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# 1 Fine scale sampling unveils diazotroph patchiness in the South Pacific Ocean

2  
3 **Running title:** Fine scale diazotroph distribution

4  
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## 14 **Abstract**

15  
16  
17 Diazotrophs are important contributors to reactive nitrogen availability in the ocean.  
18 Oceanographic cruise data accumulated along decades has revealed a heterogeneous  
19 distribution of diazotroph species at regional to global scales. However, the role of dynamic  
20 fine scale structures in distributing diazotrophs is not well understood. This is due to typical  
21 insufficient spatiotemporal resolution sampling and the lack of detailed physical studies in  
22 parallel. Here we show the distribution of five groups of diazotrophs in the South Pacific at  
23 an unprecedented resolution of 7-16 km. We find a patchy distribution of diazotrophs, with  
24 each group being differently affected by parameters describing fine scale structures. The  
25 observed variability could not have been revealed with a lower resolution sampling,  
26 highlighting the need to consider fine scale physics to resolve the distribution of diazotrophs  
27 in the ocean.

## 28 **Main body of text**

29  
30  
31 The surface ocean is constantly stirred by currents that swirl and mix different seawater  
32 masses creating a dynamic mosaic of biogeochemical properties [1]. Numerical modeling  
33 and satellite data have shown that ‘fine scale’ structures such as filaments and eddies (with  
34 typical spatiotemporal scales of 1 to 100 km and days to weeks) impact the distribution of  
35 phytoplankton, primary productivity and carbon export in the ocean [2–4]. While these  
36 remote approaches provide valuable synoptic views at large scales, in situ sampling remains  
37 imperative to resolve the diversity, metabolism and trophic interactions of marine microbes  
38 at fine scales. However, the spatiotemporal resolution of typical at-sea sampling efforts is  
39 too coarse to resolve fine scale processes [5], which hampers our understanding of physical-  
40 biological interactions and their impact on marine microbes [1].

41  
42 Understanding the effect of fine scales on biogeochemically relevant microbial groups is of  
43 particular importance. Dinitrogen (N<sub>2</sub>) fixers or ‘diazotrophs’ provide a significant source of  
44 bioavailable nitrogen in the ocean [6]. Some studies have shown a preferential accumulation  
45 of diazotrophs in anticyclonic eddies [7, 8], where eddy pumping deepens isopycnals  
46 impoverishing surface waters in inorganic nitrogen presumably favoring diazotroph growth  
47 [reviewed in 9]. However, other studies have reported accumulations of diazotrophs in  
48 cyclonic eddies instead, attributed to wind-driven Ekman pumping [10]. Diazotrophs  
49 encompass a wide diversity of prokaryotic microorganisms with different tolerance to  
50 environmental and nutrient availability conditions. For example, cyanobacteria such as  
51 *Trichodesmium* and UCYN-B abound in oligotrophic (sub)tropical waters, while UCYN-A  
52 displays a wide geographical distribution spanning from the tropics to the polar seas [6].  
53 Non-cyanobacterial diazotrophs cannot photosynthesize and obtain carbon and energy from  
54 organic matter compounds, which presents fundamentally different bottom-up controls as

55 compared to cyanobacterial diazotrophs [11]. With such divergent physiologies, it is unlikely  
56 that different diazotrophs respond to fine scale physical forcing in the same way.

57

58 Resolving these ambiguities needs coupling fine scale structure and diazotroph  
59 activity/abundance measurements at high spatiotemporal resolution. The vast majority of  
60 diazotroph activity/abundance data available in the literature up to 2012 stemmed from  
61 locations situated ~160 km apart (median distance between stations in the database  
62 compiled by Luo et al [12]). Recent methodological developments have provided underway  
63 N<sub>2</sub> fixation and diazotroph abundance data at a spatial resolution of ~18 km [13, 14]. While  
64 such resolution may be appropriate to resolve fine scale processes, previous studies have  
65 not sought to explain diazotroph distributions through the lens of fine scale oceanography.  
66

67 Here we investigate the fine scale variability of diazotrophs in the Southwest Pacific Ocean  
68 during a cruise in austral summer 2019 (Fig. 1). Zones of intense fine scale activity were  
69 selected for high-resolution sampling according to satellite and Lagrangian product maps  
70 received onboard on a daily basis [15]. These included sea surface temperature, chlorophyll,  
71 geostrophic current based on absolute dynamic topography (ADT), and the Lagrangian  
72 products finite size Lyapunov exponents (FSLE) and Okubo-Weiss parameter (OW)  
73 (Supplementary Information; Table S1; Fig. S1). Planktonic biomass was collected with an  
74 automated filtration system at an unprecedented resolution of 7-16 km. DNA extracted from  
75 the filters was used to quantify five diazotroph groups (*Trichodesmium*, UCYN-A1, UCYN-B,  
76 UCYN-C and Gamma A) in quantitative PCR assays (Supplementary Information). Only in  
77 zone 3 inorganic nutrient concentrations and N<sub>2</sub> fixation rates were also measured  
78 (Supplementary Information).

79

80 Our results reveal a patchy distribution of diazotrophs, driven by a heterogeneous effect of  
81 fine scale parameters on each diazotroph group (Fig. 1; Fig. S2; Table S2). *Trichodesmium*  
82 correlated positively with ADT (Fig. 1; Fig. S2; Table S2), and accumulated at positive-  
83 negative OW transition and high FSLE regions located at ~170°E in zone 1, 176°E in zone 2  
84 and 171°W in zone 3 (Fig. 2). High FSLE values depict fronts created by horizontal  
85 transport, which are susceptible to accumulate floating particles such as *Trichodesmium*  
86 colonies which harbor gas vesicles [16]. The accumulation of *Trichodesmium* at the  
87 convergence of two counter-rotating eddies in zone 2 (maximum abundance of  $3 \times 10^7$  *nifH*  
88 gene copies L<sup>-1</sup>; Fig. 1) was likely driven by Langmuir circulation [17]. Remarkably, the  
89 temperature of the two counter-rotating eddies of zone 2 differed by >1.5°C (Fig. S4). The  
90 abundance of UCYN-A1 ranged between 10<sup>4</sup> and 10<sup>6</sup> *nifH* gene copies L<sup>-1</sup>, with lower  
91 abundances along the southern transect in zone 3 (Fig. 1). UCYN-A1 were more  
92 homogeneously distributed independently of fine scale features and were negatively related  
93 to FSLE (Table S2) and to *Trichodesmium* (Figs. S2, S3), adding up to the antagonistic  
94 biogeographic trends of these two diazotrophs groups witnessed at larger spatial scales [12].  
95 UCYN-B were more abundant in zone 3 (up to 10<sup>6</sup> *nifH* gene copies L<sup>-1</sup>) than in zones 1 and  
96 2 (up to 10<sup>3</sup> *nifH* gene copies L<sup>-1</sup>) (Fig. 1). They were relatively more abundant at the edges  
97 of eddies (Fig. 1) coinciding with higher FSLE values (Fig. 2), although they were not  
98 statistically related to physical parameters (Table S2). UCYN-C were significantly related to  
99 both ADT and FSLE (Table S2), but were the least abundant group (up to 10<sup>3</sup> *nifH* gene  
100 copies L<sup>-1</sup>; Fig. 1) likely due to their presumed coastal origin [6]. Finally, Gamma A were  
101 significantly related to ADT (Table 2) and accumulated in frontal zones with high FSLE (up to  
102 10<sup>5</sup> *nifH* gene copies L<sup>-1</sup>), which agrees with their putative particle-attached lifestyle [18].

103

104 In zone 3, nitrate concentrations were typically <0.2 μM (Fig. S5a). The relatively high  
105 concentrations of phosphate east of ~175°W (Fig. S5b) likely sustained only moderate N<sub>2</sub>  
106 fixation rates (1-5 nmol N L<sup>-1</sup> d<sup>-1</sup>; Fig. S5c), which correlated with the abundance of  
107 *Trichodesmium* (Spearman, p= 0.008). Low N<sub>2</sub> fixation rates in this region are thought to be  
108 caused by the scarcity of iron east of the Tonga volcanic arc [19]. Nutrients and temperature  
109 typically used to define the biogeography of diazotrophs on regional to global scales [12].

110 Despite the remarkably homogeneous distribution of these factors in zone 3 (Fig. S4g, Fig.  
111 S5a-b), the distribution of diazotrophs revealed high spatial variability at the fine scale (Fig.  
112 1). Such variability would have gone unseen at a coarser resolution, stressing the role of fine  
113 scale dynamics in diazotroph distribution. The patchiness observed likely responds to a  
114 combination of bottom-up and top-down interactions between diazotrophs' competitors,  
115 predators and the surrounding biogeochemical environment. Documenting such  
116 mechanisms at fine scale resolution warrants exciting research avenues in the near future.

117

### 118 **Conflict of interest**

119

120 The authors declare no conflict of interest.

121

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123

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135

### 136 **Competing Interests**

137

138 The authors declare that they have no conflict of interest.

139

### 140 **References**

141

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## 190 Figure legends

191 **Fig. 1: Fine scale resolution abundances of diazotrophs along three selected**

192 **sampling zones.** The central image shows a chlorophyll MODIS composite averaged for

193 November 2019 at a resolution of 4 km and the location of the three selected sampling

194 zones. Zoom-out panels (in dotted squares) show the abundance of diazotrophs in each

195 selected zone as *nifH* gene copies per liter of seawater. Diazotroph abundances (*nifH* gene

196 copies L<sup>-1</sup>) are superimposed on absolute dynamic topography (ADT, color scale) and

197 geostrophic velocity (arrows). ADT data were retrieved for each zone on 2<sup>nd</sup>, 4<sup>th</sup> and 22<sup>nd</sup>

198 November 2019 for zones 1, 2 and 3, respectively. To provide an overview, this figure only

199 presents abundances of *Trichodesmium*, UCYN-A1 and Gamma A. The abundances of the

200 other groups (UCYN-B and UCYN-C) are shown in Fig. S3.

201 **Fig. 2: Lagrangian diagnostics parameters.** Panels a), d) and g) show values of the

202 Okubo-Weiss (OW) in zones 1, 2 and 3, respectively. Panels b), e) and h) show values of

203 finite Lyapunov finite size Lyapunov exponents (FSLE) in zones 1, 2 and 3, respectively.

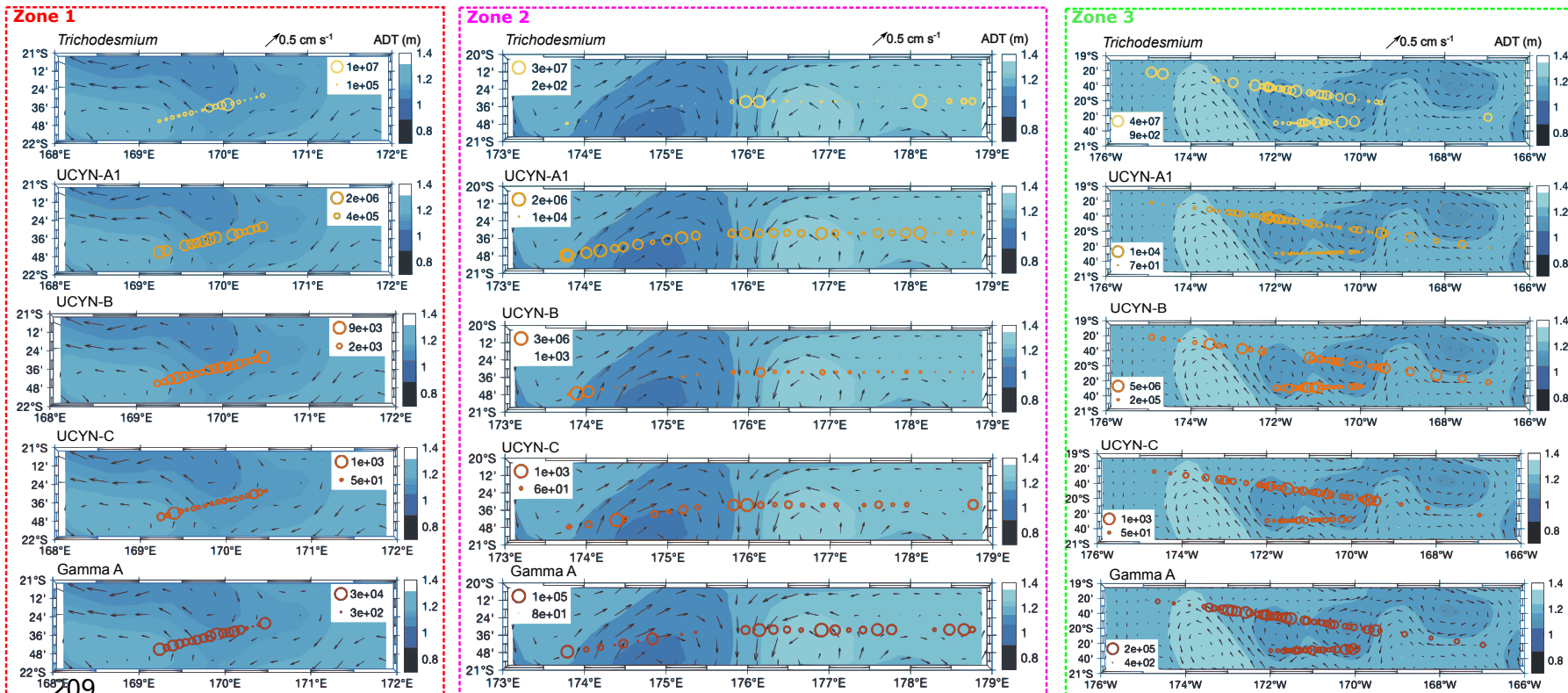
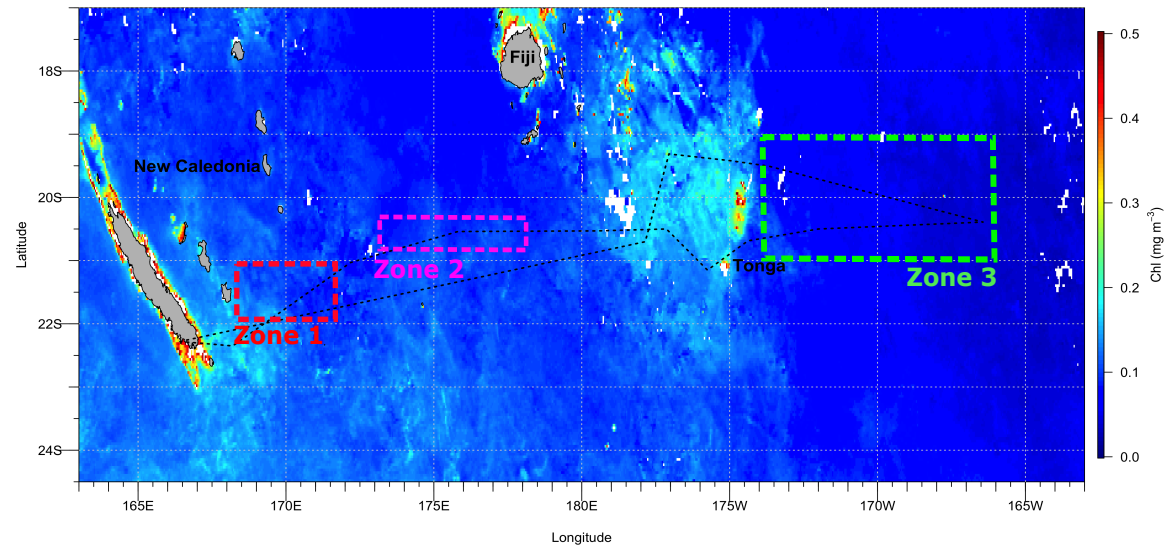
204 White dots represent sampling locations.

205

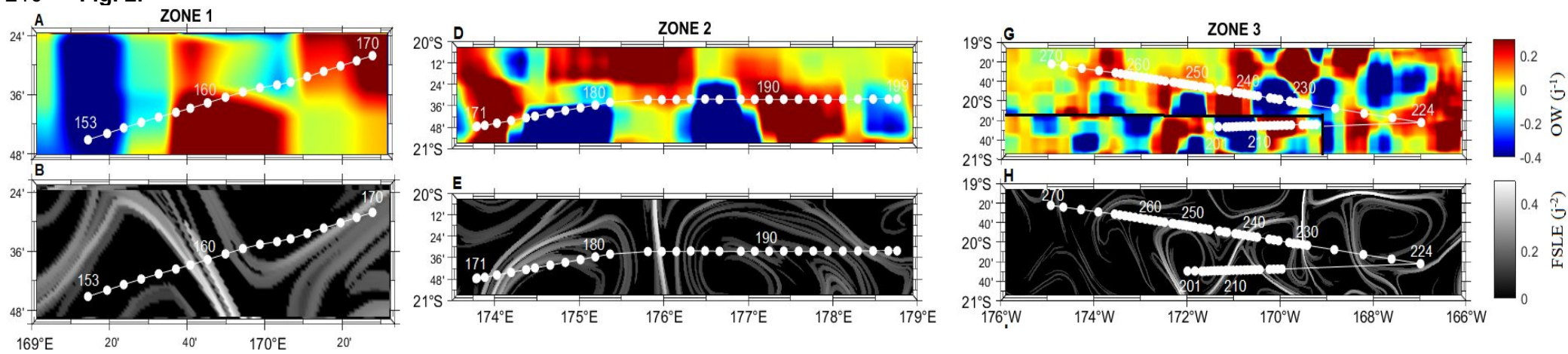
206

207





210 Fig. 2.



211