface along isopycnals *via* submesoscale fronts at the cyclone  
351 edges (Guidi et al., 2012; Lévy et al., 2012; Omand et al., 2015; Resplandy et al., 2019; Stukel et  
352 al., 2017), particularly during the intensification stage of the eddies (Guo et al., 2024).

353 Regardless of the mechanism(s) resulting in the accrual of excess nutrients at the subsurface,  
354 this feature was not evident below the euphotic zone of the anticyclone, wherein [N+N] and  
355 AOU values were similar to those at out-stations along corresponding density horizons.

356 At the center of the cyclonic eddy, the uplifted isopycnals resulted in a larger nutrient  
357 reservoir directly below the euphotic zone than mean conditions, leading to a proportionally  
358 greater flux of nutrients into the euphotic zone from turbulent mixing across isopycnals –  
359 providing a means for the cyclonic eddy to remain productive after the initial isopycnal uplift  
360 into the euphotic zone (Barone et al., 2022). The so-called “eddy-pumping” of nutrients  
361 (Falkowski et al., 1991; McGillicuddy et al., 1998), borne of the uplift of isopycnals occurred  
362 before the onset of the field survey, and was thus not captured. Barone et al. (2022) estimated  
363 a diapycnal N flux directly across the top of the nutricline of  $0.08 \text{ mmol N m}^{-2} \text{ d}^{-1}$  in the cyclone  
364 and  $0.009 \text{ mmol N m}^{-2} \text{ d}^{-1}$  in the anticyclone. These values are appreciably lower than the  
365 diapycnal flux estimated by Benitez-Nelson et al. (2007) at the center of a cyclonic eddy on the  
366 lee side of Hawaiian islands – a difference deriving largely from the assumption of a greater

367 diapycnal diffusivity of  $5 - 8 \times 10^{-5} \text{ m}^2 \text{ s}^{-1}$  versus  $1.1 \times 10^{-5} \text{ m}^2 \text{ s}^{-1}$  assumed by Barone et al.  
 368 (2022).

369 In addition to mixing across isopycnals, mixing along isopycnals may also provide an  
 370 important conduit of nutrients into the euphotic zone of the cyclone (Cao et al., 2024; Freilich &  
 371 Mahadevan, 2019). Subsurface nutrients along the  $\sigma_\theta \approx 25.0 \text{ kg m}^{-3}$  isopycnal were apt to mix  
 372 into the uplifted center of the cyclone wherein nutrients were depleted. We estimate the  
 373 isopycnal mixing flux in the cyclone and anticyclone for a diffusivity,  $k_{iso}$ , of  $1 \text{ m}^2 \text{ s}^{-1}$  (Okubo,  
 374 1971; Shcherbina et al., 2015). To this end, we first compute the volume-specific flux,  $F_{iso,vol}$   
 375 ( $\text{mmol N m}^{-3} \text{ d}^{-1}$ ) from  $F_{iso,vol} = k_{iso} (\partial^2 N / \partial x^2 + \partial^2 N / \partial y^2)$ , where  $x$  and  $y$  are the respective  
 376 zonal and meridional directions. Assuming symmetric eddies, we derive the isopycnal flux along  
 377 the hydrographic transect,  $F'_{iso,vol} = k_{iso} (2\partial^2 N / \partial x'^2)$ , where  $x'$  is the direction along  
 378 transect. The volumetric flux  $F'_{iso,vol}$  integrated over the depth range of density  $\sigma_\theta = 24.6 -$   
 379  $25.4 \text{ kg m}^{-3}$ , yields an isopycnal flux of  $0.002 \text{ mmol N m}^{-2} \text{ d}^{-1}$  in the center of the cyclone,  
 380 compared to  $-0.0003 \text{ mmol N m}^{-2} \text{ d}^{-1}$  in the center of the anticyclone. The isopycnal mixing flux  
 381 of N thus appears to be one order of magnitude lower than the diapycnal mixing flux. We note  
 382 that our calculation may underestimate isopycnal fluxes because the horizontal resolution of  
 383 the measurements was relatively coarse, with distances between the cyclone center and its  
 384 peripheral stations of  $\geq 38 \text{ km}$ . Excess subsurface nutrients accrued in closer proximity to the  
 385 cyclone center would result in a steeper along-isopycnal concentration gradient. For example,  
 386 given a similar nutrient gradient along an arbitrary distance of  $10 \text{ km}$  (along the  $x'$  direction)  
 387 from the cyclone center, isopycnal mixing would result in a flux of  $0.04 \text{ mmol N m}^{-2} \text{ d}^{-1}$ , of the  
 388 same order of magnitude as the diapycnal flux. This hypothesis is supported by a recent  
 389 investigation of energetic submesoscale dynamics in a long-lived cyclonic eddy that revealed  
 390 significant isopycnal fluxes of nutrients to the DCM (Cao et al., 2024). We thus submit that  
 391 isopycnal mixing may be a means by which production is sustained beyond the initial “eddy  
 392 injection.”

393 In all, our observations suggest that a substantive fraction of the particulate organic  
 394 material generated in the euphotic zone was remineralized directly below the euphotic zone.  
 395 Given the cyclone’s nonlinear nature, remineralized nutrients were retained within the eddy,

396 accruing at the subsurface. Remineralized nutrients at shallow depths directly below the  
397 euphotic zone were then apt to be re-supplied to the euphotic zone, allowing the cyclonic eddy  
398 to sustain primary production in the deep euphotic zone beyond that fueled by the initial uplift  
399 of isopycnals. Such “rejuvenation” of nutrients was actualized in eddy-resolving simulations of  
400 the Northern Canary upwelling system, wherein the particulate organic nitrogen (PON) stock  
401 generated at the surface of long-lived mesoscale eddies was largely regenerated at the shallow  
402 subsurface and re-supplied to the euphotic zone on timescale of  $\sim 1.5$  months – thus  
403 rejuvenating multiple times over the lifetime of long-lived ( $\sim 14$  months) cyclonic eddies  
404 (Lovecchio et al., 2022). While increased primary productivity in cyclonic eddies is initiated  
405 during intensification (*e.g.*, Guo et al., 2024), higher productivity than the surrounding may be  
406 sustained thereon by the re-supply of nutrients accrued from remineralization at the shallow  
407 subsurface.

408 The excess nutrients observed here were focused between 125 – 150 m, depths shallower  
409 than the sediment traps, suggesting that a sizeable fraction of the export flux in the cyclone was  
410 remineralized above the traps. This fraction of the exported production from the cyclone  
411 manifestly did not reach depths where carbon is effectively sequestered away from the  
412 atmosphere (DeVries et al., 2012; DeVries & Weber, 2017). This inference conforms to the  
413 notion that warmer waters promote shallower remineralization of labile organic material  
414 (Marsay et al., 2015). It is also consistent with inverse model analyses suggesting that the  
415 transfer efficiency of sinking organic particles to the ocean interior is relatively low in  
416 subtropical gyres (Weber et al., 2016). Particle remineralization and fragmentation were  
417 recently shown to be enhanced at the DCM inside a decaying cyclonic eddy in the oligotrophic  
418 South China Sea, leading to weak carbon export (Zhu et al., 2023). Much of the enhanced  
419 production during the maturing and decaying stages of regional cyclonic mesoscale eddies may  
420 be subject to shallow remineralization, such that the remineralized carbon will resurface on  
421 sub-annual to decadal time scales.

422 Surprisingly, the organic particulate flux recorded in the sediment traps at 150 m was of  
423 similar magnitude in the cyclonic vs. anticyclonic eddy in terms of both PON and POC, on the  
424 order of  $0.4 \pm 0.1 \text{ mmol N m}^{-2} \text{ d}^{-1}$  for PON – whereas particulate inorganic carbon and

425 particulate silicate fluxes were notably greater in the cyclone (Barone et al., 2022). Similar  
426 observations in subtropical gyres have led to the conclusion that regional cyclonic eddies  
427 function as effective silica pumps but inefficient organic carbon pumps (Benitez-Nelson et al.,  
428 2007; Buesseler et al., 2008; Maiti et al., 2008; Rii et al., 2008; K. Zhou et al., 2020; Zhu et al.,  
429 2023). Barone et al., (2022) nevertheless posited that organic material produced in the cyclone  
430 during the initial isopycnal uplift was exported to deeper waters prior to the sampling  
431 campaign. In this regard, examination of multiple eddies in the NPSG revealed that carbon and  
432 nitrogen flux anomalies were negatively correlated to the eddy age, with higher export  
433 anomalies occurring during early maturity (Zhou et al., 2021). Guo et al. (2024) similarly  
434 observed enhanced POC export during the intensifying stage of a cyclonic eddy, a high  
435 percentage of which was transferred to the base of the mesopelagic layer. A recent survey of  
436 regional eddies further revealed that O<sub>2</sub> minima at mid-depths (between 600 - 900 m) were  
437 generally more prominent in cyclonic eddies than in surrounding waters, while less prominent  
438 in anticyclonic eddies, suggesting greater export to mid-depths in cyclonic eddies (Xiu & Chai,  
439 2020). While organic material exported from the cyclone surface was ostensibly remineralized  
440 directly below the euphotic zone, the export of organic carbon to mid depths may nevertheless  
441 have been greater in the cyclone than the anticyclone over their respective lifetime.

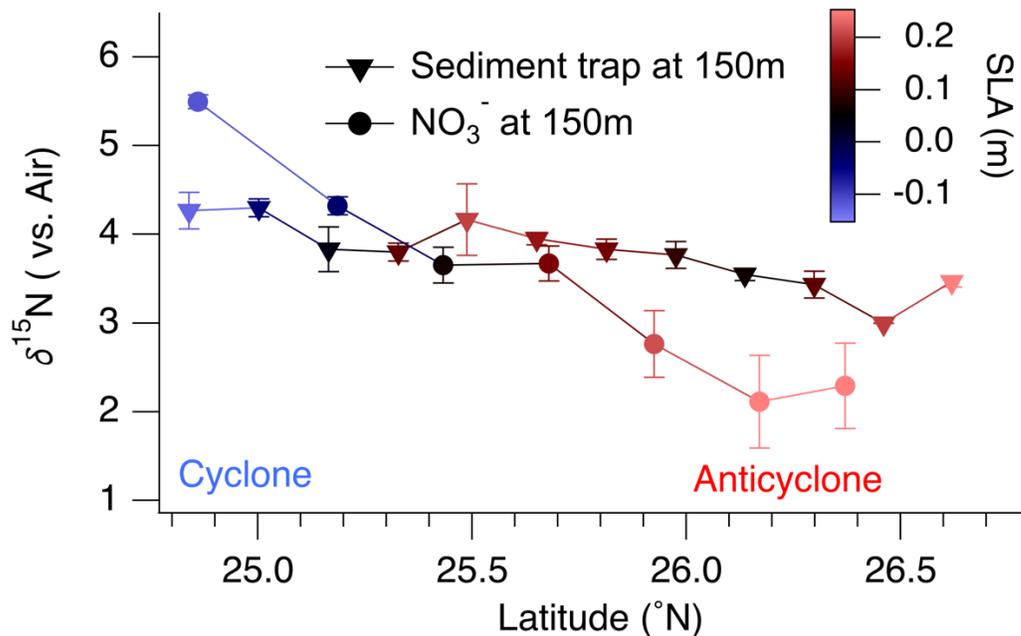
#### 442 **4.2 Stoichiometric anomalies at the subsurface**

443 A salient subsurface feature in subtropical gyres is the incidence of so-called “negative”  
444 preformed nutrients (Emerson & Hayward, 1995; Fawcett et al., 2018; Johnson et al., 2010).  
445 Given adherence to Redfield stoichiometry, negative preformed nutrients may signal the  
446 respiration of O<sub>2</sub> (and organic carbon) without the commensurate remineralization of nutrients,  
447 or the consumption of nutrients without the proportional production of O<sub>2</sub> during  
448 photosynthesis (Abell et al., 2005; Emerson & Hayward, 1995). This feature could arise from the  
449 entrainment of N-poor dissolved organic matter from the surface and/or from the gravitational  
450 flux and remineralization of C-rich gel-like organic matter (*aka*, transparent exopolymer) – the  
451 respiration of which could instigate heterotrophic nitrate assimilation (Abell et al., 2005;  
452 Emerson & Hayward, 1995; Fawcett et al., 2018; Smyth & Letscher, 2023) – or from nutrient  
453 transport by migrating plankton (Johnson et al., 2010; Letscher & Villareal, 2018; Villareal et al.,

454 1999). The association of the extrema in negative preNO<sub>3</sub><sup>-</sup> with the upward increases in δ<sup>15</sup>N<sub>NO<sub>3</sub></sub>  
455 values from partial assimilation of nitrate may arise from the consumption of C-rich organic  
456 material by heterotrophic bacteria.

#### 457 **4.3 N isotope mass balance to infer N<sub>2</sub> fixation in mesoscale eddies**

458 New and export production in the NPSG are cited to be fueled in part by biological N<sub>2</sub>  
459 fixation (Karl et al., 1997). Incubation-based estimates of N<sub>2</sub> fixation in the euphotic zone from  
460 the HOT time series average of 230 ± 136 μmol N m<sup>-2</sup> d<sup>-1</sup> (Böttjer et al., 2017) for measurements  
461 made between 2005 and 2013. These may be biased by a number of methodological artifacts  
462 that have been uncovered in recent years (Dabundo et al., 2014; Mohr et al., 2010; White et al.,  
463 2020), albeit the potential for these biases to be evident was considered in Böttjer et al. (2017)  
464 and more recent measurements have found rates were found to be similar or higher than  
465 previously reported (Dugenne et al. 2023). Independent estimates of the contribution of N<sub>2</sub>  
466 fixation to export production cover a broad range, from negligible to nearly 50 % of N export  
467 (Barone et al., 2022; Böttjer et al., 2017; Casciotti et al., 2008; Karl et al., 1997; Mahaffey et al.,  
468 2008). The latter derive from mass balance exercises where the δ<sup>15</sup>N of sinking material  
469 recovered in shallow sediment traps is compared to the δ<sup>15</sup>N<sub>NO<sub>3</sub></sub> supplied to the euphotic zone  
470 to infer the fraction of export flux from biological N<sub>2</sub> fixation (Altabet, 1988; Barone et al., 2022;  
471 Böttjer et al., 2017; Casciotti et al., 2008; Karl et al., 1997; Knapp et al., 2005, 2008, 2016;  
472 Mahaffey et al., 2008). The higher range of these estimates presumed a relatively enriched  
473 δ<sup>15</sup>N<sub>NO<sub>3</sub></sub> end-member akin to that in intermediate depth waters, lacking direct measurements of  
474 δ<sup>15</sup>N<sub>NO<sub>3</sub></sub> at shallower depths (Karl et al. 1997).



475  
 476 **Figure 6.**  $\delta^{15}\text{N}_{\text{NO}_3}$  values at 150 m and sediment trap  $\delta^{15}\text{N}_{\text{PON}}$  values plotted against latitudes  
 477 **along the hydrographic transect. Colors represent sea level anomaly. Error bars are the**  
 478 **analytical uncertainties (standard deviation) from measurement for  $\delta^{15}\text{N}_{\text{PON}}$  and  $\delta^{15}\text{N}_{\text{NO}_3}$ .**

479 The incubation-based  $\text{N}_2$  fixation rates estimated during the deployment were substantially  
 480 higher in the anticyclone ( $670 \mu\text{mol N m}^{-2} \text{d}^{-1}$ ) than in the cyclone ( $115 \mu\text{mol N m}^{-2} \text{d}^{-1}$ ; Dugenne  
 481 et al., 2023) – a dynamic that may expectedly manifest in the  $\delta^{15}\text{N}$  of the sinking flux. The high-  
 482 resolution  $\delta^{15}\text{N}_{\text{NO}_3}$  profiles measured here allow us to constrain the  $\delta^{15}\text{N}_{\text{NO}_3}$  supplied to the  
 483 euphotic zone, and evaluate whether these values can be exploited to estimate the  
 484 contribution of biological  $\text{N}_2$  fixation to shallow particle export in the respective mesoscale  
 485 eddies. The  $\delta^{15}\text{N}$  of particulate material collected in shallow sediment traps deployed at 150 m  
 486 ranged from 3.0 to 4.3 ‰, with a lower range of values observed in the traps deployed in the  
 487 anticyclone (3.0 – 4.2 ‰) compared to the cyclone (3.8 – 4.3 ‰; Fig. 6; Barone et al., 2022). We  
 488 presume here the  $\delta^{15}\text{N}_{\text{NO}_3}$  values at 150 m (the depth of sediment traps) corresponded to the  
 489 nitrate supplied to the euphotic zone. Because some of these values were imprinted by the  
 490 partial assimilation of nitrate, we extrapolate the  $\delta^{15}\text{N}_{\text{NO}_3}$  to values in contiguous density  
 491 horizons not influenced by partial assimilation (Fig. 3h, S4). At corresponding stations along the  
 492 transect, the  $\delta^{15}\text{N}_{\text{PON}}$  values of material recovered in sediment traps in the cyclone were lower  
 493 than the  $\delta^{15}\text{N}_{\text{NO}_3}$  values at 150 m, whereas the  $\delta^{15}\text{N}_{\text{PON}}$  values of particles collected in the

494 anticyclone were higher than the  $\delta^{15}\text{N}_{\text{NO}_3}$  values at 150 m (Fig. 6). Assuming the  $\delta^{15}\text{N}_{\text{NO}_3}$  of  
495 newly fixed N is  $0 \pm 1$  ‰, the contribution of  $\text{N}_2$  fixation to export production consequently  
496 inferred for the cyclonic eddy is on the order of  $13 \pm 3$  %, whereas that for the anticyclonic eddy  
497 yields a negative value of  $-29 \pm 14$  %. Alternative assumptions to characterize the  $\delta^{15}\text{N}_{\text{NO}_3}$  of  
498 the upward nitrate flux yield similarly confounding results (Supporting Information Text S2;  
499 Table S1; Fig. S5). These results are clearly problematic, arising because mesoscale eddies are  
500 not a steady-state system with respect to the nutrient supply to the surface and the coincident  
501 export of organic material therefrom. The regional  $\delta^{15}\text{N}_{\text{NO}_3}$  gradient with density (and depth) is  
502 remarkably steep – notably steeper than that near Bermuda in the North Atlantic Subtropical  
503 Gyre (Knapp et al., 2005) – rendering the  $\delta^{15}\text{N}_{\text{NO}_3}$  supplied to the euphotic zone highly sensitive  
504 to SLA. The SLA in mesoscale eddies changes on relatively short time scales, such that the  
505 sinking material captured in the traps was not necessarily produced from the nitrate (and  
506 associated  $\delta^{15}\text{N}_{\text{NO}_3}$ ) co-located at the base of the euphotic zone.

507 We nevertheless exploit the coherence of  $\delta^{15}\text{N}_{\text{NO}_3}$  along isopycnals to infer the mean depth-  
508 distribution of  $\delta^{15}\text{N}_{\text{NO}_3}$  at Station ALOHA. The  $\sigma_\theta = 24.8 \text{ kg m}^{-3}$  isopycnal is that which commonly  
509 resides at 150 – 175 m depth, and has a  $\delta^{15}\text{N}_{\text{NO}_3}$  of  $3.1 \pm 0.4$  ‰. The mean  $\delta^{15}\text{N}_{\text{PON}}$  of sinking  
510 particles recovered monthly in sediment traps at Station ALOHA for 31 years was  $3.3 \pm 1.0$  ‰,  
511 squarely in the  $\delta^{15}\text{N}_{\text{NO}_3}$  range of  $\sigma_\theta = 24.8 \text{ kg m}^{-3}$  isopycnal. Given no detectable secular change  
512 in the  $\delta^{15}\text{N}_{\text{PON}}$  of sinking particles over this time (Fig. S6), and presuming no change in the  
513 corresponding  $\delta^{15}\text{N}_{\text{NO}_3}$ , the fractional contribution of  $\text{N}_2$  fixation to export production thus  
514 estimated is within the margin of error,  $-6 \pm 35$  % – rendering this estimate uncertain. In  
515 contrast, Knapp et al. (2018) reported that the material captured in shallow sediment traps in  
516 the southwestern Pacific had  $\delta^{15}\text{N}$  values of  $0.6 \pm 1$  ‰, compared to subsurface  $\delta^{15}\text{N}_{\text{NO}_3}$  values  
517 of 7.0 to 8.4 ‰, arguing for an unambiguous contribution of newly fixed N to the sinking flux,  
518 corroborating markedly elevated incubation-based estimates of  $\text{N}_2$  fixation at this site.

519 The similarity of the long-term  $\delta^{15}\text{N}$  average of sinking flux compared to mean  $\delta^{15}\text{N}_{\text{NO}_3}$  at  
520 subsurface is perplexing in light of the magnitude of *in situ* estimates of biological  $\text{N}_2$  fixation at  
521 Station ALOHA. For a net regional community production of  $287 \pm 100 \text{ mmol N m}^{-2} \text{ y}^{-1}$  (Johnson  
522 et al., 2010), the corresponding contribution of  $\text{N}_2$  fixation to the export flux is  $29 \pm 20$  % for a

523 N<sub>2</sub> fixation rate of  $230 \pm 136 \mu\text{mol N m}^{-2} \text{d}^{-1}$  (Böttjer et al., 2017), which should result in a  
524 difference of at least  $\sim 1\%$  of sinking flux from the N isotope mass balance for a N<sub>2</sub>-fixation  
525 endmember of 0 ‰. On the basis that biological N<sub>2</sub> fixation contributes significantly to new  
526 production at Station ALOHA, the discrepancy could arise if newly fixed N accumulates as DON  
527 in the euphotic zone. This premise was queried by Knapp et al., (2005) in the Sargasso Sea,  
528 wherein the  $\delta^{15}\text{N}$  of DON in the euphotic zone was not detectably lower than at depth – noting  
529 that N<sub>2</sub> fixation is not thought to contribute substantively to the export flux in this region  
530 (Altabet, 1988; Knapp et al., 2008). The particulate flux of newly fixed N at Station ALOHA may  
531 otherwise be episodic and thus not well aliased by shallow trap deployments (Karl et al., 2012).  
532 Alternatively, newly fixed N may remain associated with prokaryotic microbes, on the premise  
533 that eukaryotes rely predominantly on nitrate (Fawcett et al., 2011); the former may be  
534 exported and remineralized at shallower depths than the sediment traps. Finally, we note that  
535 estimates of the supply of new nitrate to the surface of the NPSG are uncertain (*e.g.*, Johnson  
536 et al., 2010) and may thus be under-estimated.

537 Another uncertainty regarding the N isotope mass balance that warrants consideration is  
538 that it may be biased by isotopic fractionation during particle remineralization (Lehmann et al.,  
539 2002). Casciotti et al. (2008) observed a shift in the  $\delta^{15}\text{N}$  of sinking PON near station ALOHA,  
540 from 2.5 ‰ at 150 m to 3.5 ‰ at 300 m, attributed to isotope fractionation during  
541 remineralization. Given sizeable remineralization occurring above 150 m, the preferential  
542 production of low  $\delta^{15}\text{N}$  nitrate from remineralization would result in the capture of PON at 150  
543 m with a higher  $\delta^{15}\text{N}$  than exited from the euphotic zone – leading to an under-estimation of  
544 the contribution of biological N<sub>2</sub> fixation to the PON flux. The  $\delta^{15}\text{N}$  increase in sinking PON with  
545 depth could also conceivably reflect the differential export of respective plankton groups  
546 assimilating different N sources hypothesized above (*e.g.*, Fawcett et al., 2011), and/or the  
547 depth-sensitive disaggregation and repackaging of sinking particles (*e.g.*, Briggs et al., 2020;  
548 Lampitt et al., 1990; Wilson et al., 2008). The low  $\delta^{15}\text{N}$  nitrate at the base of the euphotic zone  
549 throughout the NPSG could thus arise from these dynamics. We thus submit that nitrate  
550 isotope ratios can provide a more robust accounting of the input of newly fixed N to the  
551 regional nitrate inventory when considering the whole of intermediate water column wherein

552 bulk remineralization occurs (*e.g.*, Casciotti et al., 2008; Marconi et al., 2017; Marshall et al.,  
553 2022; 2023) - rather than an N isotope mass balances restricted to the top of the nutricline.

## 554 **5 Conclusions**

555 Our analysis reveals that the increased production in the cyclone was patently  
556 remineralized at the cyclone edges, directly below the euphotic zone – rather than exported to  
557 depths where CO<sub>2</sub> is effectively sequestered. This material was remineralized at depths above  
558 the sediment traps, potentially explaining the similarity of the POC and PON export fluxes  
559 between the cyclonic and anticyclonic eddies. The shallow nutrient reservoir borne of  
560 remineralization within the eddy may provide a means to fuel primary production in mature  
561 and decaying stages of cyclonic eddy from cross-isopycnal (and potentially along-isopycnal)  
562 mixing of nutrients – promoting the continuous “rejuvenation” of nutrients over the lifetime of  
563 the eddy.

564 The coincidence of a subsurface nitrate assimilation signal (from  $\delta^{15}\text{N}_{\text{NO}_3}$ ) with negative  
565 preformed nutrients supports the notion that the deviations from canonical elemental  
566 stoichiometry may arise from the shallow export and remineralization of C-rich material,  
567 promoting the assimilation of nitrate by heterotrophic bacteria.

568 Substantially higher biological N<sub>2</sub> fixation was detected in the anticyclone (Dugenne et al.,  
569 2023), yet this dynamic was not discernible from the  $\delta^{15}\text{N}_{\text{PON}}$  of sinking particles recovered in  
570 sediment traps compared to the nitrate  $\delta^{15}\text{N}_{\text{NO}_3}$  at 150 m due to the non-steady state nature of  
571 the system. A steep isopycnal gradient of nitrate  $\delta^{15}\text{N}_{\text{NO}_3}$  renders subsurface values sensitive to  
572 SLA, such that the  $\delta^{15}\text{N}_{\text{PON}}$  along transect mirrored corresponding differences in the  $\delta^{15}\text{N}_{\text{NO}_3}$  of  
573 the nitrate that fueled new production. Averaged over long timescales, the N isotope mass  
574 balance of the euphotic zone did not appear sensitive to the export flux of newly fixed N at  
575 Station ALOHA, for reasons that remain unclear.

576 Our study highlights the need to better characterize the physical mechanisms of nutrient  
577 delivery to the surface oligotrophic ocean, particularly in light of increased surface ocean  
578 stratification (Li et al., 2020; Polovina et al., 2008; Sallée et al., 2021). Studies that achieve high  
579 vertical and horizontal resolution of mesoscale features will allow for better characterization of  
580 the fate of export production based on the subsurface nutrient reservoir. Our study also impels

581 consideration of how to better constrain the significance of N<sub>2</sub> fixation to the export flux in the  
582 NPSG.

### 583 **Acknowledgements**

584 The authors thank D. Karl for insightful comments on the manuscript. The authors are  
585 grateful to V. Rollinson and P. Ruffino for their technical assistance with mass spectrometry  
586 analyses. This work was supported by CAREER award to J.G. from the US National Science  
587 Foundation Division of Ocean Sciences (OCE-1554474) and by the Simons Collaboration on  
588 Ocean Processes and Ecology program (#329104 to A.W.) which supported the field sampling  
589 effort.

### 590 **Open Research**

591 Nitrate  $\delta^{15}\text{N}_{\text{NO}_3}$  measurements in this study are being archived with BCO-DMO. Hydrographic  
592 and biogeochemical measurements are from Barone et al. (2022), and are archived here:  
593 <https://doi.org/10.5281/zenodo.5048504>. The Hawaii Ocean Time-series observations are  
594 available at the BCO-DMO project page (<https://www.bco-dmo.org/project/2101>) and the  
595 program data site: <http://hahana.soest.hawaii.edu/hot/hot-dogs/>. The altimetric Mesoscale  
596 Eddy Trajectories Atlas (META3.2 DT) was produced by SSALTO/DUACS and distributed by AVISO+  
597 (<https://aviso.altimetry.fr>) with support from CNES, in collaboration with IMEDEA.

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