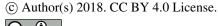
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### Silicon cycle in the Tropical South Pacific: evidence for an active

### 2 pico-sized siliceous plankton

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#### 13 1 Abstract

- 14 This article presents data regarding the Si biogeochemical cycle during two oceanographic cruises
- 15 conducted in the Southern Tropical Pacific (BIOSOPE and OUTPACE cruises) in 2005 and 2015.
- 16 It involves the first Si stock measurements in this understudied region, encompassing various
- oceanic systems from New Caledonia to the Chilean upwelling between 8 and 34° S. Some of the
- 18 lowest levels of biogenic silica standing stocks ever measured were found in this area, notably in
- 19 the Southern Pacific Gyre, where Chlorophyll a concentrations are most depleted worldwide.
- 20 Integrated biogenic silica stocks are as low as 1.08 ± 0.95 mmol m<sup>-2</sup>, and are the lowest stocks
- 21 measured in the Southern Pacific. Size-fractionated biogenic silica concentrations revealed a non-
- 22 negligible contribution of the pico-sized fraction (<2-3 μm) to biogenic silica standing stocks,
- representing  $26 \pm 12$  % of total biogenic silica during the OUTPACE cruise and  $11 \pm 9$  % during
- 24 the BIOSOPE cruise. These results indicate significant accumulation in this size-class, which was
- 25 undocumented for in 2005, but has since then been related to Si uptake by Synechococcus cells.
- Our Si kinetic uptake experiments carried out during BIOSOPE confirmed biological Si uptake by
- 27 this size-fraction. We further present diatoms community structure associated with the stock
- 28 measurements for a global overview of the Si cycle in the Southern Tropical Pacific.

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#### 2 Introduction

Siliceous phytoplankton, especially diatoms, are often associated with nutrient-rich eutrophic 30 31 ecosystems. However, the global budget of biogenic silica production by Nelson et al. (1995) 32 already pointed out the importance of these organisms in oligotrophic areas where, despite their 33 low concentration and due to the geographical extension of these systems, their silica production 34 would be comparable to the total for all areas of diatomaceous sediment accumulation combined. 35 However, studies that have documented the Si cycle in the Pacific Ocean, the largest oligotrophic 36 area of the World Ocean, mainly focused on the Equatorial region, and the northern Subtropical 37 gyre. This article presents the first set of field results from the Southern Pacific Ocean between 8 38 and 34° S spanning from New Caledonia over to the Chilean upwelling, and notably, from the most 39 Chla-depleted region at a worldwide scale (Ras et al., 2008): the South Pacific Gyre (SPG). 40 Diatoms are known to contribute more importantly to primary production in meso- to eutrophic 41 systems, yet several studies have emphasized that even if they are not dominant in oligotrophic regions, they may still contribute up to 10-20 % of C primary production in the Equatorial Pacific 42 43 (Blain et al., 1997). In the oligotrophic Sargasso Sea, their contribution may be as high as 26-48 % 44 of new annual primary production (Brzezinski and Nelson, 1995) and they may represent up to 30 45 % of Particulate Organic Carbon (POC) export (Nelson and Brzezinski, 1997). In the Eastern 46 Equatorial Pacific (EEP), it has been shown that diatoms experience chronic Si-limitation along 47 the Eastern Equatorial divergence in the so-called High Nutrient Low Silicate Low Chlorophyll (HNLSiLC) system (Dugdale and Wilkerson, 1998) as well as Si-Fe co-limitation (Blain et al., 48 49 1997; Leynaert et al., 2001). Furthermore, oligotrophic regions are known to experience 50 considerable variability in nutrient injections leading to episodical blooms depending on the 51 occurrence of internal waves (Wilson, 2011), meso-scale eddies (Krause et al., 2010) storms 52 (Krause et al., 2009), or dust deposition events (Wilson, 2003). In nitrogen (N) depleted areas, 53 punctual diatom blooms in the form of Diatom Diazotroph Associations (DDAs) are also known 54 to occur and to contribute both to new primary production (Dore et al., 2008; Brzezinski et al., 55 2011) but also to benefit to non-diazotrophic diatoms through secondary N-release (Bonnet et al., 56 2016; Leblanc et al., 2016). 57 While biogenic silica was classically associated to the largest size fractions, especially 58 microplankton, a series of recent studies have furthermore evidenced a role for picophytoplankton

such as Synechococcus in the Si cycle, showing that this ubiquitous lineage is able to take up and

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60 accumulate Si (Baines et al., 2012; Ohnemus et al., 2016; Krause et al., 2017; Brzezinski et al., 61 2017). This was evidenced in the field in the Equatorial Pacific, the Sargasso Sea, as well as in culture work, suggesting a widespread diffuse role for this organism, which could be more 62 63 prominent in oligotrophic environments where diatoms are in low abundance. In the EEP, and 64 despite very variable cellular Si content, Synechococcus represented for instance 40 % of water column biogenic silica (BSi) inventory compared to diatoms in 2004, and twice that of diatoms the 65 following year (Baines et al., 2012). The role of small nano-sized diatoms has also probably been 66 67 overlooked and we recently pointed out their general occurrence at the worldwide scale and their 68 occasional regional importance in diatom blooms (Leblanc et al., 2018). 69 Here we present the first set of field results from the Southern Pacific Ocean between 8 and 34° S 70 spanning from New Caledonia over to the Chilean upwelling, and notably, from the most depleted 71 Chla region worldwide (Ras et al., 2008), the South Pacific Gyre (SPG). Results were obtained 72 from two cruises carried out a decade apart following longitudinal sections first in the South Eastern 73 Pacific (SEP) between the Marquesas Islands and the Chilean upwelling, crossing the South Pacific 74 Gyre (BIOSOPE cruise, Oct-Dec 2004) and next in the Southern Western Pacific (SWP) between 75 New Caledonia and Tahiti (OUTPACE cruise, Feb-Apr. 2015). Very similar sampling strategies 76 and homogeneous analyses were conducted regarding the Si cycle and provide new data in this 77 under sampled region. We detail size-fractionated BSi inventories in the water column, Si export 78 fluxes, associated diatom community structure composition as well Si uptake and kinetic rates in 79 the Southern Pacific. Our key results show some of the lowest BSi stocks ever measured, which

#### 82 3 Material and methods

#### 83 **3.1 Sampling strategy**

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84 Results presented here encompass data from two French oceanographic cruises located in the

may warrant for a revision of the contribution of oligotrophic areas to the global Si cycle, and

confirm recent findings of an active biological uptake of Si in the pico-sized fraction.

85 Southern Pacific Ocean (from 10 to 30° S), covering two transects with similar sampling strategies

86 of short and long duration stations. The BIOSOPE (Blogeochemistry and Optics SOuth Pacific

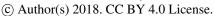
87 Experiment) cruise was undertaken in 2004, while the OUTPACE cruise took place in 2015, both

88 aboard the R/V L'Atalante. The BIOSOPE transect was sampled between the Marquesas Islands

89 (141° W, 8° S) and Concepción (Chile) (72° W, 35° S), between October 24<sup>th</sup> and November 12<sup>th</sup>

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- 90 2004. The OUTPACE transect was sampled between New Caledonia (159° W, 22° S) and Tahiti
- 91 (160° W, 20° S) between February  $18^{th}$  and April  $3^{rd}$  2015 (Fig. 1).

#### 92 **3.2 Hydrology**

- 93 Water sampling and measurements of temperature and salinity were performed using a SeaBird
- 94 SBE 911plus CTD/Carousel system fitted with an in situ fluorometer and 24 Niskin bottles. More
- 95 details about the BIOSOPE cruise strategy are given in the Biogeoscience special issue
- 96 introductory article by Claustre et al., (2008) while the OUTPACE cruise strategy is detailed in
- 97 Moutin et al. (2017). Euphotic layer depths (Ze) were calculated as described in Raimbault et al.
- 98 (2008) and Moutin et al. (2018).

#### 99 3.3 Inorganic nutrients

- 100 Nutrients were collected in 20 mL PE vials and analyzed directly on a SEAL Analytical auto-
- 101 analyzer following Aminot and Kérouel (2007) on board during BIOSOPE and at the laboratory
- during OUTPACE from frozen (-20°C) samples.

#### 103 3.4 Particulate Organic Carbon (POC)

- 104 Seawater samples (~2 L) were filtered through pre-combusted 25 mm GF/F filters, dried at 60 °C
- and stored in 1.5 mL eppendorfs PE tubes. Particulate Organic Carbon (POC) was analyzed on a
- 106 CHN elemental analyzer (Perkin Elmer, 2400 series).

#### 107 **3.5 Total Chlorophyll a (TChla)**

- 108 For pigment analyses, 2 L of seawater were filtered through 25 mm GF/F filters and stored in liquid
- 109 nitrogen and -80°C until processing. Extraction was done in 3 mL 100% methanol, followed by
- sonication and clarification by filtration on a new GF/F filter. Extracted pigments (Chl $\alpha$  and
- 111 fucoxanthin) were then analyzed by HPLC (High Performance Liquid Chromatography) according
- to the procedure detailed in Ras et al. (2008).

#### 113 3.6 Particulate Biogenic and Lithogenic Silica (BSi/LSi)

- 114 Samples were collected for silicon stocks as particulate biogenic and lithogenic silica (BSi and LSi)
- and dissolved orthosilicic acid (Si(OH)<sub>4</sub>) similarly on both cruises. For BSi/LSi, between 1.5 and
- 116 2.5 L Niskin samples were filtered through cascading polycarbonate 47 mm filters. During

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117 BIOSOPE, whole samples were filtered through three cascading filters of 0.2, 2, and 10 μm. During 118 OUTPACE, the size-fractionation used was 0.4 and 3 µm respectively. Filters were rinsed with 0.2 um filtered seawater, folded in 4 and placed in Petri dishes and dried overnight at 60°C. Filters 119 120 were then stored at room temperature and analyzed in the laboratory. BSi and LSi were measured 121 using Paasche (1973) as modified by Nelson et al. (1989): BSi and LSi were extracted on the same 122 filter after successive basic and acid treatments. BSi was extracted during a hot sodium hydroxide (NaOH 0.2 N) attack (60 min), which converted BSi into the dissolved orthosilicic acid form. 123 124 Si(OH)<sub>4</sub> was then quantified using the Strickland and Parsons (1972) spectrophotometric method. 125 After the first basic attack, filters were rinsed free of remaining Si(OH)<sub>4</sub> and dried again at 60°C. LSi, preserved in the sample, was then treated with hydrofluoric acid (HF 2.9 N) for 48 h. In the 126 same way, LSi was measured through quantification of the dissolved Si(OH)4 form. Precisions for 127 BSi and LSi measurements were 4 and 6 nmol L-1 respectively (twice the standard deviation of 128 129 blanks). It has been demonstrated that for coastal samples, significant leaching of orthosilicic acid 130 from LSi could occur during the first NaOH attack (up to 15 %) (Ragueneau and Tréguer, 1994). 131 This is particularly the case when high LSi concentrations are present. Kinetic assays of orthosilicic 132 acid were conducted in some samples from the Marquesas, Gyre, East-Gyre and near Upwelling 133 stations during BIOSOPE, but results revealed negligible LSi interferences after an extraction time 134 of 60 min. Biogenic silica export fluxes were determined from drifting sediment traps deployed at three depths 135 (153, 328, 519 m) at the three long duration stations of the OUTPACE cruise. Each trap was 136 137 deployed for 4 consecutive days, and the average daily flux was quantified by adding the amount 138 of dissolved Si in each trap to the measured BSi concentration to account for BSi dissolution in the 139 trap samples during storage. This step proved necessary, as BSi dissolution ranged between 16 and 140 90 % depending on the samples.

#### 3.7 Si bulk and specific uptake rates (\rho Si/VSi)

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During BIOSOPE, dawn-to-dawn in situ Si uptake experiments were performed using an immersed production line, at six incubation depths (50 %, 25 %, 15 %, 8 %, 4 % and 1 % light level). Seawater (275 mL) samples were spiked with 632 Bq of radiolabeled <sup>32</sup>Si-silicic acid solution (specific activity of 23.46 kBq µg-Si <sup>-1</sup>). For all samples, Si(OH)<sub>4</sub> addition did not exceed 0.4 % of the initial concentration. After incubation, samples were filtered through cascading polycarbonate

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- 147 membranes (0.2, 2 and 10 μm, 47 mm). Filters were rinsed with filtered (0.2 μm) seawater, and
- 148 placed in scintillation vials. The <sup>32</sup>Si uptake was measured in a Packard 1600-TR scintillation
- 149 counter by Cerenkov effect, following the method described by Tréguer and Lindner (1991) and
- Leynaert (1993). Precision of the method averages 10 % to 25 % for the less productive station.

#### 151 3.8 Si uptake kinetics

- 152 Samples used were collected from the same Niskin bottles as those used for in situ incubation at
- the depth of the Chla maximum. Six samples from each depth received non-radioactive Si(OH)<sub>4</sub>
- 154 additions so that concentrations increased respectively by 0, 1.1, 2.3, 4.5, 13.6, 36.4 μM. Bottles
- 155 were incubated on board in a deck incubator for 8h using neutral nickel screens. Samples were
- 156 thereafter treated as described for in situ samples. Kinetic parameters Ks and Vmax were calculated
- by fitting the data to a hyperbolic curve using the Sigmaplot® hyperbola fit.

#### 158 **3.9 Siliceous phytoplankton determinations**

- 159 Seawater samples were preserved with acidified Lugol's solution and stored at 4°C. A 500 mL
- 160 aliquot of the sample was concentrated by sedimentation in glass cylinders for six days. Diatoms
- were counted following the method described by Gomez et al. (2007).

#### 162 **3.10 Phytoplankton net samples**

- During the OUTPACE cruise, additional phyto-net hauls were undertaken at each site integrating
- the 0-150 m water column, except at stations LD-C, 14 and 15 where they integrated the 0-200 m
- water column due to the presence of a very deep Deep Chlorophyll a Maximum (DCM). Samples
- 166 were preserved in acidified lugol, and observed in a Sedgewick-rafter chamber. A semi-quantitative
- species list (dominant, common, rare) was established.

#### 168 **4 Results**

#### 169 4.1 Hydrological systems and nutrient availability

- 170 The hydrological structures crossed during the two transects have been carefully detailed in
- 171 companion papers (Claustre et al., 2008; Moutin et al., 2018; Fumenia et al., 2018) and will not be
- 172 presented in detail here. For the sake of clarity in the present article, main hydrological systems are
- 173 described as follows. During the BIOSOPE cruise, five main hydrological systems were defined

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174 from West to East: the HNLC system comprising long duration (LD) stations MAR (Marquesas)

175 and HNL and station 1; the South Tropical Pacific (STP) system from stations 2 to 6; the central

176 part of the South Pacific Gyre (SPG) from station 7 to 13 including the LD station GYR; the Eastern

177 Gyre HNLC area from stations 14 to 19 including LD station EGY (Eastern Gyre); and the coastal

178 Peru-Chile Upwelling system from station 20 to 21 including LD stations UPW and UPX. During

179 OUTPACE, two main systems were encountered, from West to East, the MA (Melanesian

180 Archipelago) from stations 1 to 12 and including LD stations A and B, and the South Pacific Gyre

181 (SPG) from stations 13 to 15 and including LD station C.

During both cruises, eutrophic to ultra-oligotrophic conditions were encountered. During

183 OUTPACE, Si(OH)<sub>4</sub> concentrations were <1 μM at all stations in the surface layer, with values as

low as  $0.3-0.6 \,\mu\text{M}$  at 5 m depth at certain stations (Fig. 2). The 1  $\mu\text{M}$  isoline was centered at ~100

m in the western part of the MA, and deepened to ~200 m in the SPG. Concentrations at 300 m

186 were quite low (<2 μM) over the entire transect. Nitrate concentrations were similarly depleted in

the surface layer, with values <0.05-0.1 μM in the first 80 m in the western part of the MA (until

188 station 6), which deepened to 100 m over the rest of the transect. Yet nitrate concentrations

189 increased with depth more rapidly than orthosilicic acid, reaching concentrations close to 7 μM at

190 300 m depth.

191 Phosphate was below detection limits in the western part of the MA (stations 1 to 11, and station

192 B) over the first 50 m, but increased to values comprised between 0.1 and 0.2 μM in the SPG.

193 Concentrations only increased to 0.6-0.7 µM at 300 m depth.

194 During BIOSOPE, both the nitracline and phosphacline extended very deeply (~200 m) in the

195 regions of the STP, SPG and Eastern Gyre (Fig. 3). They surfaced at both ends of the transect in

196 the upwelling system and near the Marquesas Islands, but contrary to nitrate which was severely

197 depleted, phosphate was never found <0.1 μM in the surface layer (except at the subsurface at site

198 14). The distribution of orthosilicic acid concentrations were less clearly contrasted, with general

199 surface values comprised between 0.5 and 1  $\mu M$  in the surface layer, except in the western part of

200 the transect from station 1 to the GYR station, and in the upwelling system, where concentrations

were  $> 1 \mu M$  and up to 8.9  $\mu M$  at the surface and increasing rapidly with depth.

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#### 4.2 Total Chla and fucoxanthin distribution

Total Chla (TChla) distributions are presented for both cruises along longitudinal transects together 203 204 with fucoxanthin concentrations, a diagnostic pigment for diatoms (Fig. 4a, b). During OUTPACE, 205 the Melanesian Archipelago system was clearly enriched in TChla compared to the South Pacific 206 Gyre and showed non-negligible concentrations in surface layers as well as a pronounced DCM 207 reaching up to 0.45 µg L<sup>-1</sup> at station 11. The observed DCM progressively deepened eastwards, from 70 m depth at LD-A to 108 m at station 12. The DCM depth generally closely followed the 208 209 euphotic layer depth (Zeu) or was located just below it. The highest surface concentrations were 210 found at stations 1 to 6, between New Caledonia and Vanuatu (0.17 to 0.34 µg L<sup>-1</sup>) while the SPG 211 surface water stations showed a depletion in Chla (0.02 to 0.04 µg L<sup>-1</sup>). A DCM subsisted in this region, but was observed to be deeper (125 to 150 m) and of lower amplitude (0.17 to 0.23 µg L<sup>-1</sup>) 212 213 than in the MA region. Fucoxanthin concentrations closely followed the DCM, but were extremely 214 low over the entire transect, with a maximum concentration of 17 ng L<sup>-1</sup> in the MA and of 4 ng L<sup>-</sup> 215 <sup>1</sup> in the SPG. 216 The BIOSOPE cruise evidenced a very similar Chla distribution in the central SPG than during the 217 OUTPACE cruise, with extremely low surface concentrations and a very deep Chla maximum 218 located between 180 - 200 m ranging between 0.15 and 0.18 µg L<sup>-1</sup>. On both sides of the central 219 SPG, the DCM shoaled towards the surface at the MAR station at the western end of the transect 220 (0.48 µg L<sup>-1</sup> at 30 m) and at the UPW station at the eastern end of the transect (3.06 µg L<sup>-1</sup> at 40 m). Fucoxanthin concentrations did not exceed 9 ng L-1 at any station between the STP and the 221 222 Eastern Gyre (between LD-HNL and station 17), thus showing ranges similar to the OUTPACE cruise measurements. Fucoxanthin increased moderately at the MAR station (85 ng L-1), while it 223 peaked in the Peru-Chile upwelling system with concentrations reaching 1,595 ng L<sup>-1</sup> at LD-UPW 224 225 but remained much lower at the LD-UPX station (200 ng L<sup>-1</sup>).

#### 4.3 Total and size-fractionated Biogenic and Lithogenic Silica standing stocks

Total Biogenic silica (BSi) concentrations were extremely low during the OUTPACE cruise (Fig. 5a) and ranged between 2 and 121 nmol L<sup>-1</sup> in the surface layers, with an average concentration of 17 nmol L<sup>-1</sup>. Similarly to TChla and fucoxanthin, the highest BSi levels were encountered over the MA, with peak values mostly found at the surface, at stations 1 and 2 and from stations 4 to 7, and with very moderate increases at depth (stations 5 and 10). The average BSi concentration decreased

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232 from 20 to 8 nmol L-1 from the MA to the SPG. In the SPG, maximum BSi levels were found at the DCM, between 125 and 150 m. Total Lithogenic Silica (LSi) concentrations were measured in 233 a very similar range (Fig. 5b), between 2 and 195 nmol L<sup>-1</sup>, with a peak value at station 2 at 100 m. 234 235 Also, LSi was ranged from 5 to 30 nmol L<sup>-1</sup> over the transect, with highest values observed close 236 to 100 m, while averaged concentrations followed the same trend as BSi, decreasing from 16 to 9 237 nmol L-1 between the MA and the SPG. During the BIOSOPE cruise, three main regions could be differentiated: a first region covering the 238 ultra-oligotrophic central area from station 1 to station 20, where average BSi concentrations were 239 as low as 8 nmol L-1 (Fig. 5c). At the western end of the transect, the first three stations in the 240 241 vicinity of the Marquesas Islands had higher concentrations with average values of 104 nmol L-1. The eastern end of the transect, located in the Peru-Chile Upwelling system, displayed much higher 242 and variable values, averaging 644 nmol L-1, with a maximum concentration of 2,440 nmol L-1 at 243 244 the UPW station at 60 m. At both ends of the transect, siliceous biomass was mainly distributed in 245 the upper 100 m. Lithogenic silica followed the same trends (Fig. 5d), with extremely low values 246 over the central area (average of 7 nmol L<sup>-1</sup>) with a few peaks close to 30 nmol L<sup>-1</sup> (stations 12 and EGY). LSi was again higher at both ends of the transect but with less amplitude than BSi, with 247 average values of 26 nmol L<sup>-1</sup> close to the Marquesas, and of 57 nmol L<sup>-1</sup> in the coastal upwelling 248 system. The maximum values close to 150 nmol L-1 were associated to the BSi maximums at the 249 UPW sites. 250 251 Size-fractionated integrated BSi stocks were calculated for both cruises over the 0-125 m layer, 252 except for the BIOSOPE cruise at station UPW1, which was only integrated over 50 m and at 253 stations UPX1 and UPX2 which were integrated over 100 m (Fig. 6a, b, Appendix 1). Total BSi 254 stocks were similarly very low in the ultra oligotrophic central gyre and averaged 1 mmol Si m<sup>-2</sup> 255 during both cruises. During BIOSOPE, the stocks measured closed to the Marquesas averaged 9.85 mmol Si m<sup>-2</sup> (with a peak of 24.12 mmol Si m<sup>-2</sup> at the MAR station). On the eastern end of the 256 transect, stocks increased to a peak value of 142.81 mmol Si m<sup>-2</sup> at the UPW2 station and averaged 257 258 65.68 mmol Si m<sup>-2</sup> over the coastal upwelling system. Size-fractionation was only carried out at 259 the long duration stations, but showed an overall non negligible contribution of the pico-sized 260 fraction (0.2-2  $\mu$ m) to BSi standing stocks of 11  $\pm$  9 %. This contribution of the pico-size fraction 261 to integrated siliceous biomass was highest at the GYR, EGY and UPX1 stations reaching 25, 18 262 and 24 % respectively.

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- 263 During OUTPACE, integrated BSi stocks ranged between 1.25 and 4.11 mmol Si m<sup>-2</sup> over the MA,
- and decreased to 0.84 to 1.28 mmol Si m<sup>-2</sup> over the SPG (Fig. 6c, Appendix 2). Here, size-
- 265 fractionation was conducted at all sites and the contribution of the 0.4 3 µm, which will be
- assimilated to the pico-size fraction hereafter, was higher than during BIOSOPE, with an average
- 267 contribution of  $26 \pm 12$  %. The importance of the picoplanktonic Si biomass was higher in the SPG
- 268  $(36 \pm 12 \%)$  than over the MA  $(22 \pm 10 \%)$ .

#### 4.4 Si uptake rates and kinetic constants

- 270 Si uptake rate measurements using the <sup>32</sup>Si radioactive isotope were only conducted during the
- 271 BIOSOPE cruise. The same size-fractionation was applied to production and kinetic experiment
- 272 samples. Vertical profiles of gross production rates (ρSi) confirm the previous stock information
- and show that the most productive stations, in decreasing order of importance, are the UPW, UPX
- and MAR stations (Fig. 7a), with 1.98, 1.19 and 0.22 μmol Si L<sup>-1</sup> d<sup>-1</sup> at 10 m respectively. Si uptake
- 275 rates remained below 0.015 µmol Si L<sup>-1</sup> d<sup>-1</sup> at central HNLC and oligotrophic stations HNL, EGY
- and GYR. Si uptake rates in the picoplanktonic size fraction showed similar trends (Fig. 7b),
- 277 despite higher values at UPX (0.076 μmol Si L<sup>-1</sup> d<sup>-1</sup>) than at UPW (0.034 μmol Si L<sup>-1</sup> d<sup>-1</sup>). Uptake
- 278 rates in that size fraction were intermediate at the MAR station with maximum value of 0.005 µmol
- 279 Si L<sup>-1</sup> d<sup>-1</sup>, while it remained below 0.001 μmol Si L<sup>-1</sup> d<sup>-1</sup> at the central stations. Specific Si uptake
- 280 (VSi normalized to BSi) rates for the picoplanktonic size fraction were even more elevated and
- 281 reached maximum values of 3.64, 1.32, 0.75, 0.37 and 0.14 d<sup>-1</sup> at the UPW, UPX, HNL, EGY and
- 282 MAR stations respectively. Total specific Si uptake rates were extremely high in the coastal
- upwelling system, with values of 2.57 and 1.75 d<sup>-1</sup> at UPX and UPW respectively, and lower but
- still elevated values at the MAR station (0.75 d<sup>-1</sup>). VSi at the central stations (HNL, EGY, GYR)
- were moderate to low and ranged between 0.02 and 0.24 d<sup>-1</sup>.
- 286 Total ΣρSi reached 52.4 mmol Si m<sup>-2</sup> d<sup>-1</sup> at UPW2 station, an order of magnitude higher that the
- 287 rate measured at the MAR station (5.9 mmol Si m<sup>-2</sup> d<sup>-1</sup>) and 3 orders of magnitude higher than at
- 288 EGY, where the lowest value was obtained (0.04 mmol Si m<sup>-2</sup> d<sup>-1</sup>). Integrated picoplanktonic Si
- 289 uptake rates (ΣρSi for 0.2-2 μm) were highest at both upwelling stations (Table 1), followed by the
- 290 MAR station. The relative average contribution of the picoplanktonic size fraction to total Si uptake
- 291 rates was highest at the central stations (32 % at GYR, 19 % at EGY and 11 % at HNL) while it
- was lowest on both ends of the transect (5 % at MAR, and 3 and 7 % at UPW and UPX stations).

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293 Si uptake kinetic experiments were conducted at some long duration stations at the surface and/or 294 depth of the DCM depending on the location of biomass. Results for the picoplanktonic fraction clearly indicate an active biological uptake (Fig. 8), generally following hyperbolic uptake kinetics. 295 296 The hyperbolic curve fitting failed for only 2 out of the 8 kinetic uptake experiments performed on 297 the 0.2-2 µm size-fraction (at the DCM at the HNL station and at the surface at the UPX station). 298 Maximum theoretical specific uptake rates (V<sub>max</sub>) values were high, ranging from 1.9 d<sup>-1</sup> at the 299 MAR station to 6.1 d<sup>-1</sup> at the surface at the UPX station. Half-saturation constants (K<sub>S</sub>) were also elevated ranging from 5.4 µM at the MAR station to as much as 38.3 µM at the UPX station and 300 301 in all cases much higher than ambient Si(OH)<sub>4</sub> concentrations.

#### 4.5 Diatom distribution and community structure

303 Microscopical examinations confirmed the presence of diatoms at every station during both cruises. 304 Diatoms were found in very low abundances during the OUTPACE cruise and only reached maximum values of 20,000-30,000 cells L-1 on two occasions, at stations LD-B at the surface and 305 306 at station 5 at the DCM (Fig. 9a). Mean diatom concentrations in the MA at the surface were 4,440  $\pm$  7,650 cells L<sup>-1</sup> while at the DCM, mean concentrations were about 2-fold lower (2,250  $\pm$  4,990 307 cells L<sup>-1</sup>). Diatom abundance decreased dramatically in the SPG, with values as low as  $25 \pm 19$ 308 cells L<sup>-1</sup> at the surface layers and  $145 \pm 54$  cells L<sup>-1</sup> at the DCM. The richness of diatoms was higher 309 310 in the MA than in the SPG, with an average number of taxa of respectively  $9 \pm 4$  and  $2 \pm 1$  in the surface layer (Fig. 9b). The richness increased at the DCM level, with  $12 \pm 8$  taxa in the MA and 311 312  $5 \pm 1$  taxa in the SPG. Diatom contribution to biomass was accordingly extremely low and remained 313 below 3 % (Fig. 9c). The diatom contribution to C biomass increased more significantly only at two stations: at station LD-B (9 % at the surface) and at station 5 where the maximum value for 314 the cruise was observed (11.5 % at the DCM). 315 During BIOSOPE, the central stations showed a record low diatom abundance with less than 100 316 317 cells L-1 from stations 2 to EGY (Fig. 10). The eastern part of the SPG and the HNL stations were 318 characterized by slightly higher abundances (from 100 to 1,000 cells L-1), followed by the UPX 319 station, where abundances were similar to the MAR station at the surface (~25,000 cells L-1). Highest abundances were observed at the UPW, with bloom values of 256,000 cells L-1 on average 320 (with a peak abundance of 565,000 cells L<sup>-1</sup> at the surface). Similar results compared to OUTPACE 321 322 showed an extremely low richness at all central stations (data not shown) with on average  $3 \pm 2$ 

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4.6 Si export fluxes

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323 diatom taxa, while richness increased at the western HNLC region with  $13 \pm 4$  taxa at the MAR 324 and HNL stations. Richness was highest at the UPW station with  $20 \pm 4$  taxa and decreased again 325 at the UPX station  $(5 \pm 3)$ . 326 The dominant diatom species for each system sampled over the course of the two cruises are 327 summarized in Table 1 and Appendix 3. During OUTPACE, very similar species were encountered 328 in both regions and were mainly dominated by pennate species such as Pseudo-nitzschia spp., P. 329 delicatissima, Cylindrotheca closterium and Mastogloia woodiana. However, Diatom-Diazotroph 330 Associations (DDAs) such as Rhizosolenia styliformis, Climacodium frauenfeldianum and 331 Hemiaulus hauckii were more abundantly found in the MA. Other siliceous organisms such as 332 radiolaria were also more abundant in the SPG and at LD-B than in the MA (Appendix 3). Overall 333 microplanktonic diazotroph abundance were much higher over the MA than in the gyre, with a 334 predominance in plankton nets of Trichodesmium, Richelia intracellularis (alone or in DDAs), Crocosphaera and other filamentous cyanobacteria such as Katagnymene (Appendix 3). 335 Diatom community structure for the BIOSOPE cruise has already been discussed extensively in 336 337 Gomez et al. (2007). In summary, the stations characterized by medium diatom abundances such as MAR, HNL, 18, 20 and EGY (Fig. 10) were mainly dominated by the pennate diatom Pseudo-338 339 nitzschia delicatissima in particular at the MAR station, where it represented on average 90 % of 340 all diatoms over the 0-100 m layer. Extremely low abundance stations (< 200 cells L-1) from the 341 middle of the SPG (stations 2 to 14) did not show any consistent community, with varying dominant 342 species across stations and along vertical profiles as well. Maximum abundances at these sites were 343 consistenly found at depth, between 100 and 200 m. In the Peru-Chile upwelling, diatom 344 community structure was mostly dominated by small and colonial centric species such as 345 Chaetoceros compressus and Bacteriastrum spp. at the UPW station where abundances were 346 highest (565,000 cells L-1) and such as Skeletonema sp. and Thalassiosira anguste-lineata at the 347 UPX station where abundances decreased to 10,000-40,000 cells L<sup>-1</sup>. In this system, the highest 348 abundances were found in the first 10 m.

Particulate silica export fluxes were measured from drifting trap deployments at each long duration station during OUTPACE and are presented in Table 3. BSi daily export fluxes below the mixed

layer at 153, 328 and 529 m were extremely low at all sites, with lowest values at site A (0.5 to 0.1

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353 μmol Si m<sup>-2</sup> d<sup>-1</sup>), highest at site B (3 to 5 μmol Si m<sup>-2</sup> d<sup>-1</sup>) and intermediate at site C (0.5 to 2 μmol

354 Si m<sup>-2</sup> d<sup>-1</sup>).

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#### 5 Discussion

#### 5.1 Si budgets for the South Pacific

In the following section, values from previous studies are compared (Table 4) with the results obtained across this under-studied region of the Pacific Ocean, which is characterized by the most oligotrophic and Chla depleted waters worldwide (Ras et al., 2008). On one hand, size-fractionated biomass and export fluxes were obtained during the OUTPACE program, while on the other hand, size-fractionated production and biomass budgets were quantified during the BIOSOPE program. Regarding values obtained at both ends of the BIOSOPE transects, i.e. in the Peru-Chile upwelling system and in the HNLC system surrounding the Marquesas Islandss,  $\Sigma \rho Si$  rates compare well with previous studies from other similar regions (Table 4). Integrated Si production rates at the UPW stations are in the middle range (42-52 mmol Si m<sup>-2</sup> d<sup>-1</sup>) of what was previously found in coastal upwellings. Values are however almost double to what was previously observed in the Peru upwelling by Nelson et al. (1981), although less productive than the Monterey Bay and Baja Californian upwelling systems (Nelson and Goering, 1978; Brzezinski et al., 1997). For oceanic HNLC areas, values obtained (0.8 to 5.6 mmol Si m<sup>-2</sup> d<sup>-1</sup>) cover the range of rates measured in HNLC to mesotrophic systems of the North Atlantic, Central Equatorial Pacific and Mediterranean Sea. However, integrated rates obtained for the oligotrophic area of the South Eastern Pacific Gyre are to our knowledge among the lowest ever measured. Indeed, values range from 0.04 to 0.20 mmol Si m<sup>-2</sup> d<sup>-1</sup>, they are thus lower than average values previously measured at BATS and ALOHA stations (0.42 and 0.19 mmol Si m<sup>-2</sup> d<sup>-1</sup> respectively) (Brzezinski and Kosman, 1996; Nelson and Brzezinski, 1997; Brzezinski et al., 2011). However, they are similar to measurements performed in autumn (0.04-0.08 mmol Si m<sup>-2</sup> d<sup>-1</sup>) in a severely Si-limited regime of the North Atlantic (Leblanc et al., 2005b). Previous studies have evidenced limitation of diatom Si production by Si (Leynaert et al., 2001), but more recently evidence of co-limitation by both Si and Fe was found in the central Equatorial Pacific (Brzezinski et al., 2008). This would be a more than likely scenario for the SPG, given the very low silicic acid (Fig.2 & 3) and Fe concentrations (0.1 nM and ferricline below 350 m depth, Blain et al., 2008) measured during both cruises. The approximate surface area of mid-ocean gyres was estimated to be 1.3 x 10<sup>8</sup> km<sup>2</sup> (representing

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383 approximately 1/3 of the global ocean) yielding a global contribution of only 26 Tmol Si y-1 gross silica production, i.e. approximately 9-13% of the budget calculated for the global ocean of 240 384 Tmol Si y<sup>-1</sup> according to Nelson et al. (1995). This budget has been recently revised down to 13 385 386 Tmol Si y<sup>-1</sup> reducing the contribution of subtropical gyres to 5-7% of global marine silica 387 production (Brzezinksi et al., 2011; Tréguer and de La Rocha, 2013). However, the range provided 388 in Nelson et al. (1995) in the calculation of their global Si production fluxes for mid-ocean gyres was of 0.2 – 1.6 mmol m<sup>-2</sup> d<sup>-1</sup>. Our values would, once again, lower the contribution of these vast 389 oceanic regions to global Si production, although the present data is only based on two production 390 391 station measurements and warrants further measurements for this region. Nevertheless, it can be 392 expected that the most ultra-oligotrophic region of the world ocean would contribute even less to 393 total Si production than the other oligotrophic systems listed in Table 4 and that in particular, the 394 Si production in the ultra-oligotrophic Southern Tropical Gyre would be lower than the Northern 395 Tropical Gyre. 396 Integrated Si biomass also reflects the very low contribution of diatoms in this system, which was 397 more than 2-fold lower in in the South Pacific Gyre than in the Melanesian Archipelago (Table 5). In the SPG, the lowest Si stocks were measured (~1 mmol Si m<sup>-2</sup>), and were similar to lower-end 398 399 values found in the ultra-oligotrophic Eastern Mediterranean Basin in autumn and in other 400 oligotrophic areas of the North Pacific Subtropical Gyre and of the Sargasso Sea (Table 5 and 401 references therein). It is probable that  $\Sigma \rho Si$  production and BSi stocks could have been slightly 402 higher less than a month earlier in the season on the western part of the OUTPACE transect in the MA. Indeed, the satellite-based temporal evolution of Chla at stations LD-A and LD-B showed 403 404 decreasing concentrations at the time of sampling (de Verneil et al., 2018), while the situation did 405 not show any temporal evolution for the SPG, thus suggesting that the biogenic silica budget for 406 this area is quite conservative under a close to steady-state situation. Lastly, our Si export flux measurements by drifting sediment traps are the lowest ever measured 407 408 and are about two orders of magnitude lower than those from other oligotrophic sites such as BATS in the Atlantic or ALOHA in the Pacific Ocean (Table 6). They represent a strongly negligible 409 410 fraction of surface Si stocks, implying no sedimentation at the time of sampling, and that active 411 recycling and grazing occurred in the surface layer. Indeed, surface temperatures higher than 29°C 412 at all long duration sites, may favor intense dissolution in the upper layer, while active zooplankton grazing was also documented, removing between 3 and 21% of phytoplankton stocks daily (Carlotti 413

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et al., 2018). The virtual absence of silica export from the surface layer well agrees with the conclusion of Nelson *et al.* (1995) that no siliceous sediment is accumulating beneath the central ocean gyres.

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418 5.2 Siliceous plankton community structure in the South Tropical Pacific 419 The main feature observed during OUTPACE was a bi-modal distribution of diatom communities, 420 either at the surface and/or at the DCM level depending on stations, which deepened towards the 421 East, following the increasing oligotrophy gradient, similarly to what was previously described in 422 the Mediterranean Sea (Crombet et al., 2011). A similar feature, showing a particularly deep DCM, up to 190 m in the SPG at 1.2-fold the euphotic depth (Ras et al., 2008), was observed during 423 424 BIOSOPE, revealing a known strategy for autotrophic plankton cells in nutrient depleted waters to 425 stay at the depth where the best light vs nutrient ratio is obtained (Quéguiner, 2013). 426 If the presence of DCMs in oligotrophic mid-ocean gyres are well known, associated to the dominance of small pico-sized phytoplankton (Chavez et al., 1996), studies documenting 427 428 phytoplankton community structure in the South Tropical Pacific Ocean, an area formerly called a 429 « biological desert », are still very scarce. In the review of planktonic diatom distribution by 430 Guillard and Kilham (1977) referencing biocenoses for all main oceanic water bodies and for which 431 thousands of articles were processed, the diatom composition for the South Tropical region was referred to as « No species given (flora too poor) ». Since then only a few studies mentioning 432 433 phytoplankton community structure, mostly located along the equator were published, such as 434 Chavez et al. (1990); Chavez et al. (1991); Iriarte and Fryxell (1995); Kaczmarska and Fryxell (1995); and Blain et al. (1997). In Semina and Levashova (1993) some biogeographical distribution 435 436 of phytoplankton including diatoms is given for the entire Pacific region, yet the Southern tropical 437 region is limited to more historical Russian data and rely on very few stations. The only diatom 438 distribution for the South Tropical Gyre was published for the present data set by Gomez et al. 439 (2007) in the BIOSOPE special issue. Hence the present data contributes to documenting a severely 440 understudied, yet vast area of the world ocean. 441 The oceanic regions covered during both cruises may be clustered into three main ecological 442 systems with relatively similar diatom community structures: the nutrient-rich coastal upwelling system near the Peru-Chile coast, where diatom concentrations exceeded 100,000 cells L<sup>-1</sup>, the Fe-443

fertilized areas of the Melanesian Archipelago and West of Marquesas Islands, where

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445 concentrations could locally exceed 10,000 cells L-1, and all the other ultra-oligotrophic regions (mainly the South Pacific Gyre system) characterized by extremely low diatom abundances, 446 447 usually <200 cells L<sup>-1</sup>. 448 The upwelling area was characterized by a distinct community, not found in the other regions, 449 composed of typical neritic and centric colonial species such as Skeletonema sp., Bacteriastrum 450 spp., Chaetoceros compressus, Thalassiosira subtilis and T. anguste-lineata. These first three species were already documented as abundant in the Chile upwelling by Avaria and Munoz (1987), 451 452 whereas T. anguste-lineata was reported along the Chilean coast from 20°S to 36°S (Rivera et al., 453 1996) and was also documented in the upwelling system West of the Galapagos Islands (Jimenez, 454 1981). The highest pSi production values were measured at the offshore UPW station where 455 Bacteriastrum spp. and Chaetoceros compressus co-occurred as the two dominant species, whereas 456 ρSi rates were halved at the closest coastal station UPX, associated to lower abundances of diatoms, 457 with co-occurring dominance by Skeletonema sp. and Thalassiosira anguste-lineata. 458 The HNLC regions off the Marquesas Islands (MAR) and in the Eastern Gyre (stations 14-20, 459 BIOSOPE) and the oligotrophic region (N-deprived but Fe-fertilized region of the MA), with bloom situations at stations 5 and LD-B (OUTPACE), showed strong similarities in terms of 460 461 diatom community structure and were all mainly dominated by the medium-sized pennate diatoms 462 of the Pseudo-nitzschia delicatissima/subpacifica species complex. These pennate species are 463 commonly reported for the Central and Equatorial Pacific Ocean (Guillard and Kilham, 1977; 464 Iriarte and Fryxell, 1995; Blain et al., 1997). During BIOSOPE, Pseudo-nitzschia delicatissima 465 were often seen forming « needle balls » of ~100 μm diameter which suggests an anti-grazing 466 strategy from micro-grazers (Gomez et al., 2007), a strategy already described by several authors (Hasle, 1960; Buck and Chavez, 1994; Iriarte and Fryxell, 1995). Predominance of pennate diatoms 467 468 over centrics has previously been observed in the N-depleted environment of the Equatorial Pacific 469 (Blain et al., 1997; Kobayashi and Takahashi, 2002), and could correspond to an ecological 470 response to diffusion-limited uptake rates, favoring elongated shapes, as suggested by Chisholm 471 (1992). Furthermore, net samples from the OUTPACE cruise showed a numerically dominant 472 contribution of Cylindrotheca closterium over 0-150 m at most stations of the MA (Appendix 3), 473 with a strong dominance at LD-B, even though their contribution to biomass is minor given their 474 small size. Pseudo-nitzschia sp. and Cylindrotheca closterium have been shown to bloom upon Fe-

addition experiments (Chavez et al., 1991; Fryxell and Kaczmarska, 1994; Leblanc et al., 2005a;

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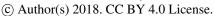




476 Assmy et al., 2007) and may reflect the significantly higher dissolved Fe concentrations measured 477 in the MA (average 1.9 nM in the first 100 m) compared to the SPG (0.3 nM) (Guieu et al., in rev). In the Equatorial Pacific, Fe-amendment experiments evidenced the rapid growth of Cylindrotheca 478 479 closterium, with a high doubling rate close to 3 d<sup>-1</sup> (Fryxell and Kaczmarska, 1994), which can explain why this species is often numerically dominant. 480 Fast growing colonial centric diatoms such as Chaetoceros spp. were notably absent from the MA, 481 except at stations 5 and LD-B, where mesoscale circulation increased fertilization (de Verneil et 482 483 al., 2018) and allowed a moderate growth (observed in both Niskin samples and net hauls), 484 resulting in an increased contribution of diatoms to total C biomass of approximately 10% (Fig. 485 9c). Other typical bloom species such as *Thalassiosira* spp. were completely absent from the 486 species from the Niskin samples but observed at low abundance in some net haul samples. 487 Nonetheless, very large centrics typical of oligotrophic waters such as Rhizsolenia calcar-avis 488 (Guillard and Kilham, 1977) were present in low numbers at all stations and in all net hauls, and 489 represented a non-negligible contribution to biomass despite their low abundance. 490 One difference with the N-replete Marquesas HNLC system was that the hydrological conditions of the MA were highly favorable for the growth of diazotrophs, with warm waters (>29°C), 491 492 depleted N in the surface layer associated to high Fe levels, while P was likely the ultimate controlling factor of N-input by N<sub>2</sub>-fixation in this region (Moutin et al., 2008; Moutin et al., 2018). 493 494 N<sub>2</sub>-fixation rates were among the highest ever measured in the open ocean during OUTPACE in 495 this region (Bonnet et al., 2017), and the development of a mixed community, composed of 496 filamenteous cyanobacteria such as Trichodesmium spp. and other spiraled-shaped species, 497 unicellular diazotrophs such as UCYN, Crocosphaera watsonii, and Diatom-Diazotroph 498 Associations (DDAs) was observed (Appendix 3). The highest rates were measured at the surface 499 at stations 1, 5, 6 and LD-B (Caffin et al., this issue) and the major contributor to N<sub>2</sub>-fixation in 500 MA waters was by far Trichodesmium (Bonnet et al., 2018). In the Niskin cell counts, DDAs known 501 to live in association with the diazotroph Richelia intracellularis such as Hemiaulus hauckii, 502 Chaetoceros compressus and several species of Rhizosolenia such as R. styliformis, R. bergonii, R. 503 imbricata and the centric Climacodium frauenfeldianum known to harbor a genus related to 504 Cyanothece sp. (Carpenter, 2002) were all found in low abundance in the water sample cell counts, 505 contributing to less than 1% of total diatoms. Exceptions were observed at sites 1 and 2 where their 506 contributions increased to 2.3 and 8% respectively. The low contribution of DDAs to the

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diazotrophs community was confirmed by direct cell counts and nifH gene sequencing (Stenegren et al., 2018). Notably, the presence of *Richelia intracellularis* was not observed in the Niskin lugolfixed water samples, but Rhizosolenia styliformis with Richelia, and some isolated Richelia cells were observed abundantly in net hauls. The latter were found to be dominant at stations 1 and LD-B, where the highest fixation rates were measured. Richelia, alone or in association with R. styliformis were much less abundant in the South Pacific Gyre, where Fe is prone to be the limiting nutrient for N<sub>2</sub>-fixation rates despite higher P availability, pointing to less favorable growth conditions for diazotrophs. Yet, the overall dominance of Trichodesmium, Crocosphaera and other filamenteous cyanobacteria (Appendix 3) in the net samples reveals that DDAs were very minor contributors to N2-fixation during OUTPACE. This was also evidenced through NanoSIMS analyses (Caffin et al., 2018). In order to explain the growth of diatoms in this severely N-depleted region, one can quote the use of diazotroph-derived nitrogen (DDN), i.e. the secondary release of N<sub>2</sub> fixed by diazotrophs, which showed to be efficiently channeled through the entire plankton community during the VAHINE mesocosm experiment (Bonnet et al., 2016). In this latter study off shore New Caledonia, Cylindrotheca closterium grew extensively after a stimulation of diazotrophy after P-addition in large volume in situ mesocosms in New Caledonia (Leblanc et al., 2016). As previous studies had already observed a co-occurrence of elevated C. closterium with several diazotrophs (Devassy et al., 1978; Bonnet et al., 2016), this recurrent association tends to confirm our previous hypothesis of a likely efficient use of DDN released as NH<sub>4</sub> by this fast growing species (Leblanc et al., 2016). This could be another factor, besides Fe-availability, explaining its success. A similar hypothesis may be invoked for the presence of Mastogloia woodiana, a pennate diatom known to be occasionally dominant in the North Pacific Subtropical Gyre blooms (Dore et al., 2008; Villareal et al., 2011). It is also a characteristic species of oligotrophic areas (Guillard and Kilham, 1977), often observed in association with other DDAs, which could similarly benefit from secondary N-release (Villareal et al., 2011; Krause et al., 2013). Lastly, the ultra-oligotrophic region of the SPG investigated both during OUTPACE and BIOSOPE revealed a base-line contribution of diatoms with often less than 200 cells L-1 at the DCM and close to zero at the surface. In addition, a dominance of small and large pennate species was observed, such as Nitzschia bicapitata, Pseudo-nitzschia delicatissima, Thalassiothrix longissima, Thalassionema elegans and Pseudoeunotia sp., that have already been documented for the Equatorial Pacific by Guillard and Kilham (1977). Occasional occurrences of some emblematic

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538 species of oligotrophic regions were also observed, such as Chaetoceros dadayi, C. peruvianus, C.

539 tetrastichon or Planktoniella sol. It can be noted that radiolarians were also more abundant and

540 more diverse in the ultra-oligtrophic SPG during OUTPACE than in the MA, while unfortunately

541 no information regarding radiolarians is available for the BIOSOPE cruise.

#### 542 5.3 Evidence for active Si uptake in the pico-planktonic size-fraction in the South Tropical

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The pico-size fraction (<2-3 µm) represented on average 11% of BSi stocks during BIOSOPE, and 26% of BSi stocks during OUTPACE (Fig. 6), which is a non-negligible contribution. If the importance of pico-size fraction in the BSi stock could be explained by detrital components, its contribution to Si(OH)4 uptake during BIOSOPE was really surprising but could be explained in the light of new findings. Indeed, recent studies have evidenced that the pico-phytoplanktonic cyanobacteria Synechococcus can assimilate Si (Baines et al., 2012; Ohnemus et al., 2016; Krause et al., 2017; Brzezinski et al., 2017), which could explain why Si stocks were detected in this size fraction. The first hypothesis was to consider broken fragments of siliceous cells passing through the filter or interferences with lithogenic silica, but these hypotheses were invalidated during BIOSOPE when Si uptake measurements using <sup>32</sup>Si were also carried out on this pico-size fraction and revealed a non-negligible uptake, mainly in the Chilean upwelling systems (Fig. 7). It is also excluded that some broken parts of active nano-planktonic diatoms labelled with 32Si could have passed through the filters because of breakage during filtration, as a kinetic type response was observed in most samples (Fig. 8), implying truly active organisms in the 0.2-2 μm size fraction. Our results are thus in line with previous findings, as no other organisms below 2-3 µm are known to assimilate Si, except some small size Parmales, a poorly described siliceous armored planktonic group which span over the 2-10 µm size class, such as *Tetraparma* sp. (Ichinomiya, 2016), or small nano-planktonic diatoms such as *Minidiscus* (Leblanc et al., 2018), close to the 2 µm limit (Fig. 11 a,b). The latter two species could occur in the 2-3 µm size-fraction, but are very easily missed in light microscopy and require SEM imaging or molecular work for correct identification. Presence of Parmales or nano-planktonic diatoms may explain the measurement of BSi in this  $0.4 - 3 \mu m$ size-class for the OUTPACE cruise, but can be excluded as responsible for the Si uptake measured during BIOSOPE on filters below 2 µm. Rather, during OUTPACE, NanoSIMS imaging revealed that cytometrically sorted Synechococcus cells accumulated Si (Fig. 11c), confirming their potential role in the Si cycle in the South Tropical Gyre.

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According to Baines et al. (2012), the Si content of Synechococcus, in some cases, could exceed that of diatoms, but these authors suggested that they might exert a larger control on the Si cycle in nutrient-poor waters where these organisms are dominant. In the present study, the largest contribution of the pico-size fraction to absolute  $\Sigma \rho Si$  uptake rates occurred at both ends of the transect in the Peru-Chile upwelling region and at the MAR station (Table 1), locations which also corresponded to the highest concentrations of Synechococcus observed (Grob et al., 2007). However, compared to diatoms, this only represented 1 to 5 % of total ΣρSi uptake, which is probably not likely to drive the Si drawdown in this environment. This low relative contribution to ΣρSi was similarly found at the other end of the transect at HNL and MAR station, but where absolute uptake rates were moderate. The largest contribution of the pico-size fraction was measured in the SPG (GYR and EGY sites), where despite very low ρSi values, the relative ΣρSi uptake between 0.2 and 2 µm reached 16 to 25 %. Station GYR as well as stations 13 to 15 are areas that are highly depleted in orthosilicic acid, with concentrations <1 µM from the surface to as deep as 240 m. Hence, it is probable that Synechococcus could play a major role in depleting the Si of surface waters in this area, which are devoid of diatoms. During the OUTPACE cruise, there were no clear correlations between Synechococcus distributions and the measured 0.4-3 µm BSi concentrations. This could be explained by the extremely wide range of individual cellular Si quotas estimated to vary between 1 and 4700 amol Si cell-1 (with an average value of 43) from cells collected in the North Western Atlantic (Ohnemus et al., 2016), where Synechococcus contributed up to 23.5 % of  $\Sigma$ BSi (Krause et al., 2017). In the latter study, a first-order estimate of the contribution of Synechococcus to the global annual Si production flux amounted to 0.7-3.5%, which is certainly low, but comparable to some other important input or output fluxes of Si (Tréguer and De la Rocha, 2013).

#### 6 Conclusion

The Sargasso Sea (BATS) and the North Tropical Pacific Ocean (ALOHA) were until now the only two subtropical gyres where the Si cycle was fully investigated during time-series surveys. In this paper, we provide the first complementary data from two cruises documenting production, biomass and export fluxes from the oligotrophic to ultra-oligotrophic conditions in the South Tropical Pacific Gyre, which may lower the estimates of diatom contribution to primary

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598 productivity and export fluxes for the Pacific Ocean and for mid-ocean gyres in general. The mid-599 ocean gyres (representing 1/3 of the global ocean) are severely under-sampled regarding the Si 600 cycle, and may encompass very different situations, in particular in the vicinity of Islands and 601 archipelagos with reduced bathymetry, and nutrient-fertilized surface waters, to HNLC waters and 602 even HNLSiLC along the equatorial divergence (Dugdale and Wilkerson, 1998). The mid-ocean 603 gyres contribution to Si production was recently revised down to 5-7% of the total by Brzezinski et al. (2011) building on estimates from the North Subtropical Pacific Gyre. The present study 604 605 points to even lower values for the South Pacific Gyre, confirming its ultra-oligotrophic nature, 606 and should further decrease this estimate. These findings clearly warrant for improved coverage of 607 these areas and for more complete elemental studies (from Si production to export). 608 Diatom community structure and contribution to total biomass could be summarized by 609 differentiating 3 main ecosystems: (i) the eutrophic Peru-Chile coastal upwelling, where colonial 610 neritic centric diatoms such as Skeletonema sp., Chaetoceros sp. and Thalassiosira sp. contributed 611 to elevated abundances (>100,000 cells L<sup>-1</sup>) and very high Si uptake rates; (ii) the HNLC region 612 off the Marquesas Islands and the nutrient depleted but Fe-fertilized region of the Melanesian 613 Archipelago, where a distinct community largely dominated by small and medium-sized pennates 614 such as Cylindrotheca closterium and Pseudo-nitzschia delicatissima developed to moderate levels (<30,000 cells L-1), while Fe levels in the MA further stimulated diazotrophs and DDAs which 615 616 could have stimulated diatom growth through secondary N release; (iii) the SPG, characterized by 617 ultra-oligotrophic conditions and Fe-limitation, where diatoms reached negligible abundances 618 (<200 cells L-1) with species typical of oligotrophic regions, such as Nitzschia bicapitata, 619 Mastogloia woodiana, Planktoniella sol as well as radiolarians. 620 Finally, thanks to both size-fractionated biomass and Si uptake measurements, we were able to 621 confirm a potential role for Synechococcus cells in Si uptake in all environments, which may be of 622 importance relative to diatoms in oligotrophic regions, but probably negligible in highly productive 623 regions such as coastal upwellings. Mechanisms linked to Si uptake in Synechococcus and its 624 ecological function still need to be elucidated, and further attention to the Si cycle needs to be 625 placed on this elusive pico- and nano-sized fraction.

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#### 626 **7 Data availability**

#### **8 Author contribution**

- 628 KL treated all data and wrote the paper. BQ and PR sampled on board and analyzed Si data from
- 629 the BIOSOPE cruise. SH-N and O.G. collected nutrient samples on board and analyzed nutrient
- 630 data from the OUTPACE cruise. VC sampled for all BSi data and diatom diversity on board, and
- 631 analyzed plankton net samples on the OUTPACE cruise. CB analyzed all Si data and ran diatom
- 632 cell counts during her Masters thesis. HC and JR were in charge of all pigment data for both cruises.
- 633 NL collected and analyzed Si export flux data from the OUTPACE drifting sediment traps.

#### 634 9 Competing interests

The authors declare that they have no conflict of interest.

#### 636 **10 Special Issue Statement**

- 637 This article is part of the special issue "Interactions between planktonic organisms and
- 638 biogeochemical cycles across trophic and N<sub>2</sub> fixation gradients in the western tropical South Pacific
- 639 Ocean: a multidisciplinary approach (OUTPACE experiment)"

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869 870 871	Figure 1: Bathymetric map of the stations sampled in the South Pacific Ocean during the OUTPACE cruise (FebApr. 2015) and the BIOSOPE cruise (OctNov. 2004). Short-term duration stations are indicated in white, and long-term duration stations (typically 2-3d) in black.
872	Figure 2: Nutrient distribution (orthosilicic acid, nitrate, phosphate, in $\mu M$ ) along the OUTPACE cruise transect.
873	Figure 3: Nutrient distribution (orthosilicic acid, nitrate, phosphate, in $\mu M$ ) along the BIOSOPE cruise transect.
874 875 876	<b>Figure 4 :</b> Top panel: TChl $\alpha$ distribution during the OUTPACE cruise in the SW Pacific (in $\mu$ g L $^{-1}$ ) with fucoxanthin overlay lines in white (in ng L $^{-1}$ ). Lower panel: TChl $\alpha$ distribution during the BIOSOPE cruise in the SW Pacific (in $\mu$ g L $^{-1}$ ) with fucoxanthin overlay lines in white (in ng L $^{-1}$ ). Black dots indicated the Ze depth.
877 878	Figure 5: a.c Biogenic silica (BSi) and b.d. Lithogenic Silica (LSi) distribution during the OUTPACE and BIOSOPE cruises respectively (in $\mu$ mol $L^{-1}$ ).
879 880 881 882 883	Figure 6: a.b Size-fractionated integrated Biogenic silica ( $\Sigma$ BSi) standing stocks (0-125 m) during the BIOSOPE cruise. UPW1 stations was only integrated over 50 m and UPX1 and UPX2 over 100 m. The b panel shows a zoom over the central section where integrated BSi stocks are an order of magnitude lower than at the two extremities of the transect. Grey bars indicate that no size-fractionation was conducted and represent the total $\Sigma$ BSi. C. Size-fractionated integrated Biogenic silica ( $\Sigma$ BSi) standing stocks (0-125 m) during the OUTPACE cruise.
884 885	Figure 7: a. Total absolute Si uptake rates ( $\rho$ Si) vertical profiles (in $\mu$ mol $L^{-1}$ $d^{-1}$ ) at the LD stations MAR, HNL, GYR, EGY, UPX and UPW. b. $\rho$ Si in the 0.2 - 2 $\mu$ m size fraction at the same sites.
886 887 888	Figure 8: Si uptake kinetic experiments conducted at the LD stations MAR, HNL, GYR, EGY, UPX at various euphotic depths. Specific Si uptake rates (in $d^{-1}$ ) are plotted vs Si(OH) <sub>4</sub> increasing concentrations. Data was adjusted with hyperbolic curves when statistically relevant and $V_{max}$ and $K_S$ values indicated below each curve.
889 890	Figure 9: Diatoms cellular concentrations (cells $L^{-1}$ ) derived from a. Niskin cell counts, b. number of taxa and c. relative contribution to POC biomass (%) at the surface and DCM levels during the OUTPACE cruise.
891 892	Figure 10: Diatoms cellular concentrations (cells $L^{-1}$ ) derived from Niskin cell counts at several depths during the BIOSOPE cruise (data from Gomez et al. 2007).
893 894 895	<b>Figure 11:</b> Potential siliceous organisms in the picoplanktonic (<2-3 μm) size fraction. a.Siliceous scale-bearing Parmale ( <i>Tetraparma pelagica</i> in SEM, photo courtesy of Dr. J. Young), b. centric diatom ( <i>Minidiscus trioculatus</i> ), c. <i>Synechoccocus</i> cell showing Si assimilation in red ( <sup>28</sup> Si) in NanoSIMS (photo courtesy of M. Caffin).
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#### 14 Tables

Table 1: Size-fractionated integrated Si production rates in mmol Si  $m^{-2}$   $d^{-1}$  in the SEP (BIOSOPE). Integrated Si production was measured over the 0-1% light depth range for each site (in parenthesis in column 5), and normalized over 100 m considering a zero production at 100 m in the last column.

Stations	ΣρSi <2μm	ΣρSi 2-10 μm	ΣρSi >10μm	Total ΣρSi	Total ΣρSi over 0-100 m
MAR1	0.15	0.51	4.37	5.02 (50 m)	5.87
HNL1	0.05	0.12	0.58	0.75 (80 m)	0.77
GYR2	0.01	0.01	0.02	0.04 (110 m)	0.04
EGY	0.03	0.07	0.09	0.19 (100 m)	0.19
UPW2	0.62	2.88	39.66	43.16 (35 m)	52.36
UPX1	1.07	5.90	13.49	20.46 (30 m)	42.46

Table 2: Dominant diatom species in each main system of the BIOSOPE and OUTPACE cruises. Taxonomic information for the OUTPACE cruise are derived from discrete samplings at the surface and DCM and phytoplankton nets, while information for the BIOSOPE cruise were obtained through an average of six discrete samples over the euphotic layer (see Gomez et al., 2007).

Cruise	Oceanic system	Dominant diatom species
OUTPACE	Melanesian Archipelago	Pseudo-nitzschia spp. & Pseudo-nitzschia delicatissima, Cylindrotheca closterium, Mastogloia woodiana, Leptocylindrus mediterraneus, Hemiaulus membranaceus, Chaetoceros spp. (hyalochaete), Pseudosolenia calcar- avis, Climacodium frauenfeldianum, Planktoniella sol
	South Pacific Gyre	Climacodium frauenfeldianum, Pseudo-nitzschia spp., Chaetoceros spp. (hyalochaete), Pseudo-nitzschia delicatissima, Mastogloia woodiana
BIOSOPE	Western HNLC area (Marquesas)	Pseudo-nitzschia delicatissima, Rhizosolenia bergonii, Thalassiothrix longissima, Plagiotropis spp., Pseudo- nitzschia pungens, P. subpacifica
	South Tropical Pacific	Nitzschia bicapitata species complex, Nitzschia sp., Thalassiothrix longissima, Pseudo-nitzschia delicatissima
	South Pacific Gyre	Hemiaulus hauckii, Chaetoceros curvisetus, Bacteriastrum cf. comosum
	Eastern Gyre	Pseudo-nitzschia cf. delicatissima, Pseudo-nitzschia cf. subpacifica, Pseudoeunotia sp.
	Peru-Chile Upwelling	Chaetoceros compressus, Bacteriastrum sp., Thalassiosira subtilis, Chaetoceros cf. diadema, Skeletonema sp., Pseudo-nitzschia sp.

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Table 3: Particulate biogenic and lithogenic (BSi and LSi) Silica in drifting sediment traps at each long duration station during OUTPACE cruise, at 153, 328 and 519 m depth.

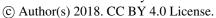
915				
016		Trap depth	BSi	LSi
916		m	μmol Si m <sup>-2</sup> d <sup>-1</sup>	μmol Si m <sup>-2</sup> d <sup>-1</sup>
917	A	153	0.5	23.1
<i>711</i>		328	0.2	4.6
918		519	0.1	5.2
	В	153	2.6	0.4
919		328	2.9	0.6
020		519	4.8	1.1
920	C	153	1.8	0.5
921		328	0.5	0.2

Table 4: Integrated Si production rates in various systems for comparison with our study from direct  $^{32}$ Si uptake measurements or from indirect silicate utilization ( $\Delta$ SiO<sub>4</sub>) estimates (\*).

Region	Integrated Si production	References
	rate	
	ΣρSi (mmol m <sup>-2</sup> d <sup>-1</sup> )	
Coastal upwellings		
BIOSOPE: Peru-Chile upwelling	42 – 52 (UPW)	This study
Baja California	89	Nelson and Goering, 1978
Monterey Bay	70	Brzezinski et al., 1997
Peru	27	Nelson et al., 1981
Southern California Current coastal waters	1.7 - 5.6	Krause et al., 2015
Oceanic area		
BIOSOPE: South Eastern Pacific (HNLC)	0.8 - 5.6 (HNL - MAR)	This study
Gulf Stream warm rings	6.4	Brzezinski and Nelson, 1989
Central Equatorial Pacific (HNLC)	3.9	Blain et al., 1997
North Pacific (OSP)	5.1	Wong and Matear, 1999*
North Atlantic (POMME)	1.7	Leblanc et al., 2005b
North Atlantic (Bengal)	0.9	Ragueneau et al., 2000
Mediterranean Sea (SOFI)	0.8	Leblanc et al., 2003
Oligotrophic area		
BIOSOPE: South Eastern Pacific Gyre	0.04 (GYR) - 0.2 (EGY)	This study
Central Equatorial Pacific	0.8 - 2.1	Blain et al., 1997
Eastern Equatorial Pacific	0.2 - 2.5	Leynaert et al., 2001; Adjou et al., 2011; Krause
-		et al., 2011, Demarest et al., 2011
Central North Pacific	0.5 - 2.9	Brzezinski et al., 1998
North Pacific Subtropical Gyre	0.1 - 1.7	Krause et al., 2013
North Pacific Subtropical Gyre (ALOHA)	0.1 - 0.5	Brzezinski et al., 2011
Sargasso Sea	0.5	Brzezinski and Nelson, 1995
Sargasso Sea (BATS)	0.1 - 0.9	Brzezinski and Kosman, 1996 (1996), Nelson an Brzezinski, 1997

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Table 5: Summary of  $\Sigma BSi$  stocks in mmol Si m<sup>-2</sup> for the OUTPACE and BIOSOPE and other oceanic and oligotrophic systems.

	Region	Average Integrated	References
)		Si biomass	
		ΣBSi (mmol m <sup>-2</sup> )	
	Coastal upwellings		
	BIOSOPE: Peru-Chile upwelling	$65.7 \pm 53.8$	This study
,	Southern California Current coastal waters	$53.2 \pm 39.3$	Krause et al., 2015
	Oceanic area		
	Southern California Current oceanic waters	$1.6 \pm 0.3$	Krause et al., 2015
931 932 933 934 935 936	BIOSOPE: South Eastern Pacific (HNLC)	11.9 ± 10.9	This study
	Oligotrophic area		
	Mediterranean Sea (BOUM)	1.1 - 28.2	Crombet et al., 2011
931 932 933 934 935	Sargasso Sea (BATS)	$4.0 \pm 6.8$	Nelson et al., 1995
932 S6 933 S6 934 O 935 S6 936 N N 937 E B O	Sargasso Sea	0.9 - 6.1	Krause et al., 2017
	North Pacific Subtropical Gyre	1.6 - 12.8	Krause et al., 2013
	North Pacific Subtropical Gyre (ALOHA)	$3.0 \pm 1.1$	Brzezinski et al., 2011
	Central North Pacific	$7.1 \pm 3.0$	Brzezinski et al., 1998
	Eastern Equatorial Pacific	3.8 - 18.0	Krause et al., 2011
	BIOSOPE: South Eastern Pacific Gyre	1.1 ± 1.1	This study
	OUTPACE: South Western Pacific Gyre	$1.0 \pm 0.2$	This study
3	OUTPACE: Melanesian Archipalago	$2.4 \pm 1.0$	This study

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# Table 6: Summary of Si export fluxes in sediment traps at various depths in µmol Si m<sup>-2</sup> d<sup>-1</sup> for the OUTPACE cruise compared to other studies.

Region	Sediment trap depth (m)	Average Si export fluxes (µmol m <sup>-2</sup> d <sup>-1</sup> )	References
Coastal upwellings			
Southern California Current coastal waters	100	$8,000 \pm 5,760$	Krause et al., 2015
Oceanic area			
North Atlantic (NABE)	400	10 - 145	Honjo and Manganini, 1993
North Atlantic (POMME)	400	2 - 316	Mosseri et al., 2005; Leblanc et al., 2005b
North Pacific Subtropical Gyre (ALOHA)	150	14 - 300	Brzezinski et al., 2011
Oligotrophic area			
Sargasso Sea (BATS)	150	17 - 700	Nelson et al., 1995
Sargasso Sea (BATS)	150	130	Brzezinski and Nelson, 1995
	200	113	
	300	85	
OUTPACE: South Western Pacific Gyre	153	1.8	This study
•	328	0.5	Ž
OUTPACE: Melanesian Archipelago	153	1.6	This study
1 0	328	1.6	<b>y</b>
	519	2.5	

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#### 946 **15 Appendices**

Stations	ΣBSi 0.2-2 μm (mmol m <sup>-2</sup> )	ΣBSi 2-10 μm (mmol m <sup>-2</sup> )	ΣBSi >10 μm (mmol m <sup>-2</sup> )	Total ΣBSi (mmol m <sup>-2</sup> )
MAR1	0.36	3.49	20.28	24.12
NUK1	0.34	0.66	2.40	3.40
HNL1	0.20	2.34	5.54	8.09
1				3.79
2				0.40
3				0.48
4				0.31
5				0.20
6				0.18
7				0.20
8				0.49
GYR2	0.30	0.37	0.55	1.23
GYR5	0.13	0.24	0.39	0.75
11				0.42
12				0.82
13				0.16
14				0.47
15				1.03
EGY2	0.29	0.45	0.87	1.60
EGY4	0.15	0.25	0.65	1.05
17				2.36
18				2.47
19				0.45
20				1.50
21				3.48
UPW1*	1.27	5.36	55.43	62.05
UPW2	3.75	15.28	124.10	142.81
UPX1**	7.66	9.80	14.64	32.00
UPX2**	2.27	8.12	15.49	25.88

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Appendix 1: Integrated size-fractionated Biogenic Silica concentrations ( $\Sigma$ BSi) in the South Eastern Pacific (BIOSOPE cruise) over 0-125 m. 0-50 m for \* and 0-100 m for \*\*.

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C4-4!	ΣBSi 0.4-3 μm	ΣBSi > 3 µm	Total ΣBSi
Stations	(mmol m <sup>-2</sup> )	(mmol m <sup>-2</sup> )	(mmol m <sup>-2</sup> )
1	1.24	2.52	3.76
2	0.39	3.56	3.95
3	0.43	1.83	2.26
A	0.26	1.83	2.09
4	1.06	2.24	3.30
5	0.51	3.60	4.11
6	0.70	1.80	2.49
7	0.39	1.95	2.34
8	0.39	1.12	1.51
9	0.50	1.45	1.96
10	0.77	0.98	1.75
11	0.24	1.00	1.24
12	0.17	1.29	1.46
В	0.30	1.60	1.89
13	0.17	0.96	1.13
C*	0.50	0.93	1.43
C*	0.59	1.03	1.61
14*	0.68	1.02	1.70
15*	0.76	1.38	2.14

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Appendix 2: Integrated size-fractionated Biogenic Silica concentrations (  $\Sigma\,BSi)$  in the South Western Pacific (OUTPACE cruise) over 0-125 m and 0-200 m for \*.

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STATION	1	2	3	Α	Α	Α	Α	Α	4	5	6	7	8	9	10	11	12	В	В	В	В	В	С	С	С	С	С	14	ı
Date	22/02	23/02	24/02	26/02	27/02	28/02	1/3	2/3	4/3	2/3	6/3	2/3	8/3	8/3	10/3	11/3	12/3	15/3	16/3	17/3	18/3	19/3	23/3	24/3	25/3	26/3	27/3	29/3	
Diatoms	2	2	2	2	7	7	-	┢	_	-	-	-	-	_			1	-	-	1	-	_	+ '	-	Ë		-	-	Ŧ
Asterolampra marylandica	H	H	H		H			H	-		-	-	-	-		H	-	-	-	H	-		٠	۰	٠		H	Н	t
Asteromphalus heptactis/roperianus	H	-	H		H			H						-		H	-	-	-	H		H	╆	۰	+	$\vdash$	$\vdash$	H	t
Bacillaria paxillifera		H	H					H						_		Н	_	-	-	Н	_	Н	т	т	+		_	_	t
Bacteriastrum comosum	H	Н	H		H			H	-					-		H	-			H			╁	╁	╁	<del>                                     </del>	┢	┢	t
Bacteriastrum elongatum		H						H	_					_		Н	_	-	-	Н	-		٠	۰	+	H		H	t
Cerataulina cf pelagica	H		H					H	_					_		Н	_	-	-	Н	-		т	٠	+	H	т	H	t
Chaetoceros hyalochaetae spp/	H		H		H			H	-					-		H						H	╁	۰	H				t
Chaetoceros compressus with Richelia	H		H		Ħ			Ħ												_			т	т	_		т	т	t
Chaetocer os dadayi	m	H	H		H			H	_					_		Н	_	_	_	Н	_		1	t	t			Н	t
Chaetoceros peruvianus		H		H	H				-					-		H	-			H			т	t	╁		_		t
Climacodium frauendfeldianum	H	H	Ħ	Н	Ħ			Ħ																					t
Cylindrotheca closterium		Н			Н											_							г	т	т		_		Ť
Dactyliosolen blavyanus	F	H	П	Т	H		Т		_	Т	Т	т	т	_		т	_						т	t	t	т	T	m	t
Dactyliosolen fragilissimus	H	Г	H	Н	t			Г												Н		Н	1	t	t	H	t	t	†
Dactyliosolen phuketensis	H	T	T		T			T															t	t	t	H	T	T	t
Ditylum brightwelli	H	т	Ħ	Н	Ħ			H	Н							Н		Н	Н	Н	Н	Н	1	t	t	H	H	H	†
Gossleriella tropica	H	t	t	Н	t			t						т		Н	т			Н		Н	1	t	t	H	t	t	t
Guinardia cylindrus with Richelia		Г	T	Т	T			T			П	П	П			П				П		Т	T	t	т	t	T	T	t
Guinardia striata		г	H	H	H	H	H	H	Н		Н	Н	Н	Н	H	H	Н	$\vdash$	$\vdash$	H	$\vdash$	H	╁	۳	٢	t	$\vdash$	t	†
Haslea sp.	F	Н	Ħ		Ħ			H															t	t	1	H	t	t	t
Helicotheca tamesis	H	H	Ħ		Ħ			H										_	_		_		t	t	1	H	t	t	t
Hemiaulus membranaceus	H	H			H			H															т	t	t	H	t	t	t
Hemiaulus hauckii		H	Ħ	Н	H			H															т	t	t		H	H	t
Hemidiscus sp.	m	H	H		H			H	_					_		Н	_	_	_	т	_		т	۰	t				t
Leptocylindrus mediterraneus		H	H		H			Ħ								Н		_		Н	_		t	۰	t				t
Lioloma pacificum	F	Н	H		H			Ħ	_		_	_		_			_		_				т	t	1	H	Н	Н	t
Navicula/Nitzschia/Mastogloia					H			H															т	т	T	Т	T		t
Nitzschia longissima	г	Т	Т	_	Н			т			_					$\vdash$				$\vdash$			T	t	+	$\vdash$	T	г	t
Planktoniella sol	H				H																		t	t			H	H	t
Proboscia alata	H	г												_			_	_	_				т	t	т		Н	Н	t
Pseudoguinardia recta	Н		H		Ħ			Н								_				_			Н	t	•	т	т	т	t
Pseudolenia calcar-avis			H		H																		Н	Н	+		H		t
Pseudo-nitzschia	H	H			H			t															т	т	+		H		t
Rhizosolenia sp. with Richelia		г	H		H			H						_		Н	_			-	_	_	т	Н	۰	Н	┢		t
Rhizosolenia imbricata/bergonii		Н	H		H			H	_									_	_	_	_		╁	т	٠		H		t
Rhizosolenia formosa	t	m	H	_	H		Н	H	_		_	_	Н	_		т	_	_	_	т	_		т	٠	十		H	┢	t
Skeletonema sp.	H	H	Ħ		Ħ			H								Н				Н			t	t	t	т	H	H	t
Stephanopyxis sp.	H	H						H	_					_		Н	_	-	-	Н	-		۲	٠	+	H	┢	H	t
Thalassionema sp.	H	H	H		H			H	_								_	_	_		_		٠	۰	٠		┢		t
Triceratium sp.		Н			H			H	_							Н	_	-	-	Н	-		t	t	+		H		t
Undetermined pennates < 50 μm	H	H	H		H			H								H							т	т	+	_	-		t
Undetermined pennates 100-200 µm	H	H	H		H			H	_					_		H	_			_	_		т	Н	H		H	Н	t
Undetermined pennates >200 μm		Н			H											Н							۲	t	т	Н	_	H	t
Thalassiosira-like ~15 µm		H			H			H	_					_		Н		_	_	_	_		۲	т	1	H	┢	H	t
Thalassiosira-like ~50 µm	H	H	H		H			H															H	۰	H				t
Thalassiosira-like ~100 µm	H	H			H		_	H													_		т	т	+	Н		Н	t
Radiolarians	H	H	H		H			Г	-					-									٢	۲	✝	H	F	H	t
Single radiolarians	H	Н			H			H							Н	H	H				$\vdash$		t	t	t				t
Colonial radiolarians	Н	Н			H			Н						Н	Н	Н	Н				Н		т	۲	۲			г	f
Silicoflagellates	H	Н	┢	H	┢		1	┢		1	H	H	H	H		H	H			Н	<del>                                     </del>	H	۰	۰	Г				†
Dictyocha speculum	H	H	H		H			H	Н			Н	Н	Н		H	Н	-	-	H	-	Н	╆	۲	✝	H	┢	┢	t
Diazotrophs	H	H	т		H		Н	Г	$\vdash$	Н		Н	Н	$\vdash$		H	$\vdash$	1	1	H	1	H	╁	۲	+	H	┢	H	t
Trichodesmium spp.					H													١,	١,	۱,	١,		٠	۰	٠	Н	⊢	$\vdash$	t
Richelia intracellularis					┢																		Н	۰	┲	$\vdash$	⊢		t
Croccosphera sp.		Н			┢			Н					H	H		H	H						٠	۰	٠		┢		+
Other filamenteous cyanobacteria		Н	H		┢			H															н	Н			⊢	⊢	+

Appendix 3: Semi-quantitative contribution of siliceous plankton (diatoms, radiolarians, silicoflagellates) and diazotrophs in plankton nets hauls of 35  $\mu$ m mesh size (over 0-150 m at all sites except but over 0-200 m at stations 14 and 15) during the OUTPACE cruise. Long duration stations were sampled every day. Light grey, medium grey and dark grey correspond to minor, common and dominant abundances respectively.

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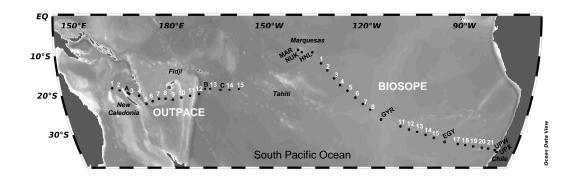






Figure 2

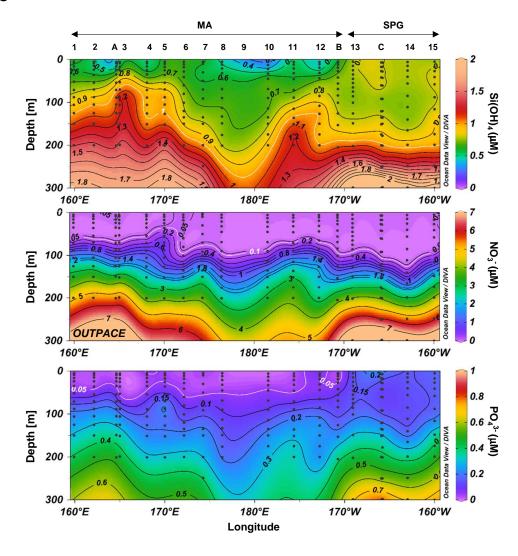
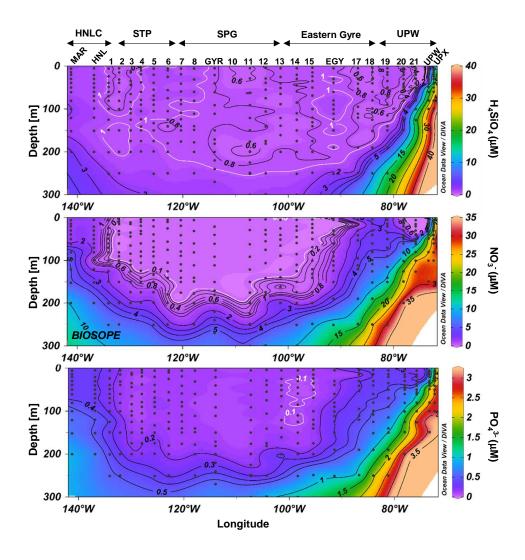






Figure 3







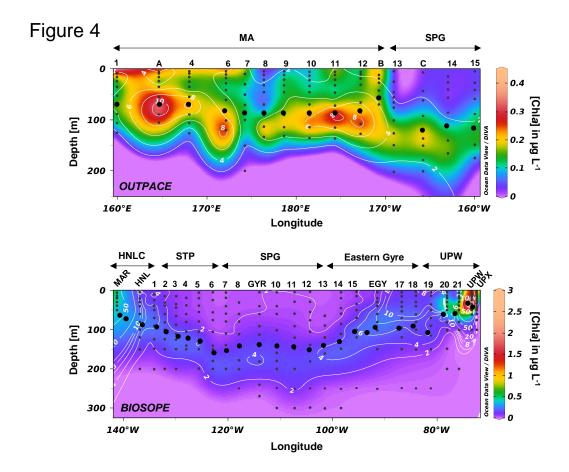
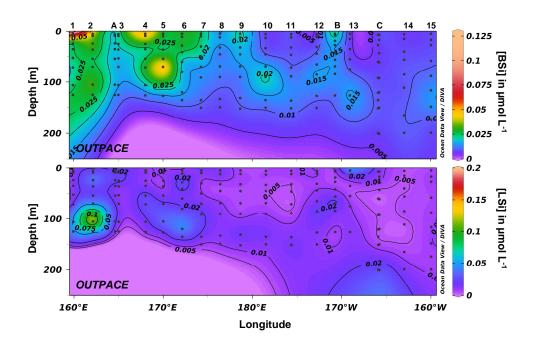






Figure 5



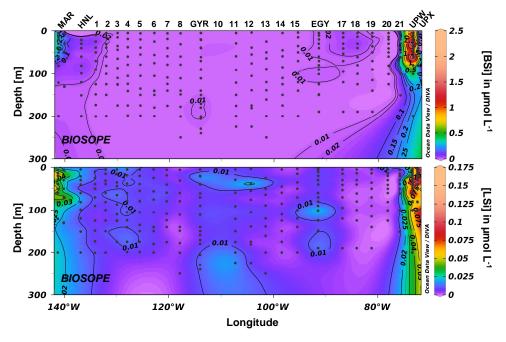
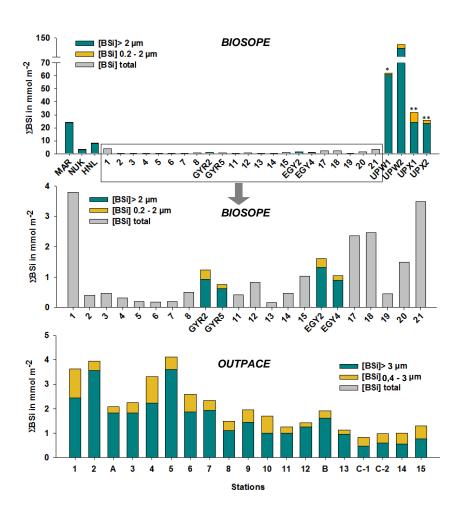






Figure 6







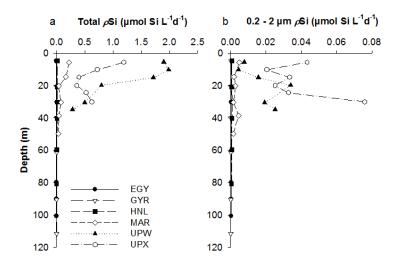
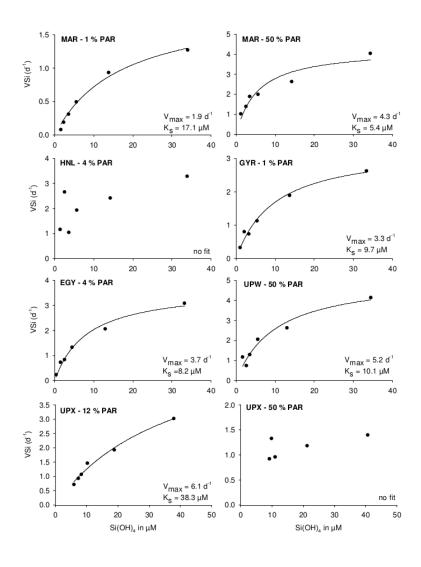




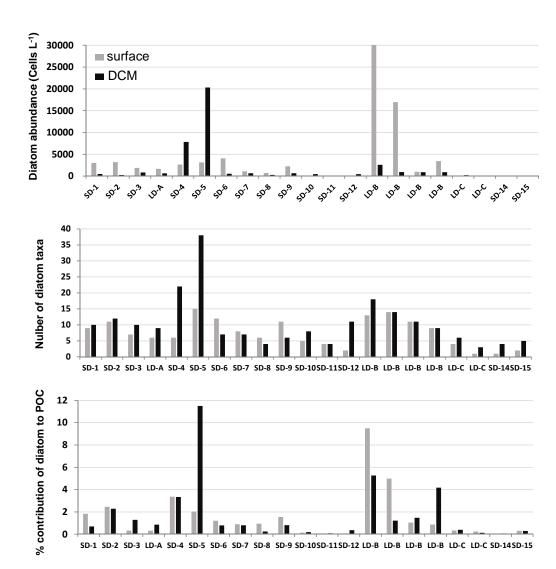


Figure 8







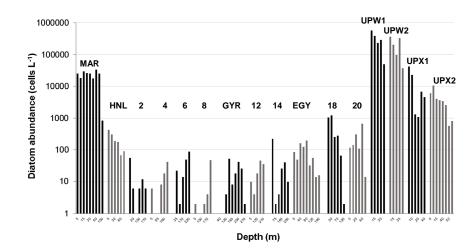


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Figure 11

