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Importance of salt fingering for new nitrogen supply in the oligotrophic ocean

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The input of new nitrogen into the euphotic zone constrains the export of organic carbon to the deep ocean and thereby the biologically mediated long-term CO₂ exchange between the ocean and atmosphere. In low-latitude open-ocean regions, turbulence-driven nitrate diffusion from the ocean's interior and biological fixation of atmospheric N₂ are the main sources of new nitrogen for phytoplankton productivity. With measurements across the tropical and subtropical Atlantic, Pacific and Indian oceans, we show that nitrate diffusion ($171 \pm 190 \mu\text{mol m}^{-2} \text{d}^{-1}$) dominates over N₂ fixation ($9.0 \pm 9.4 \mu\text{mol m}^{-2} \text{d}^{-1}$) at the time of sampling. Nitrate diffusion mediated by salt fingers is responsible for ca. 20% of the new nitrogen supply in several provinces of the Atlantic and Indian Oceans. Our results indicate that salt finger diffusion should be considered in present and future ocean nitrogen budgets, as it could supply globally $0.23\text{--}1.00 \text{Tmol N yr}^{-1}$ to the euphotic zone.

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The concept of new production, as opposed to regenerated production, has been instrumental in understanding and modelling carbon export in the ocean¹. This concept indicates that biological production susceptible of being exported outside the euphotic zone must be in balance with the input of new nutrients (as opposed to nutrient recycling) into the euphotic zone¹. Turbulent diffusion across the nitracline has been traditionally considered the dominant source for new nitrogen to the surface ocean. However, recent studies indicate that biological fixation of atmospheric N₂ by microbial diazotrophs could equal or even exceed nitrate diffusion as a mechanism for new nitrogen supply in the subtropical gyres^{2–4}. These vast biomes are responsible for approximately 30% of the global carbon export to the deep ocean^{5,6}. Below the mixed layer, turbulent diffusivity is due to mechanical processes, such as shear instabilities and internal waves, and also due to double-diffusive processes including salt fingers⁷. These develop in the tropical and subtropical central oceans, where warm and salty layers overlie cooler and fresher waters⁸. Because salt fingers mix dissolved substances more efficiently than mechanical turbulence⁹, this phenomenon could have important implications for the transport of nutrients and phytoplankton growth¹⁰. The first attempt to quantify the relevance of salt finger mixing to new production reported a sixfold increase in nitrate diffusive fluxes¹¹. Despite the subsequent development of more accurate models to estimate salt finger diffusivity from microstructure measurements¹², simultaneous estimates of the magnitudes of nitrate diffusion and N₂ fixation have so far overlooked the contribution of this process^{2–4,13}.

Between December 2010 and July 2011, during the Malaspina expedition, estimates of N₂ fixation rates and nitrate diffusive fluxes, due to mechanical turbulence and salt fingers, were obtained in 40 stations located in different biogeographical provinces¹⁴ of the tropical and subtropical Atlantic (NE Atlantic Subtropical Gyral (NASE), North Atlantic Tropical Gyral (NATR), Western Tropical Atlantic (WTRA), South Atlantic Gyral (SATL) and Caribbean (CARB)), Indian (Indian South Subtropical Gyre (ISSG)) and Pacific oceans (South Pacific Subtropical Gyre (SPSG), Pacific Equatorial Divergence (PEQD), North Pacific Equatorial Countercurrent (PNEC) and North Pacific Tropical Gyre (NPTG)) (see Methods). Four additional stations were sampled along the coast of south Australia (South Subtropical Convergence (SSTC), East Australia Coastal (AUSE) and Australia-Indonesia Coastal (AUSW)). These stations were not considered for computing the global averages provided in the text, as they were located very close to the coast and therefore they are not representative of typical open-ocean conditions. N₂ fixation was measured following the ¹⁵N₂ bubble injection uptake technique described by Montoya *et al.*¹⁵, whereas vertical diffusivity was derived from shear and temperature microstructure observations, and the St Laurent and Schmitt¹² model (see Methods). We show that, on average, nitrate diffusion dominated over N₂ fixation, and that diffusion mediated by salt fingers was responsible for ca. 20% of the new nitrogen supply in several tropical and subtropical provinces of the north and south Atlantic, and the Indian Ocean.

Results

Nitrate diffusive fluxes. Vertical diffusivity by mechanical turbulence and salt fingers computed during the expedition ranged between 0.0296×10^{-4} and $25.6 \times 10^{-4} \text{ m}^2 \text{ s}^{-1}$, with the highest values observed near the southern coast of Australia (Fig. 1 and Supplementary Table 1). Nitrate gradients were in general $> 100 \mu\text{mol m}^{-4}$ in the tropical provinces, some of them influenced by the equatorial or the Costa Rica Dome

upwelling (NATR, WTRA, PEQD and PNEC), and lower than this value in the subtropics (Table 1). Nitrate diffusive fluxes, computed as the product of vertical diffusivity and the nitrate gradient (see Methods), mostly ranged between 5.4 and $846.5 \mu\text{mol m}^{-2} \text{ d}^{-1}$ (Supplementary Table 1) (global average $171 \pm 190 (\pm \text{s.d.}) \mu\text{mol m}^{-2} \text{ d}^{-1}$). The regional variability of these fluxes was mainly driven by nitrate concentration gradients, as they were generally higher in the tropical Atlantic and Pacific (ranging $99.9\text{--}495.4 \mu\text{mol m}^{-2} \text{ d}^{-1}$ in NATR, WTRA, PEQD and PNEC), compared to the subtropical and Caribbean provinces ($25.6\text{--}177.7 \mu\text{mol m}^{-2} \text{ d}^{-1}$ in NASE, SATL, CARB, ISSG and SPSG) (Table 1). The only exception to this general pattern were the higher values observed at two stations sampled near south Australia, due to the enhanced diffusivity.

Salt finger diffusion was negligible in the Pacific, where favourable stratification conditions for their formation were scarce¹⁶, and relevant in the Atlantic provinces SATL ($0.17 \pm 0.35 \times 10^{-4} \text{ m}^2 \text{ s}^{-1}$), NASE ($0.07 \pm 0.05 \times 10^{-4} \text{ m}^2 \text{ s}^{-1}$) and WTRA ($0.07 \pm 0.11 \times 10^{-4} \text{ m}^2 \text{ s}^{-1}$), and the Indian ISSG ($0.05 \pm 0.09 \times 10^{-4} \text{ m}^2 \text{ s}^{-1}$, see Table 1). The averaged nitrate diffusive flux due to salt fingers computed using all the open-ocean stations sampled during the expedition was $24 \pm 57 \mu\text{mol m}^{-2} \text{ d}^{-1}$. However, stratification conditions favourable for salt fingers were only found in 21 stations. The average flux using only these stations was $46 \pm 76 \mu\text{mol m}^{-2} \text{ d}^{-1}$. The higher nitrate fluxes due to salt finger mixing were computed for the tropical Atlantic WTRA ($162.8 \pm 239.1 \mu\text{mol m}^{-2} \text{ d}^{-1}$), followed by the Atlantic and Indian subtropical provinces NASE, SATL and ISSG ($20.5\text{--}34.9 \mu\text{mol m}^{-2} \text{ d}^{-1}$).

N₂ fixation and diazotrophic microplankton. Photic layer depth-integrated N₂ fixation rates ranged between 0.031 and $59.5 \mu\text{mol m}^{-2} \text{ d}^{-1}$ (average $9.0 \pm 9.4 \mu\text{mol m}^{-2} \text{ d}^{-1}$), but in most cases were below $10 \mu\text{mol m}^{-2} \text{ d}^{-1}$ (Fig. 2 and Supplementary Table 1). The maximum rate of $59.5 \mu\text{mol m}^{-2} \text{ d}^{-1}$ was measured in the eastern Indian ocean, and the highest province-averaged rate corresponded to the south Atlantic SATL ($17.8 \pm 14.8 \mu\text{mol m}^{-2} \text{ d}^{-1}$) (Table 1). The abundance of the colony-forming diazotrophic cyanobacterium *Trichodesmium* spp. was higher ($> 40 \times 10^6$ filaments m^{-2}) in the Atlantic WTRA and CARB, followed by the Atlantic NATR and the Pacific SPSG ($> 20 \times 10^6$ filaments m^{-2}) (Table 2). The diazotrophic endosymbiont *Richelia intracellularis* and its hosts, the diatoms *Hemiaulus hauckii* and *Rhizosolenia* spp., were more abundant in the SATL (Fig. 3 and Table 2).

Relative contributions to the new nitrogen supply. The relative contribution of nitrate diffusive fluxes (due both to mechanical turbulence and salt fingers) and N₂ fixation to the new nitrogen supply, here considered as the total amount of new nitrogen supplied by these processes, is reported in Fig. 4, Table 1 and Supplementary Table 1. It is important to note that several other mechanisms, such as mesoscale and submesoscale turbulence, lateral transport, atmospheric deposition and the more complex three-dimensional dynamics, today recognized as important contributors to the supply of new nitrogen^{17–20}, were not considered in our study. On average N₂ fixation represented $10 \pm 15\%$ of the new nitrogen supply. This process represented $> 50\%$ of the new nitrogen supply only in one station, located in the western SATL, where relatively high N₂ fixation rates coincided with low diffusive fluxes. Other than that, the higher contributions of N₂ fixation occurred in the Atlantic provinces SATL (21%) and CARB (19%) (Table 1). The global averaged contribution of salt finger mixing was $11 \pm 18\%$. Although the averaged contribution of N₂ fixation and salt finger mixing to the

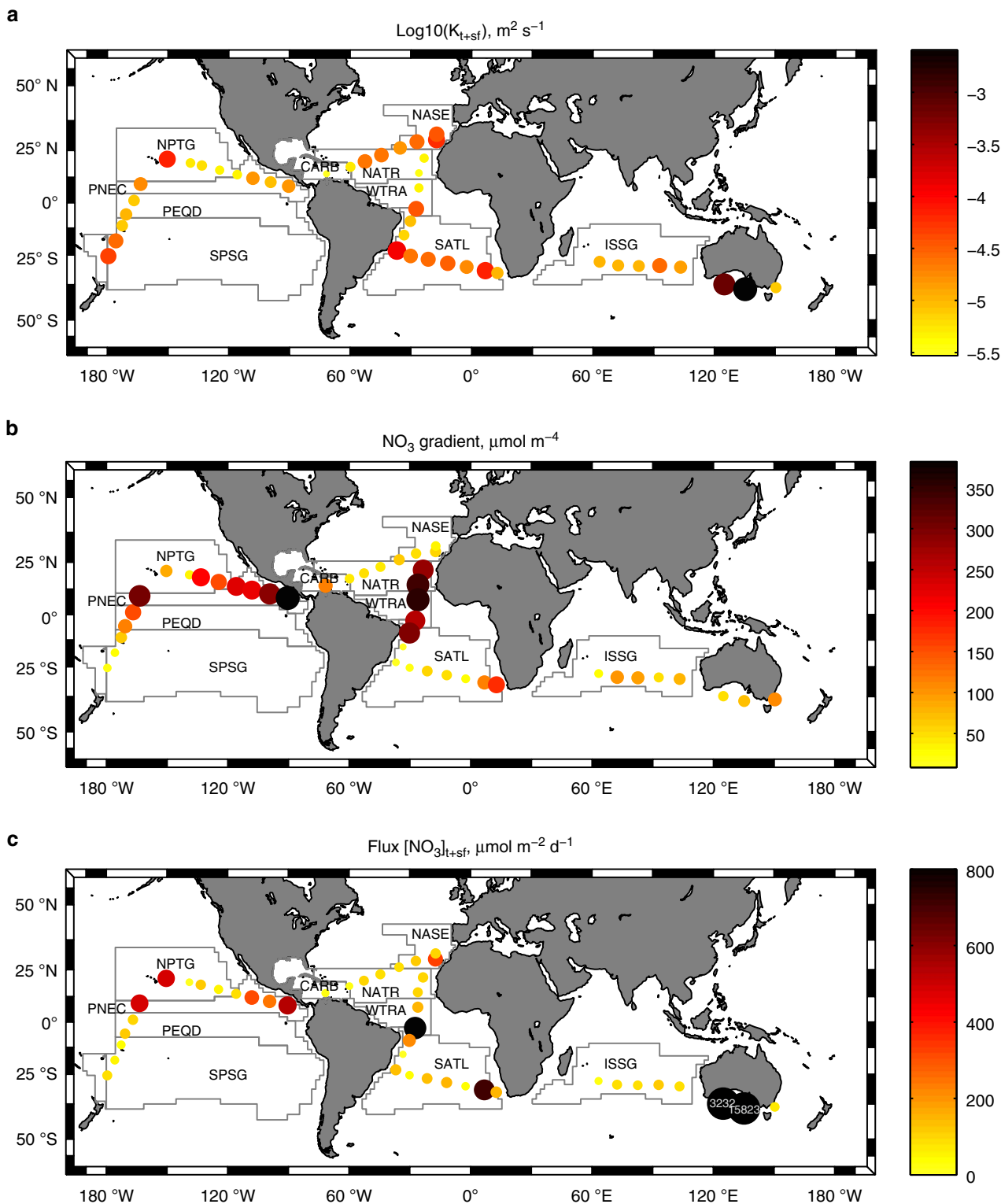


Figure 1 | Nitrate diffusive fluxes during the Malaspina expedition. (a) Averaged vertical diffusivity including the effect of salt fingers plus mechanical turbulence (K_{t+sf}), (b) nitrate gradient, and (c) nitrate diffusive fluxes across the nutricline. White numbers in black bubbles indicate values above the range shown in the colour bar. Main tropical and subtropical biogeographical provinces¹⁴ crossed during the expedition are shown: NASE (NE Atlantic Subtropical Gyral), NATR (North Atlantic Tropical Gyral), WTRA (Western Tropical Atlantic), SATL (South Atlantic Gyral) and CARB (Caribbean) in the Atlantic; ISSG (Indian South Subtropical Gyre) in the Indian; and SPSG (South Pacific Subtropical Gyre), PEQD (Pacific Equatorial Divergence), PNEC (North Pacific Equatorial Countercurrent) and NPTG (North Pacific Tropical Gyre) in the Pacific Oceans. Three other stations sampled along the coastal regions of Australia (SSTC, South Subtropical Convergence, AUSE, East Australia Coastal and AUSW, Australia-Indonesia Coastal) are also included.

Table 1 | Contribution of N₂ fixation and nitrate diffusive fluxes to the new nitrogen supply during the Malaspina expedition.

Prov.	n_T (n_p)	N ₂ fix. $\mu\text{mol m}^{-2} \text{d}^{-1}$	$\partial [\text{NO}_3^-]/\partial z$ $\mu\text{mol m}^{-4}$	K_{t+sf} $10^{-4} \text{m}^2 \text{s}^{-1}$	Flux _{t+sf} NO ₃ $\mu\text{mol m}^{-2} \text{d}^{-1}$	K_{sf} $10^{-4} \text{m}^2 \text{s}^{-1}$	Flux _{sf} NO ₃ $\mu\text{mol m}^{-2} \text{d}^{-1}$	% N ₂ fix.	% sf.	N ₂ fix Luo et al. ²⁷ $\mu\text{mol m}^{-2} \text{d}^{-1}$
NASE	4 (0)	6.9 ± 3.1	- 52 ± 11	0.35 ± 0.21	160.0 ± 118.4	0.07 ± 0.05	33.8 ± 29.4	6.0 ± 4.2	19.2 ± 4.0	4.1 ± 1.2
NATR	4 (0)	8.7 ± 6.6	- 177 ± 155	0.14 ± 0.12	99.9 ± 12.6	0.01 ± 0.01	6.6 ± 5.3	8.0 ± 5.6	6.1 ± 3.9	390.4 ± 141.1
WTRA	2 (0)	5.5 ± 3.9	- 309 ± 88	0.21 ± 0.23	495.4 ± 502.9	0.07 ± 0.11	162.8 ± 239.1	2.9 ± 3.6	19.2 ± 27.1	199.9 ± 74.2
SATL	9 (1)	17.8 ± 14.8	- 85 ± 95	0.35 ± 0.37	177.7 ± 214.9	0.17 ± 0.35	34.9 ± 46.5	20.6 ± 28.1	24.1 ± 27.6	12.5 ± 4.3
CARB	2 (0)	6.1 ± 2.4	- 80 ± 56	0.04 ± 0.02	25.6 ± 7.4	0.00 ± 0.00	1.7 ± 2.4	18.8 ± 1.9	4.3 ± 6.1	756.7 ± 296.8
ISSG	5 (5)	8.7 ± 4.0	- 69 ± 32	0.15 ± 0.09	80.5 ± 37.8	0.05 ± 0.09	20.5 ± 35.7	12.4 ± 10.6	17.6 ± 26.9	- ± -
SPSG	3 (0)	5.3 ± 7.8	- 37 ± 25	0.27 ± 0.19	63.4 ± 23.9	0.00 ± 0.00	0.0 ± 0.0	7.7 ± 11.5	0.0 ± 0.0	56.6 ± 6.5
PEQD	2 (0)	0.3 ± 0.4	- 137 ± 29	0.10 ± 0.02	112.2 ± 16.0	0.00 ± 0.00	0.0 ± 0.0	0.2 ± 0.3	0.0 ± 0.0	75.8 ± 26.5
PNEC	4 (0)	2.0 ± 1.9	- 300 ± 70	0.15 ± 0.04	397.2 ± 156.0	0.00 ± 0.00	0.0 ± 0.0	0.6 ± 0.6	0.0 ± 0.0	22.6 ± 5.1
NPTG	5 (0)	9.3 ± 6.6	- 142 ± 84	0.18 ± 0.28	153.6 ± 193.5	0.02 ± 0.04	13.3 ± 30.0	10.2 ± 8.7	4.5 ± 6.3	177.9 ± 44.2

Averaged photic layer depth-integrated N₂ fixation rates (N₂ fix.), nitrate gradient ($\partial [\text{NO}_3^-]/\partial z$), vertical diffusivity (K_{t+sf}) and nitrate diffusive fluxes due to salt fingers plus mechanical turbulence (Flux_{t+sf} NO₃), vertical diffusivity (K_{sf}) and nitrate diffusive fluxes due to salt fingers (Flux_{sf} NO₃), and relative contribution of N₂ fixation (% N₂ fix.) and salt fingers (% sf.) to the new nitrogen supply computed for the tropical and subtropical biogeographical provinces crossed during the Malaspina expedition (Prov.): NASE (NE Atlantic Subtropical Gyral), NATR (North Atlantic Tropical Gyral), WTRA (Western Tropical Atlantic), SATL (South Atlantic Gyral), CARB (Caribbean), SPSG (South Pacific Subtropical Gyre), PEQD (Pacific Equatorial Divergence), PNEC (North Pacific Equatorial Countercurrent) and NPTG (North Pacific Tropical Gyre). Averaged N₂ fixation rates compiled by Luo et al.²⁷ at each province are also included. n_T is the number of stations where N₂ fixation rates and nitrate diffusive fluxes were computed for each province, and n_p corresponds to the stations where KPP diffusivities were used. Errors correspond to standard deviations of the values shown in Supplementary Table 1. Uncertainties inherent to vertical diffusivity, NO₃ gradients and nitrate diffusive flux calculations were quadratically added to standard deviations.

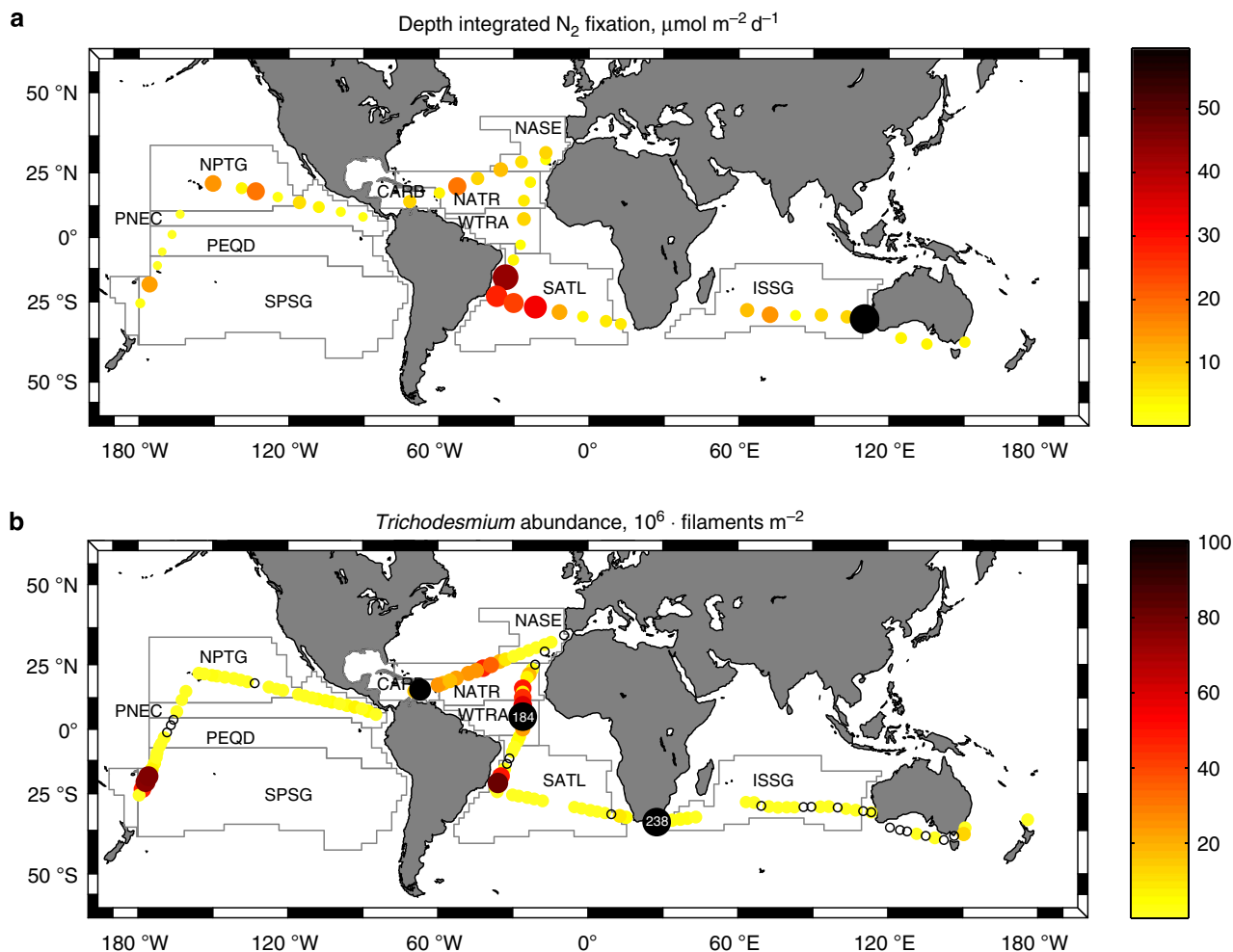


Figure 2 | N₂ fixation and *Trichodesmium* spp. abundance during the Malaspina expedition. (a) Photic layer depth-integrated N₂ fixation rates and (b) *Trichodesmium* spp. abundance estimated from vertical tows of a microplankton net in the upper 200 m (see Methods). White numbers in black bubbles indicate values above the range shown in the colour bar. White circles indicate stations where the organisms were not detected. Main tropical and subtropical biogeographical provinces¹⁴ crossed during the expedition are shown: NASE (NE Atlantic Subtropical Gyral), NATR (North Atlantic Tropical Gyral), WTRA (Western Tropical Atlantic), SATL (South Atlantic Gyral) and CARB (Caribbean) in the Atlantic; ISSG (Indian South Subtropical Gyre) in the Indian; and SPSG (South Pacific Subtropical Gyre), PEQD (Pacific Equatorial Divergence), PNEC (North Pacific Equatorial Countercurrent) and NPTG (North Pacific Tropical Gyre) in the Pacific Oceans. Four other stations sampled for N₂ fixation along the coastal regions of Australia (SSTC, South Subtropical Convergence, AUSE, East Australia Coastal and AUSW, Australia-Indonesia Coastal) are also included.

Table 2 | Diazotrophic microplankton abundance during the Malaspina expedition.

Prov	n_{Trich}	<i>Trichodesmium</i> 10^6 trichomes m^{-2}	n_{dia}	<i>Richelia</i> 10^6 colonies m^{-2}	<i>Rhizosolenia</i> 10^6 cells m^{-2}	<i>Hemiaulus Hauckii</i> 10^6 cells m^{-2}
NASE	11	3.20 ± 5.64	10	0.24 ± 0.36	0.58 ± 0.40	2.19 ± 4.16
NATR	13	25.06 ± 15.24	14	0.15 ± 0.39	1.03 ± 1.02	2.11 ± 3.18
WTRA	7	48.51 ± 63.80	7	0.02 ± 0.04	1.90 ± 3.49	0.00 ± 0.00
SATL	21	7.32 ± 20.01	24	4.64 ± 12.61	6.96 ± 18.12	21.42 ± 59.95
CARB	3	47.00 ± 46.67	5	0.28 ± 0.62	1.35 ± 1.90	2.23 ± 1.97
ISSG	19	0.92 ± 1.33	19	0.15 ± 0.37	0.61 ± 0.82	25.14 ± 98.58
SPSG	9	23.82 ± 32.98	9	0.33 ± 0.41	1.84 ± 1.40	0.21 ± 0.33
PEQD	6	0.17 ± 0.23	6	0.00 ± 0.00	1.48 ± 0.94	0.05 ± 0.13
PNEC	12	2.80 ± 2.22	12	0.00 ± 0.00	1.92 ± 3.09	0.00 ± 0.01
NPTG	15	0.93 ± 0.70	14	0.00 ± 0.00	0.33 ± 0.52	0.55 ± 1.82

Averaged photic layer depth-integrated abundance of *Trichodesmium* spp. trichomes, *Richelia* colonies, *Rhizosolenia* spp. and *Hemiaulus hauckii* spp. computed for the tropical and subtropical biogeographical provinces crossed during the Malaspina expedition (Prov.): NASE (NE Atlantic Subtropical Gyral), NATR (North Atlantic Tropical Gyral), WTRA (Western Tropical Atlantic), SATL (South Atlantic Gyral), CARB (Caribbean), SPSG (South Pacific Subtropical Gyre), PEQD (Pacific Equatorial Divergence), PNEC (North Pacific Equatorial Countercurrent) and NPTG (North Pacific Tropical Gyre). n_{Trich} and n_{dia} are the number of stations where *Trichodesmium* spp. and the other diazotrophic microphytoplankton groups were determined, respectively. Errors correspond to standard deviations.

new nitrogen supply was very similar, both processes showed a different regional distribution. The contribution of salt fingers was > 50% only in four stations, located in the Atlantic SATL, the Indian ISSG and the coastal south Australia (Supplementary Table 1). In terms of provinces, higher averaged contributions were computed for the Atlantic SATL (24%), WTRA (19%) and NASE (19%), and the Indian ISSG (18%), whereas the contribution in the Pacific provinces was < 5% (Table 1).

Discussion

Nitrate diffusive fluxes computed during the Malaspina expedition are in the range of previously reported values for open-ocean ($34\text{--}850 \mu\text{mol m}^{-2} \text{d}^{-1}$)^{3,4,21,22} and regions under the influence of equatorial upwelling ($1,300 \mu\text{mol m}^{-2} \text{d}^{-1}$)²³. Despite the relevant contribution of salt fingers to nitrate diffusion described for our data in several Atlantic and Indian provinces, our estimates are far below the five- to sixfold increase factor, with respect to mechanical turbulence, reported by Hamilton *et al.*¹¹ and Dietze *et al.*²⁴. Differently to our study, Hamilton *et al.* used the conservation equation of turbulent kinetic energy to derive salt finger mixing efficiency, by assuming that there is no mechanical generation of turbulence. However, more recent studies demonstrated that in the ocean mechanical turbulence could disrupt the effect of salt fingers, causing lower mixing efficiencies than those predicted by the Hamilton *et al.* model¹² (see Methods). On the other hand, Dietze *et al.*²⁴ computed nitrate diffusive fluxes using two parameterizations for internal waves²⁵ and salt finger diffusivity²⁶ based on conductivity–temperature–depth (CTD) and current velocity data. Simultaneous microstructure-derived and parameterized diffusivity estimates are scarce; for this reason, and also because of the different nature of both estimates, the comparison is difficult to make. In a previous study we compared microstructure-derived and K-profile parameterized (KPP) diffusivity estimates performed during the Malaspina expedition¹⁶. In general, the KPP showed a good agreement with diffusivity estimates derived from microstructure observations. However, the relative contribution of salt finger mixing derived from the KPP was higher compared to the estimates derived from microstructure observations. Our estimates are in good agreement with recent studies using the same model to estimate the contribution of salt finger mixing²¹; therefore discrepancy with previous studies is probably due to the different approaches used.

Excluding the Atlantic NASE and SATL provinces, N_2 fixation rates measured during the Malaspina expedition fall within the lower edge of previous estimates recently compiled by

Luo *et al.*²⁷ (Table 1). Some of the previously described spots of enhanced N_2 fixation, such as the Caribbean and the tropical North Atlantic^{2,28,29}, were not detected here. This was probably due to the low spatial resolution of our sampling for N_2 fixation rates (ca. 1,000 km), as these spots were indeed tracked by the higher spatial resolution of the *Trichodesmium* abundance measurements. The fact that *Trichodesmium* abundance did not show any statistically significant correlation with N_2 fixation rates ($r = -0.059$, $P = 0.71$) points to the contribution of other groups of diazotrophs. High abundances of the diatoms *Hemiaulus hauckii* and *Rhizosolenia* hosting the diazotrophic symbiont *Richelia intracelularis* found in the western SATL, could possibly be related to the enhanced N_2 fixation rates determined in this region (Fig. 3). Elevated N_2 fixation rates as the result of this symbiosis have been previously reported in the Amazon river plume region³⁰. Moreover, the symbiotic cyanobacterium UCYN-A hosted by a prymnesiophyte was also detected during the Malaspina expedition in regions of enhanced N_2 fixation rates, such as the western SATL and the eastern Indian ocean³¹. Indeed, the rates we measured in tropical and subtropical regions are in good agreement with the background N_2 fixation rates of $8\text{--}16 \mu\text{mol m}^{-2} \text{d}^{-1}$ reported for unicellular diazotrophs in the north Atlantic^{4,28}.

It has recently been reported that the $^{15}\text{N}_2$ bubble injection technique underestimates N_2 fixation rates because the injected bubble does not attain equilibrium with the water^{32,33}. According to Mohr *et al.*³² the underestimation is significantly reduced when, similar to the methodology used during the Malaspina expedition (see Methods), 24-h incubations are used. However, recent studies suggest that the underestimation could persist for 24-h incubation periods³⁴. Although there is a growing interest among the scientific community to establish a protocol to solve this problem, so far no consensus has been attained. In any case, the underestimation problem would also affect most of the previously published N_2 fixation rates²⁷.

To our knowledge only three studies have compared so far the relevance of nitrate diffusion and N_2 fixation in the open ocean^{2–4}, none of them including the contribution of salt fingers to mixing. In the tropical north Atlantic, Capone *et al.*² estimated that N_2 fixation by *Trichodesmium* spp. could equal or even exceed the vertical flux of nitrate into the euphotic zone as estimated by using a constant diffusivity. The use of a microstructure profiler along a meridional transect in the Atlantic (TRYNITROP cruise) revealed the importance of considering the variability in diffusivity³. These authors estimated a contribution of N_2 fixation to the new nitrogen supply of $44 \pm 30\%$, $22 \pm 19\%$ and $2 \pm 2\%$ in the south

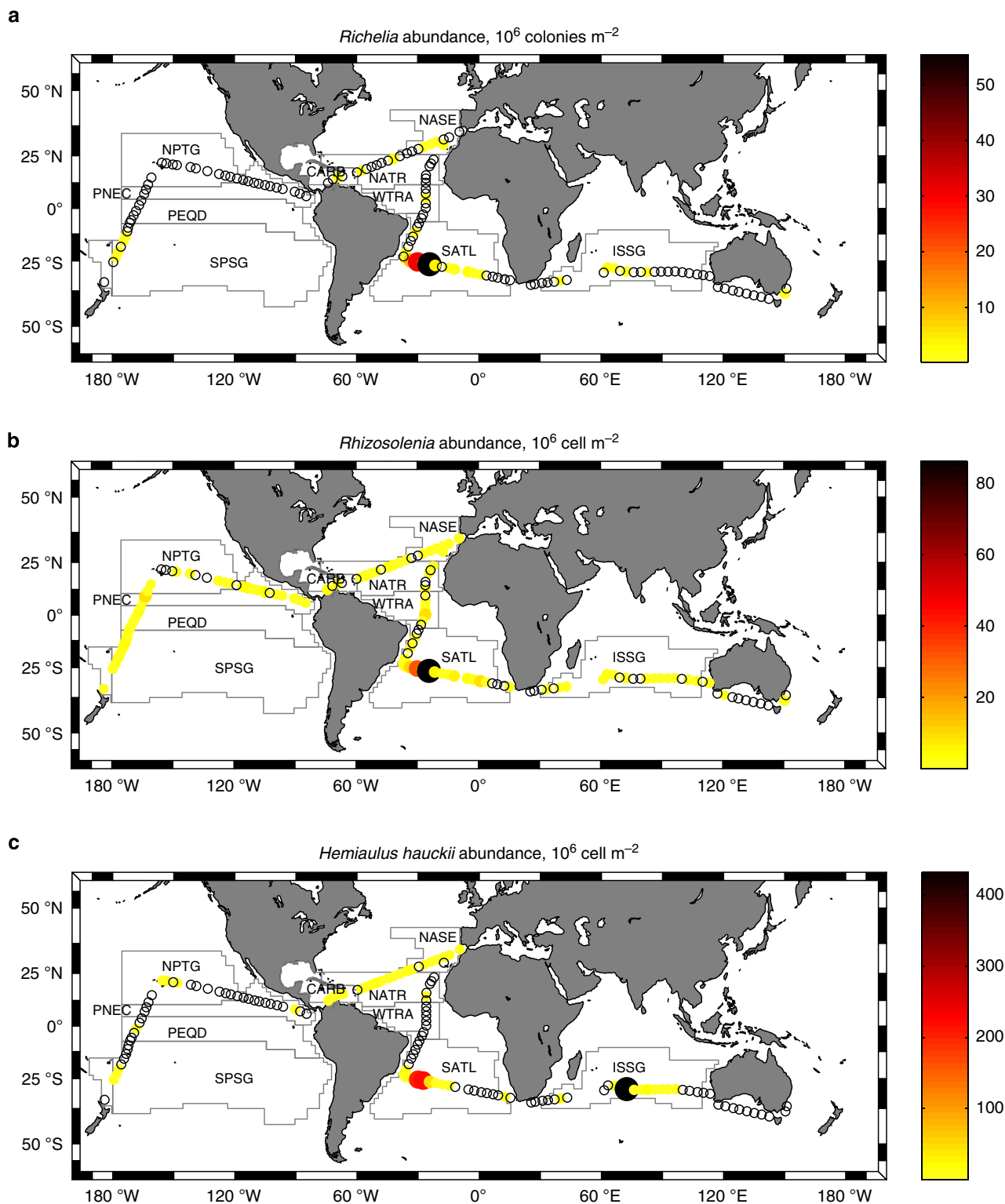


Figure 3 | Diazotrophic microplankton abundance during the Malaspina expedition. Photic layer depth-integrated abundance of (a) *Richelia* colonies, (b) *Rhizosolenia* spp. and (c) *Hemiaulus hauckii* spp. collected during the Malaspina expedition. White circles indicate stations where the organisms were not detected. Main tropical and subtropical biogeographical provinces¹⁴ crossed during the expedition are shown: NASE (NE Atlantic Subtropical Gyral), NATR (North Atlantic Tropical Gyral), WTRA (Western Tropical Atlantic), SATL (South Atlantic Gyral) and CARB (Caribbean) in the Atlantic; ISSG (Indian South Subtropical Gyre) in the Indian; and SPSG (South Pacific Subtropical Gyre), PEQD (Pacific Equatorial Divergence), PNEC (North Pacific Equatorial Countercurrent) and NPTG (North Pacific Tropical Gyre) in the Pacific Oceans.

subtropical, equatorial and north subtropical Atlantic, respectively. Finally, Painter *et al.*⁴ reported N_2 fixation rates comparable to nitrate diffusive fluxes, also derived from a

microstructure profiler, in the northeast subtropical Atlantic. The comparison of fluxes reported in different studies is sometimes problematic because nitrate diffusive fluxes are very sensitive to

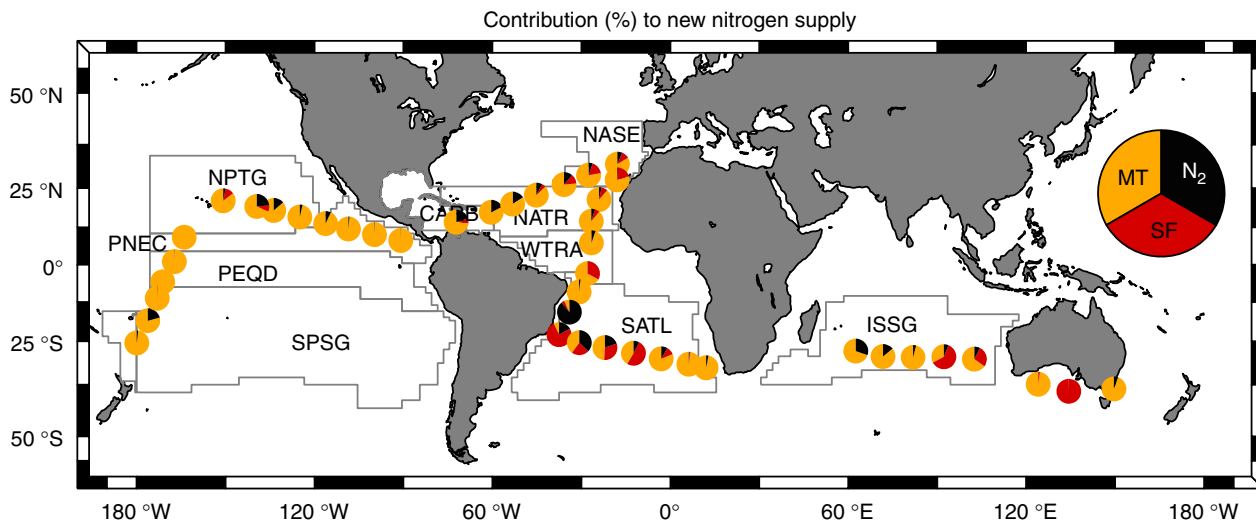


Figure 4 | Relative contribution of nitrate diffusive fluxes and N₂ fixation to the new nitrogen supply during the Malaspina expedition. Relative contribution (%) of nitrate diffusive fluxes due to mechanical turbulence (MT, orange) and salt fingers (SF, red), and N₂ fixation (N₂, black) to the new nitrogen supply, considered as the sum of these three processes. Main tropical and subtropical biogeographical provinces¹⁴ crossed during the expedition are shown: NASE (NE Atlantic Subtropical Gyral), NATR (North Atlantic Tropical Gyral), WTRA (Western Tropical Atlantic), SATL (South Atlantic Gyral) and CARB (Caribbean) in the Atlantic; ISSG (Indian South Subtropical Gyre) in the Indian; and SPSG (South Pacific Subtropical Gyre), PEQD (Pacific Equatorial Divergence), PNEC (North Pacific Equatorial Countercurrent) and NPTG (North Pacific Tropical Gyre) in the Pacific Oceans. Three other stations sampled along the coastal regions of Australia (SSTC, South Subtropical Convergence, AUSE, East Australia Coastal and AUSW, Australia-Indonesia Coastal) are shown in the map.

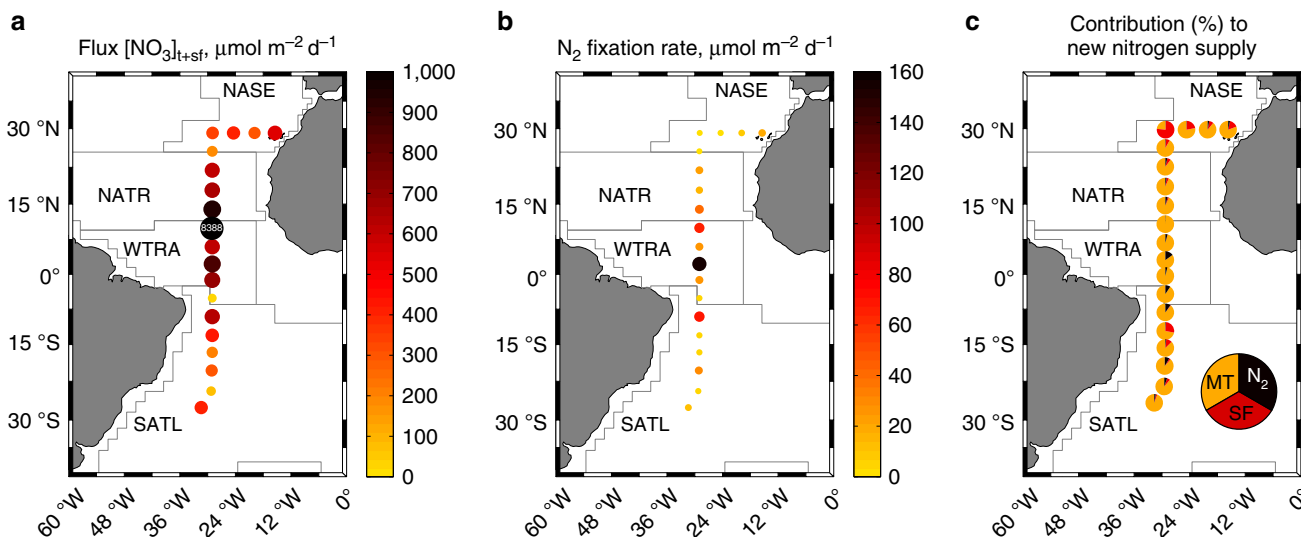


Figure 5 | N₂ fixation and nitrate diffusive fluxes during the TRYNITROP cruise. (a) Nitrate diffusive fluxes computed across the nutricline, due to mechanical turbulence plus salt finger diffusivity, (b) photic layer depth integrated N₂ fixation rates and (c) relative contribution (%) of mechanical turbulence (MT, orange), salt fingers (SF, red) and N₂ fixation (N₂, black) to the new nitrogen supply, considered as the sum of these three processes. White numbers in black bubbles indicate values above the range shown in the colour bar. Main biogeographical provinces¹⁴ crossed during the TRYNITROP cruise are shown in the map: NASE (NE Atlantic Subtropical Gyral), NATR (North Atlantic Tropical Gyral), WTRA (Western Tropical Atlantic) and SATL (South Atlantic Gyral).

the depth interval chosen for the calculation. The nitrate fluxes reported during the TRYNITROP cruise in Mouriño Carballido *et al.*³ were computed across a 10-m layer centred at the bottom of the photic layer and they were interpreted as instantaneous. Here we chose to compute the fluxes across the upper nitracline, which results from biological consumption at the surface and therefore integrates processes occurring at relatively longer temporal scales. The recalculation of nitrate diffusive fluxes during the TRYNITROP cruise following exactly the same protocol reported here, in order to include mechanical

turbulent mixing but also salt fingers (Fig. 5), shows a maximum contribution of salt finger mixing to new production in NASE (26 ± 28%) and SATL (8.3 ± 9.6%), higher than the contribution of N₂ fixation (1.7 ± 1.4% and 4.9 ± 3.6%, respectively), and consistent with the results from the Malaspina expedition.

The data set collected during the Malaspina circumnavigation allowed us to compare, for the first time, the contribution of N₂ fixation, mechanical turbulence and salt finger mixing to the supply of new nitrogen to surface euphotic waters in large regions

of the open ocean. These data reveal that nitrate diffusion dominated over N_2 fixation at the time of sampling, and highlight the importance of considering the effect of salt finger mixing in nitrogen budgets of the surface ocean. This process was an important source for new nitrogen, representing close to 20% of the new nitrogen supply in the Atlantic tropical and subtropical NASE, WTRA and SATL provinces, and the subtropical Indian ISSG (Table 1). Although salt finger mixing and N_2 fixation showed different regional distribution, on average, the contribution of both processes as sources of new nitrogen supply was comparable. Albeit the Malaspina expedition provided a unique data set, this study has limited temporal and spatial resolution. In order to provide a global estimate of nitrate diffusive fluxes due to salt finger mixing, we combined data from the World Ocean Atlas 2009 (<http://www.nodc.noaa.gov/>) and the KPP³⁵ (Supplementary Fig. 1). The computed supply flux by this process ($1.00 \pm 0.75 \text{ Tmol yr}^{-1}$) is about fourfold higher than the global estimate derived from extrapolating the averaged salt finger flux estimated from the Malaspina observations ($0.23 \text{ Tmol yr}^{-1}$). These figures are within the range of global N_2 fixation ($0.36\text{--}11 \text{ Tmol yr}^{-1}$)³⁶ and atmospheric N deposition ($2\text{--}6 \text{ Tmol yr}^{-1}$)³⁷ estimates, emphasizing the need to include salt finger mixing in present and future ocean nitrogen budgets.

Methods

Sampling. Field observations were carried out during the Malaspina circumnavigation expedition in the Atlantic, Pacific and Indian Oceans between December 2010 and July 2011 on board R/V *Hespérides* (see Supplementary Fig. 2). The cruise was divided into seven legs: leg 1 (14 December 2010, Cádiz–13 January 2011, Rio de Janeiro), leg 2 (17 January, Rio de Janeiro–6 February, Cape Town), leg 3 (11 February, Cape Town–13 March, Perth), leg 4 (17 March, Perth–30 March, Sydney), leg 5 (16 April, Auckland–8 May, Honolulu), leg 6 (13 May, Honolulu–10 June, Cartagena de Indias) and leg 7 (19 June, Cartagena de Indias–14 July, Cartagena). Leg 1 crossed the NASE, NATR, WTRA and SATL biogeographical provinces¹⁴. Leg 2 sampled a zonal transect across the SATL province, the last station being carried out in the Benguela Current Coastal (BENG). Leg 3 crossed the Indian ocean from west to east. The first three stations were carried out in the East Africa Coastal (EARF) province, whereas most of the stations sampled the ISSG province. Four provinces were sampled along the south Australian coast during leg 4: ISSG, AUSW, SSTC and AUSE provinces. During leg 5, the SPSG, PEQD, PNEC and NPTG provinces were sampled. Leg 6 crossed the NPTG and again the PNEC province. Finally, during leg 7 the CARB, NATR and NASE provinces were sampled.

CTD casts were carried out with a SBE911plus (Sea-Bird Electronics) probe attached to a rosette equipped with Niskin bottles. A Lowered Acoustic Doppler Current Profiler (LADCP) system was also mounted on the rosette. A microstructure turbulence profiler was deployed in 36 stations. Water from Niskin bottles was collected in 39 stations for nutrient analysis, in 44 stations for the determination of N_2 fixation rates and in 136 stations for microphytoplankton abundance determination. Samples for the determination of *Trichodesmium* abundance from a plankton net were collected in 132 stations.

Microstructure measurements. Measurements of microstructure shear and temperature used to infer dissipation rates of turbulent kinetic energy (ϵ) and thermal variance (χ) were conducted by using a microstructure turbulence profiler MSS³⁸, down to a maximum depth of 300 m. Averaged diffusivity due to both mechanical turbulence and salt fingers (K_{t+sf}) was modelled, according to St Laurent and Schmitt¹², as the weighed sum of diffusivity due to turbulence (K_t) and salt fingers (K_{sf}^S , where S stands for salt as we assumed that nitrate diffuses at the same rate as salinity): $K_{t+sf} = p_{sf}K_{sf}^S + (1 - p_{sf})K_t$, where p_{sf} is the weighting factor, corresponding to the fraction of bins where salt fingers are active. Favourable stratification for salt fingers was identified using the density ratio ($R_\rho = \alpha \partial_z T / \beta \partial_z S$, where α and β are the thermal expansion and salinity contraction coefficients, respectively). Although salt fingers are theoretically possible for $R_\rho > 1$, its contribution to mixing has been shown to be irrelevant for $R_\rho > 2$ (ref. 12). According to McDougall³⁹ and Hamilton *et al.*¹¹, who solved the turbulent kinetic energy equation for salt fingers, mixing efficiency for this process is expected to exceed the value of 0.2 for mechanical turbulence. Hence, we used two parameters to identify salt finger active bins: the density ratio ($1 < R_\rho < 2$) and the observed mixing efficiency ($\Gamma_{\text{Obs}} > 0.2$) (calculated as $\Gamma_{\text{Obs}} = 0.5N^2\chi/\epsilon(\partial_z T)^2$, where N is the buoyancy frequency). Diffusivity for turbulence (K_t) and salt finger (K_{sf}^S) bins was computed following the Osborn⁴⁰, $K_t = K_\epsilon = \langle 0.2\epsilon/N^2 \rangle$, and the Osborn–Cox⁴¹ models, $K_{sf}^S = K_\gamma = \langle 0.5\chi/(\partial_z T)^2 \rangle$, respectively. The Osborn–Cox⁴¹ model applies for heat. For dissolved substances (i.e., nitrate) $K_{sf}^S = \langle R_\rho \rangle^{-1} K_{sf}^T$, where

$r = 0.4\text{--}0.7$, according to the compilation of estimates carried out by St Laurent and Schmitt¹², is the salt finger flux ratio. Here we set $r = 0.7$ for coherence with the K -profile parameterization (see below). In the manuscript, salt finger diffusivity K_{sf} refers to the weighted contribution of this mechanism to total diffusivity: $p_{sf}K_{sf}^S$. Errors in turbulence plus salt fingers (K_{t+sf}) and salt fingers diffusivity (K_{sf}^S) were estimated as the standard deviation of 1,000 estimates obtained by bootstrapping the input variables: α , β , R_ρ , K_ϵ and K_γ . In this way, ϵ and χ uncertainties were treated implicitly through K_ϵ and K_γ . A 10% error estimate of the salt fingers flux ratio was added to the calculations. A sensitivity test was performed to verify that the computed diffusivity was not strongly dependent on the choice of the critical Γ value (data not shown).

During leg 3, when we sampled the Indian Ocean, and due to technical problems, no microstructure measurements were available, so diffusivity was estimated by using an adaptation of the KPP³⁵ based on CTD, LADCP and meteorological data. The salt finger term included in the KPP was considered as K_{sf} . Uncertainties of KPP diffusivity were calculated as the standard deviation of 1,000 averaged estimates resulting from bootstrapping individual 10-m vertical resolution K values within the nitracline. A detailed description of the implementation of the KPP and the comparison with diffusivity derived from microstructure observations collected during the Malaspina expedition is given in Fernández-Castro *et al.*¹⁶.

Nitrate diffusive fluxes. Nitrate diffusive fluxes across the nutricline were calculated following the Fick's law as

$$\text{FluxNO}_3 = - \langle K \rangle \frac{\partial[\text{NO}_3]}{\partial z}, \quad (1)$$

where $\frac{\partial[\text{NO}_3]}{\partial z}$ is the nitrate gradient obtained by linearly fitting nitrate concentrations in the nitracline, and $\langle K \rangle$ is averaged diffusivity for the same depth range.

A total of 7–9 samples for nitrate (NO_3) + nitrite (NO_2) concentration in the upper 300 m were directly collected from the Niskin bottles in 20 ml acid-washed polyethylene vials. They were immediately analysed on board according to classical methods using the automated colorimetric technique⁴² on a segmented flow Skalar autoanalyser. For the nitracline region, relevant for this study, vertical resolution varied between 20 and 50 m. The nitracline was determined as a region of approximately maximum and constant gradient, usually extending to 50–100 m and including 4–6 nitrate data points. In those stations where nitrate concentrations were not available (see Supplementary Fig. 2) nitrate gradients were computed from the data included in the World Ocean Atlas 2009 (WOA09) database⁴³. A good correspondence between nitrate gradients based on Malaspina observations and the WOA09 climatology was found ($r = 0.76$, $P < 0.001$, data not shown). Diffusive flux errors were calculated as the squared sum of the diffusivity error (see above) and the error of the slope resulting from the linear fit.

Nitrate diffusive fluxes due to mechanical turbulence and salt finger mixing during the TRYNITROP cruise, which sampled a meridional transect from 30°S to 30°N in the Atlantic Ocean in April–May 2008 (ref. 3), were calculated following exactly the same protocol as described for the Malaspina expedition.

N_2 fixation. Samples for the determination of N_2 fixation rates were collected at the same stations where nitrate diffusive fluxes were computed. Additionally, samples were also collected at one station located at the Indian Australia coast (AUSW). Only those stations located in tropical and subtropical regions were used for computed global open-ocean averages reported in the text. N_2 fixation was measured at four depths (surface, the depths where the photosynthetically active radiation was 20 and 10% of the surface value, and the deep chlorophyll maximum) following the $^{15}\text{N}_2$ uptake technique described by Montoya *et al.*¹⁵. For each depth, one (three during leg 6) acid-washed, clear polycarbonate bottle (4 l in volume) was filled directly from the CTD rosette and supplemented with 8 ml of $^{15}\text{N}_2$ (98 atom%; Sigma-Aldrich, lot -CX0937). Samples were incubated on deck at their original irradiance and temperature conditions during 24 h. After the incubation the whole volume was filtered through a 25-mm GF/F filter (Whatman). Afterwards, filters were dried at 40 °C for 24 h and then stored until pelletization in tin capsules. ^{15}N atom % in particulate organic matter was measured with an elemental analyser combined with a continuous-flow stable isotope mass spectrometer (Flash-EA112 + Deltaplus; ThermoFinnigan), using an acetanilide standard as reference. The equations given by Weiss⁴⁴ and Montoya *et al.*¹⁵ were used to calculate the initial N_2 concentration and N_2 fixation rates, respectively.

***Trichodesmium* spp. abundance.** Plankton samples were collected by vertical tows of a microplankton net (40 μm mesh size) through the upper 200 m of the water column. Sampling was between 10:00 and 16:00 h GMT. Abundance of the diazotroph *Trichodesmium* spp. was estimated by counts of 50-ml aliquots of the sample from the microplankton net preserved in glutaraldehyde (25% final concentration) using a FlowCAM system (Fluid Imaging Technologies). Prior to analysis, the samples were screened with a 100- μm nylon mesh to prevent clogging of the FlowCAM cell. Results are reported as number of colonies (trichomes) per square meter.

Diazotrophic microphytoplankton abundance. Samples for determining the abundance of diatom *Hemiliaulus hauckii* sp. and *Rhizosolenia* spp. hosts of the diazotrophic cyanobacteria *Richelia intracellularis*, and abundances of *Richelia intracellularis* colonies were collected at three depths from the surface to the deep chlorophyll maximum and fixed with 2% formalin–hexamine solution. Abundance was quantified using an inverted microscope, after 48-h sedimentation of 150 ml of sample in composite-settling chambers.

Global supply of nitrate due to salt finger diffusivity. A gross estimate of vertical nitrate fluxes due to salt finger diffusivity between 40°S and 40°N was computed by using data from the WOA09. Vertical nitrate gradients were computed in the upper 250 m, and the nitracline was determined as the depth of maximum gradient. Temperature⁴⁵ and salinity⁴⁶ fields were used to compute the density ratio (R_ρ). Vertical diffusivity due to salt finger mixing was calculated according to the KPP³⁵ as a function of R_ρ :

$$K_{\text{KPP}}^{\text{sf}} = 0, \quad R_\rho \geq R_\rho^0 \quad (2)$$

$$K_{\text{KPP}}^{\text{sf}} = 10 \times 10^{-4} \left(1 - \left(\frac{R_\rho - 1}{R_\rho^0 - 1} \right)^2 \right)^3, \quad 1.0 < R_\rho < R_\rho^0 \quad (3)$$

where $R_\rho^0 = 1.9$. Nitrate vertical fluxes due to salt finger mixing were calculated using equation (1). Errors were calculated by propagating standard errors of the temperature, salinity and nitrate fields.

A second global estimate was calculated by extrapolating the averaged nitrate diffusive flux due to salt fingers ($46 \pm 76 \mu\text{mol m}^{-2} \text{d}^{-1}$), computed by using only the 21 stations where stratification conditions were favourable for salt finger formation ($1 < R_\rho < 2$) during the Malaspina expedition, to the global surface area where this condition was accomplished in the nitracline (ca. $1.3 \times 10^7 \text{ km}^2$), according to the WOA09 temperature and salinity fields.

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Author contributions

Data processing was carried out by B.F.-C., P.C. and S.J.-R.; J.G., T.R., E.M. and B.M.-C. designed and supervised N₂ fixation experiments; D.B. and M.V. were responsible for nutrient concentration analysis; and A.B. and M.E. for determination of the abundance of diazotrophic microphytoplankton groups. B.F.-C., B.M.-C., E.M. and R.S. designed the study and data analysis. B.F.-C., B.M.-C., E.M., and R.S. wrote the manuscript with the contributions of D.B., A.B., M.E., M.V. and J.G.

Additional information

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