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Fine scale sampling unveils diazotroph patchiness in the South Pacific Ocean

Mar Benavides, Louis Conrardt, Sophie Bonnet, Ilana Berman-Frank,
Stéphanie Barrillon, Anne Petrenko, Andrea M. Doglioli

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

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

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5 ^{1,*}Mar Benavides, ¹Louis Conradt, ¹Sophie Bonnet, ²Ilana Berman-Frank, ¹Stéphanie
6 Barrillon, ¹Anne Petrenko, ¹Andrea M. Doglioli

7
8 ¹Aix Marseille Univ, Université de Toulon, CNRS, IRD, MIO UM 110, 13288, Marseille,
9 France

10 ²Leon H. Charney School of Marine Sciences, University of Haifa, Mt. Carmel, Haifa
11 3498838, Israel

12
13 *Corresponding author: Mar Benavides mar.benavides@ird.fr

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 (N₂) 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 N₂ 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 N₂ 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 3×10^7 *nifH*
88 gene copies L⁻¹; 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 10⁴ and 10⁶ *nifH* gene copies L⁻¹, 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 10⁶ *nifH* gene copies L⁻¹) than in zones 1 and
96 2 (up to 10³ *nifH* gene copies L⁻¹) (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 10³ *nifH* gene
100 copies L⁻¹; 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
102 10⁵ *nifH* gene copies L⁻¹), 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 N₂
106 fixation rates (1-5 nmol N L⁻¹ d⁻¹; Fig. S5c), which correlated with the abundance of
107 *Trichodesmium* (Spearman, p= 0.008). Low N₂ 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**

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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⁻¹) are superimposed on absolute dynamic topography (ADT, color scale) and

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

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

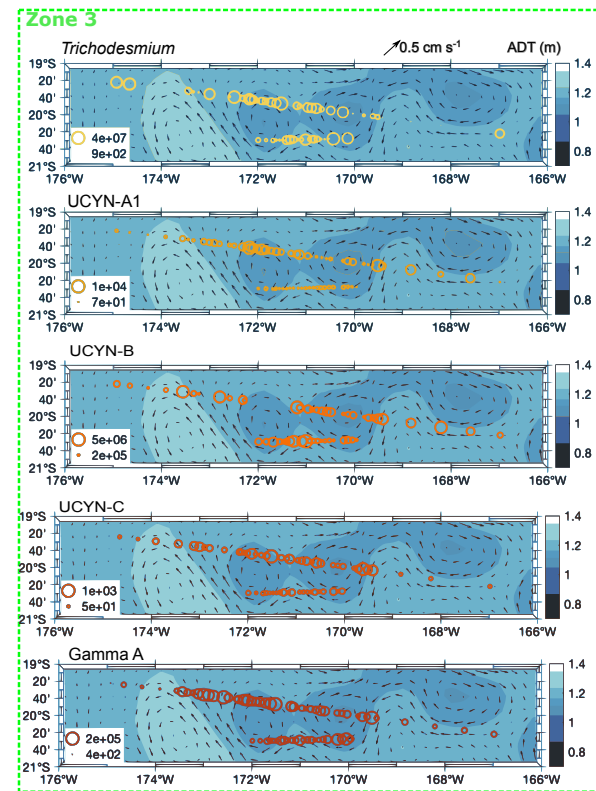
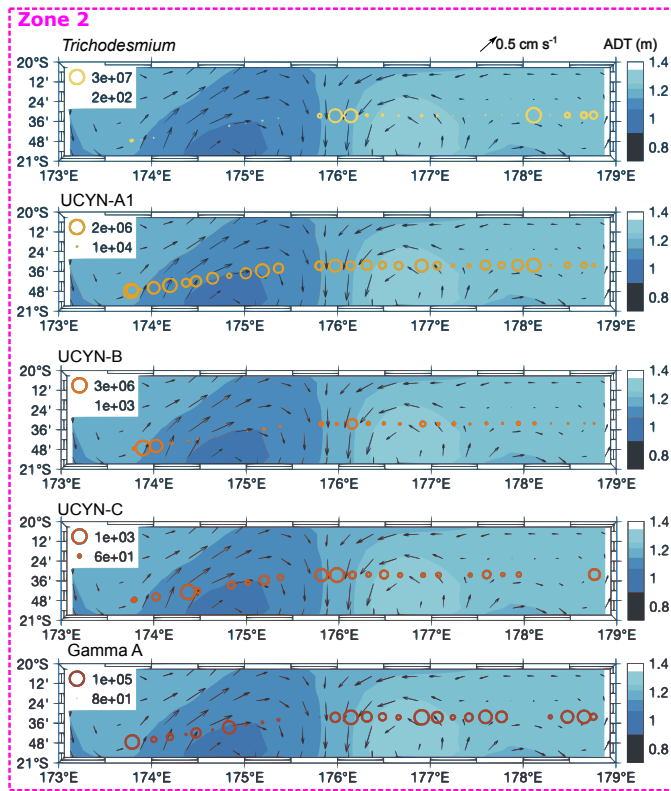
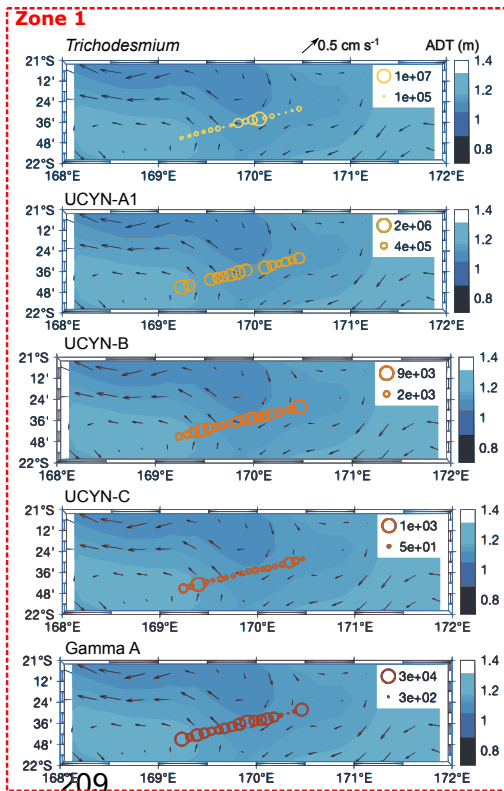
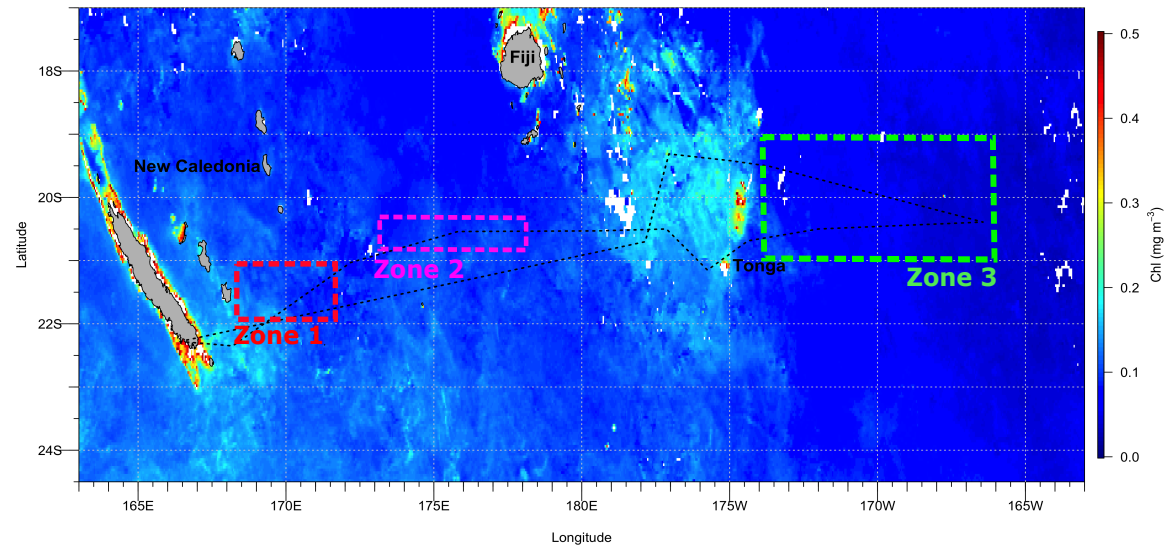
203 finite Lyapunov finite size Lyapunov exponents (FSLE) in zones 1, 2 and 3, respectively.

204 White dots represent sampling locations.

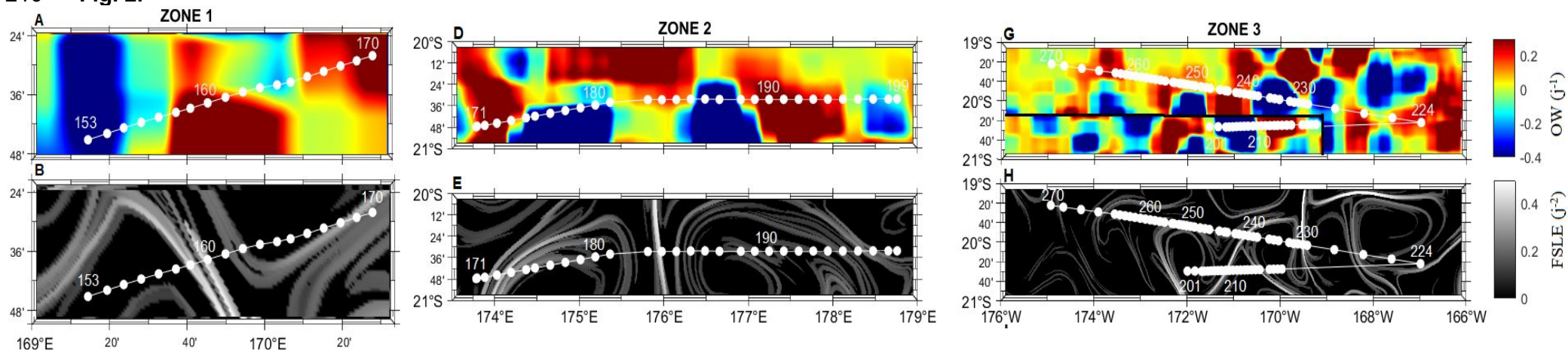
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207



210 **Fig. 2.**



211