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SUPPLEMENTARY INFORMATION

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Influence of diatom diversity on the ocean biological carbon pump

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Supplementary information

This document complements the review article. When necessary, it provides additional comments and references to some sections of the article. It also provides detailed legends of the 4 figures of the article and additional figures for Box 2.

Introduction

-With respect to the faster growth rates of diatoms also note Flori et al. (2017), reference S1, who show how the plastid thylakoid architecture optimizes photosynthesis in diatoms.

S1. Flori, S. *et al.* Plastid thylakoid architecture optimizes photosynthesis in diatoms. *Nat. Commun.* **8**, 15885 (2017).

-As regard the contribution of diatoms to primary production on Earth (about 20%) and in the ocean (about 40%), in addition to Field et al. (1998), reference 9 of the list of references (main text), also see Nelson *et al.* (1995), reference S1, Falkowski (2002), ref. S2, et Malviya *et al.* (2016), ref. 16. As mentioned in the main text our estimate (about 40%) for the contribution of diatoms to the POC export production is based on Jin *et al.* (2006), ref. 11, calculated on Si:N ratios in diatoms.

S2. Nelson, D.M. *et al.* Production and dissolution of biogenic silica in the ocean: revised global estimates, comparison with regional data and relationship to biogenic sedimentation. *Glob. Biogeochem. Cycles* **9**, 359-372 (1995).

S3. Falkowski, P.G. The ocean's invisible forest. *Sci. Am.* **287**, 54–61 (2002).

What controls the distribution of diatoms in the ocean?

Hereafter are key features that in our opinion make diatoms so unusual among the phytoplankton.
Generally speaking, the ecological success of a phytoplanktonic organism in an ecosystem depends upon its capacity to proliferate (maximization of growth terms) and to maintain its population size in the euphotic zone.
With respect to loss terms, the large size of many of the diatoms, which positively impacts sedimentation, is a disadvantage for maintenance in the surface waters (a point well developed in the manuscript). Similar to other phytoplankton groups, diatoms are also targets for pathogens, predators, and parasites (also developed in the manuscript). Trophic relationships and potential predators are starting to be identified, but these studies need to scale up to provide quantitative data, besides from % of a diatom population infected, on the outcome of such attacks on the C cycle. Viruses identification is relatively new (Nagasaki *et al.*, 2008, ref. S4) and algal viruses have been shown to be all novel and remarkably distant from any other known viruses. Parasitic chitrids (Kagami *et al.* 2007, ref. S5) are also known to infect preferentially larger diatoms, and are often considered to be highly host-specific and their importance in the environment may be largely underestimated (Scholz *et al.*, 2016, ref. S6). Nanoflagellates have also been shown to feed on specific diatoms (Drebes *et al.*, 1996, ref. S7) and can be considered as successful competitors to zooplankton in channeling C fluxes and influencing diatom species succession (Tillmann *et al.*, 1999, ref. S8). In a recent

review article, Sherr and Sherr (2007), ref. 65, have evidenced that phagotrophic heterotrophic dinoflagellates were likely to be more quantitatively significant grazers of bloom-forming diatoms than copepods and other meso-zooplankton species, but that their relative importance was probably underestimated due to methodological difficulties of accurate quantification.

But with respect to growth terms, in nutrient-replete sunlit environments diatoms appear able to grow faster than other phytoplankton groups (e.g. Lichtman *et al*. 2007, ref. 5; Edwards *et al.* 2015, ref. 6). One of the reasons for this is that diatom cell-wall silicification is a low-energy process, mostly uncoupled from photosynthesis (Martin-Jezéquel *et al*. 2000, ref. S9), as compared to the higher energy requirements for the construction of the cellulosic thecal plates in dinoflagellates for example. As regards diatom-zooplankton interactions, the large size of diatoms might be an advantage. Recorded estimates of diatom-specific loss rates from grazing have demonstrated that both microzooplankton and macrozooplankton can graze upon diatoms (in the gulf of Mexico, for example, high microzooplankton grazing rates on diatoms were recorded for cells < 20 µm, while large cells usually escaped grazing from microzooplankton, Fahnenstiel *et al*. 1995, ref. S10). Mesozooplanktonic organisms (copepods etc.) are the other dominant grazers of diatoms (although this point of view is challenged by Sherr and Sherr, 2007, cf. above). However, a global assessment of the influence of mesozooplankton grazing on primary production (PP) suggests that these organisms remove an average of 12% of the annual global PP (Calbet 2001, ref. S11). In the Southern Ocean, however, krill (*Euphausia superba*) swarms may exert a stronger control on diatom population dynamics, and clearance rates on diatoms was found to increase with size for larger mesozooplankton grazers (Schultes *et al*. 2006, ref. S12).

S4. Nagasaki, K. Dinoflagellates, diatoms, and their viruses. *J. Microbiol.* **46,** 235–243 (2008).

S5. Kagami, M. *et al.* Parasitic chytrids: Their effects on phytoplankton communities and food-web dynamics. *Hydrobiologia* **578,** 113–129 (2007).

S6. Scholz, B. *et al.* Zoosporic parasites infecting marine diatoms - A black box that needs to be opened. *Fungal Ecol.* **19**, 59-76 (2016).

S7. Drebes, G. *et al. Cryothecomonas aestivalis* sp. nov., a colourless nanoflagellate feeding on the marine centric diatom *Guinardia delicatula* (Cleve) Hasle. *Helgoländer Meeresuntersuchungen* **50**:BF02367163 https://doi.org/10.1007/BF02367163 (1996).

S8. Tillmann, U., Hesse, K.-J. & Tillmann, A. Large-scale parasitic infection of diatoms in the Northfrisian Wadden Sea. *J. Sea Res.* **42,** 255–261 (1999).

S9. Martin-Jézéquel, V. *et al.* Silicon metabolism metabolism in diatoms : implication for growth. *J. Phycol.* DOI: 10.1046/j.1529-8817.2000.00019.x (2000).

S10. Fahnenstiel, G.L. *et al.* Taxon-specific growth and loss rates for dominant phytoplankton populations from the northern Gulf of Mexico. *Mar. Ecol. Progress. Ser.* (1995).

S11. Calbet, A. Mesozooplankton grazing effect on primary production: a global comparative analysis in marine ecosystems. *Limnol. Oceanogr.* DOI: 10.4319/lo.2001.46.7.1824 (2001).

S12. Schultes, S., Verity, P. G. & Bathmann, U. V. Copepod grazing during an iron-induced diatom bloom in the Antarctic Circumpolar Current (EisenEx): I. Feeding patterns and grazing impact on prey populations. *J. Exp. Mar. Bio. Ecol.* **338,** 16–34 (2006).

Export of carbon from the photic layer: are all diatoms equal?

As regards the zoosporic parasite infection, see Scholz *et al.* (2016), ref. S13:

S13. Scholz, B. *et al.* Zoosporic parasites infecting marine diatoms - A black box that needs to be opened. *Fungal Ecol.* 19, 59–76. doi:10.1016/j.funeco.2015.09.002 (2016).

Methodology related to metabarcoding data acquisition is referred in **Box 1**, see Guidi *et al.* (2016), ref. 116.

Are diatoms efficient transporters of organic matter to the CO2 sequestration layer?

No additional comment and reference.

Can we predict the fate of diatoms in a future warm and acidified ocean?

No additional comment and reference.

Box 1

No additional comment and reference.

Box 2. Importance of incorporating diversity of diatoms into numerical models

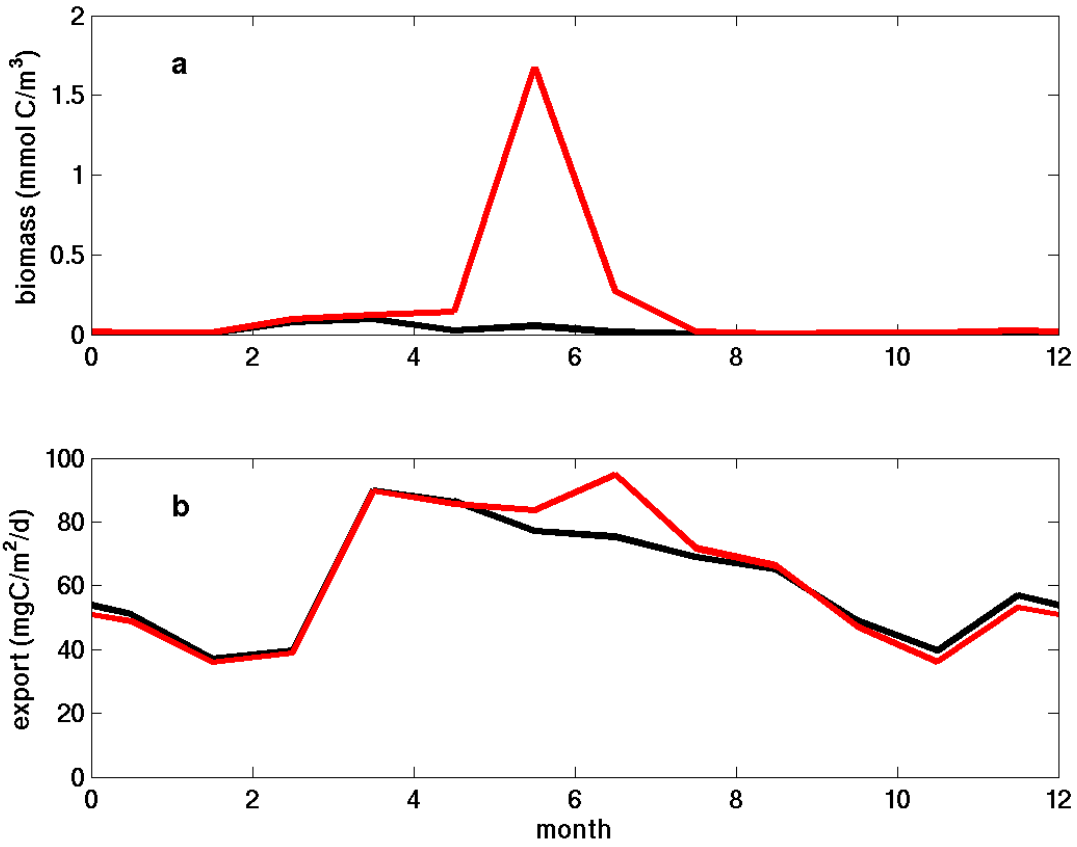


Figure S1. MIT Model monthly output for a region of the oligotrophic North Pacific of (a) surface diatom biomass (mmol C m^{-3}) ; (b) carbon export through 250m (mgC m^{-2} d^{-1}). The black line is from the simulation of Dutkiewicz *et al.* (2015), ref. 27, which includes one diatom « PFT ». The red line is from a simulation which also included a diazotroph-diatom assemblage (DDA). Relief from nitrogen limitation allows the DDA to bloom during the summer months. There is a subsequent increase in carbon export.

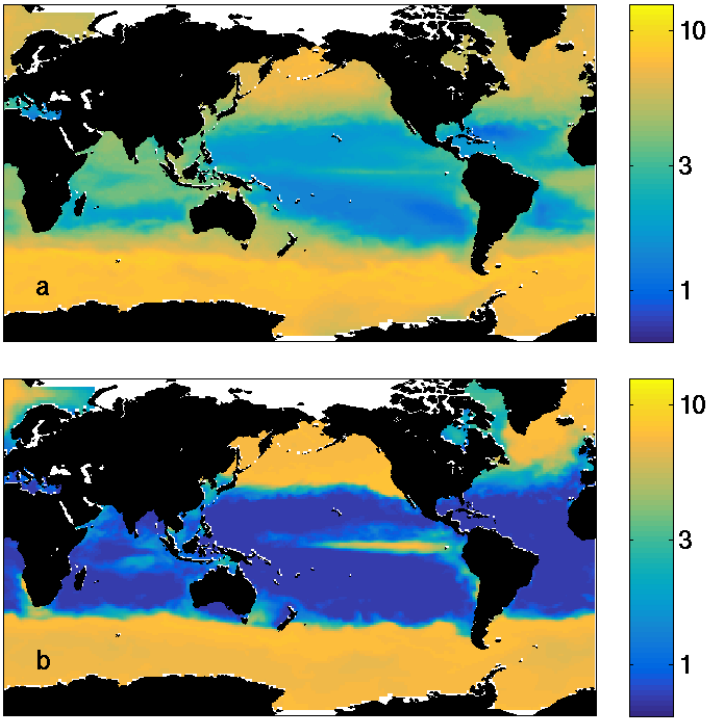


Figure S2. Mean equivalent spherical diameter (ESD, µm) of the surface phytoplankton from simulations with (a) a size-based model, and (b) a more traditional 2 PFT model. The size-based model (also shown in Figure 1) is a modifed version of Dutkiewicz *et al.* (2015), ref. 27, and Ward *et al.* (2012), ref. 32, and has16 size classes within several functional groups. Together with a range of size classes of zooplankton, the model captures observed functional group and size distributions. The diatom group has 11 size classes between 3µm to over 200µm. The 2 PFT model has one size each of pico-plankton and diatom (nominal ESD of 8µm). The size based model allows for a much more nuanced size structuring, in particular in the subtropical gyres. The physical model (Wunsch and Heimbach, 2007, ref. S14) has one degree horizontal resolution, and does not resolve the Arctic.

S14. Wunsch, C. and Heimbach, P. Practical global ocean state estimation, *Physica D*, 230, 197-208 (2007).

As regards model projections which predict decrease in NPP and restructuring of phytoplankton communities, with important regional heterogeneity, in addition to Dutkiewicz *et al.* (2013), ref. 29, Laufkötter *et al.* (2015), ref. 89, Barton *et al.* (2016), ref. 90, Dutkiewicz *et al.* (2014), ref. 91, also see Bopp *et al.* (2005), ref. S15, and Marinov *et al.* (2013), ref. S16:

S15. Bopp, L. *et al.* Response of diatoms distribution to global warming and potential implications: A global model study. *Geophys. Res. Lett*. **32**, 2– 5 (2005).

S16. Marinov, I. *et al.* North-South asymmetry in the modeled phytoplankton community response to climate change over the 21st century, *Glob. Biogeochem. Cycles* **27**, GB004599, doi:10.1002/2013GB004599 (2013).

As regards rapid evolutionary adaptations of phytoplankton traits, also see Box 2 cf. Loeuille et Loreau (2005), ref. 122, and Ward *et al* (2017), ref. S17.

S17. Ward, B.A. *et al.* The size dependence of phytoplankton growth rates: a trade-off between nutrient uptake and metabolism. *Am. Nat.* 189, 170-177 (2017).

…and mitigation of projected changes, in addition to Irwin *et al.* (2015), ref. 98, and Norberg *et al.* (2012), ref. 99, also see Li *et al.* (2017), ref. S18:

S18. Li, F. *et al.* Decreased photosynthesis and growth with reduced respiration in the model diatom *Phaeodactylum tricornotum* grown under elevated CO2 over 1800 generations. *Glob. Change Biol.* **23**, 127-137 (2017).

Figure 1, detailed caption: Diatom biogeography illustrated with the results of the MIT ecosystem model.
A clear picture of large scale patterns of diatom biogeography is difficult to obtain given the paucity of observations of diatom abundances (Leblanc et al. 2012 ref. 19; Buitenhuis et al. 2013 ref. 20; Malviya et al. 2016 ref. 16). Here we use results from a coupled physical, biogeochemical and ecosystem model to provide an illustration of the biogeography. We note that the model does not include all the processes (biological, chemical and physical) that may be important for diatom growth, and as such these maps are not definitive and should be understood as an illustration. For example, the representation of diatom abundance in coastal regions and near/under sea-ice is unsatisfactory. However, many of the features seen in these maps are indeed seen in the limited observations (Leblanc et al. 2012 ref. 19; Buitenhuis et al. 2013, ref. 20). The ecosystem component is an update from previous studies (Dutkiewicz et al. 2015 ref. 27; Ward et al. 2012, ref. 32), and describes several functional groups of phytoplankton (such as diatoms) distributed over 16 size classes. The physical fields are from a global reanalysis of the ocean circulation at 18 km resolution (http://ecco2.jpl.nasa.gov/). **a** and **b** –World ocean: model diatom concentrations (mmol C m^{-3}) at the surface for April/May/June and October/November/December) showing the large spring blooms. **c** and **d** - Transects through the Atlantic Ocean (corresponding line in a,c), showing a higher concentration of diatoms at the Deep Chlorophyll Maximum in the subtropical gyres, and seasonally at higher latitudes. **e** and **f**- The role of submesoscale fronts on the heterogeneity of diatoms is illustrated using the same ecosystem model as above, but in a higher resolution regional physical model (Lévy et al. 2014, ref. 13) nominally located in the squares shown in a,b. e- Model diatom concentrations (mmol C m^{-3}) at the surface over the Gulf Stream extension in January (daily average on January 12th). Green contours show submesoscale fronts, and red contours show the core of eddies. f- Median concentrations of depth-integrated phytoplankton abundances (boxes are quartiles, whiskers are 9th and 91st percentile) at fronts (F) and in the core of mesoscale eddies (E) compared to background conditions (B). Statistically phytoplankton are more abundant at submesoscale fronts and less abundant in the core of eddies, and this is particularly remarkable for diatoms compared to non-diatom phytoplankton types. The region covers the edge of the subtropical gyre where diatoms are not the dominant species, here the fronts are important to enhance the low background concentrations of diatoms.

Figure 2, detailed caption: Key processes influencing the contribution of diatoms to carbon export/transfer efficiency (CE/TE). (a) Taxonomic differences in cell size and shape (modified from Mann and Lazier, 2006; ref. S19), and/or the degree of cell wall silicification, both influence density (ρ, kg m^{-3}) and sinking rates of single cells or diatom chains; thereby influencing the residence time of organic C in the sunlit surface layers. For example, diatom species with higher cellular Si/C elemental ratios (mol mol^{-1}), such as *Thalassionema nitzchioides*, and *Coscinodiscus granii*, are more dense with a higher CE/TE potential. CE/TE potential is however modulated by changes in diatom population states **(b)**: physiological stressors such as light or nutrient limitation influence ρ through variations in diatom Si/C ratios, changes to life histories (e.g., induction of highly silicified resting spores), or production of Transparent Exopolymers Particles (TEP) during diatom proliferation; providing higher probability of collision, scavenging and aggregate formation. CE/TE potential is also modulated by **(c):** top-down processes involving biotic interactions with grazers, bacteria, viruses and parasites can have both direct and indirect effects; e.g., packaging of diatom fragments into fast-sinking faecal pellets (with higher Si/C ratios) reduces the residence time of undigested organic carbon in the upper surface layers. The

presence of grazers can also result in higher diatom Si/C ratios through biochemically-mediated increases in diatom cell wall silicification.

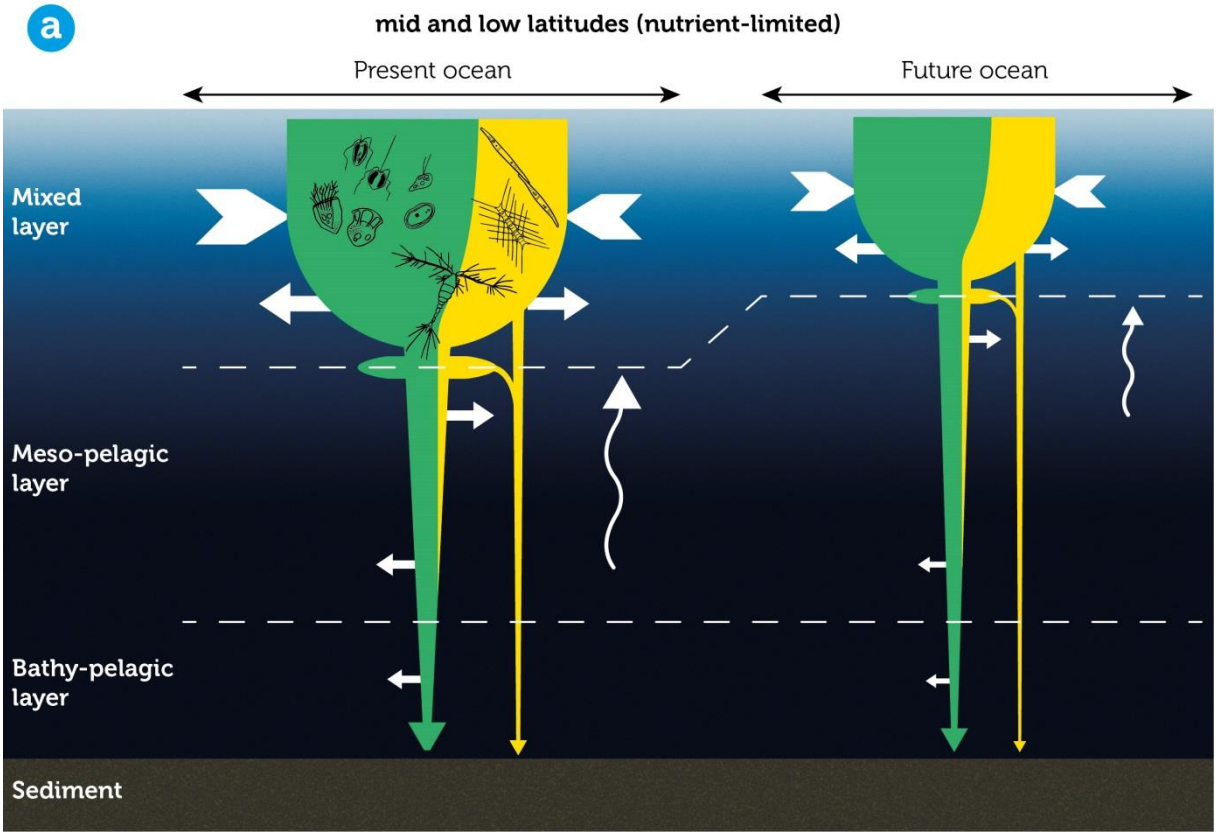
S19. Mann, K.H. and Lazier, J.R.N. Dynamics of Marine Ecosystems: Biological-Physical Interactions in the Oceans (Third Edition). Black-well Publishing, 496 pages, ISBN 1405111186 (2006).

Figure 3. detailed caption: Diatom lineages and their role in NPP and carbon export as revealed by high-throughput DNA sequence-based datasets from Tara Oceans. A regression-based modelling analysis has been used to study concomitantly a relative abundance matrix of diatoms inferred from metabarcoding data (based on 18s rDNA ribotypes (V9 region); Malviya *et al.* 2016, ref. 16) and a matrix of environmental parameters. Both matrices were extracted from the oligotrophic sampling dataset published by de Vargas *et al.* 2015 (S20) in which all sampling details can be found. In the environmental matrix, carbon export was estimated at 150 m from measurements of particle size distribution (between 250µm and 1.5cm) and concentration (for details see Guidi *et al.* 2016, ref. 116). To build the sequence metabarcoding abundance matrix, the taxonomic affiliation of the sequences has been done using a last common ancestor methodology, and had thus been performed down to species level when possible (S20 and http://taraoceans.sb-roscoff.fr/EukDiv/). Communities were sampled in the pico-nano- (0.8-5 µm), micro- (20-180 µm) and meso- plankton (180-2000 µm) fractions. In the framework of this study (and as in Guidi *et al.* 2016, ref. 116), sequences from all size fractions were pooled in order to get the most global and statistically reliable dataset of the planktonic community. Moreover, to get the most accurate vision of the diatom community, sequences showing less than 97% identity with reference sequences were excluded. Finally, each lineage has been normalized by the total sum of sequences in each sample. The final diatom relative abundance matrix used in our analyses included 103 lineages in 48 samples from 28 oligotrophic stations. The environmental matrix involved 11 environmental parameters in the same 48 samples. To compare both matrices and to model a causal relationship between the lineages (i.e., diatom metabarcode abundances) and the environmental parameters, a sparse Partial Least Squares analysis has been used in a regression mode (sPLS as implemented in the R package mixOmics (S21), which maximises the covariance between each linear combination (components) associated to each dataset. The Pearson method has been used for calculations, and parameter tuning was performed. A similar analysis (using the same options and parameters) has been applied to create the Fig. 1 from Guidi *et al.* 2016, ref. 116 (analyzing in that case the entire planktonic community). Correlations between lineages and environmental parameters are depicted as a clustered heatmap, in which the colour code corresponds to the correlation strength. This approach enabled to identify high covariations/correlations between certain lineages and carbon export or/and NPP. As a first result, NPP and carbon export appear well correlated. Second, with respect to the initial dataset of 103 lineages reduced then to 82 significant predictors (i.e., 82 lineages are finally retained), two diatom groups show high correlations with NPP and three groups with carbon export. From this regression analysis, three main groups of diatoms are thus identified. The “blue group” involves lineages showing a significant positive correlation to NPP and carbon export, with a relatively more important implication in NPP. The “green group” corresponds to lineages important in NPP and carbon export, whereas the “red group” comprises lineages that are important only with respect to carbon export. The “green” and “red” groups show a relatively higher correlation to carbon export compared to NPP. Such analysis is useful to pinpoint and focus on the main actors within the environmental communities and clearly highlights the potential contribution, and perhaps specialization of some specific lineages. Note that the dataset used for these analyses is derived primarily from samples in the oligotrophic ocean and excludes higher

latitudes in the North Pacific and North Atlantic Oceans, as well as the Southern Ocean (Guidi *et al.* 2016, ref. 116).

S20. de Vargas, C. *et al.* Eukaryotic plankton diversity in the sunlit ocean. *Science* **348**, doi:10.1126/science.1261605 (2015).

S21. Lê Cao, K. A., *et al.* Sparse PLS for Variable Selection when Integrating Omics Data. *Stat. Appl .Genet. Mol.* **7**, doi:10.2202/1544-6115.1390 (2008).


a
mid and low latitudes (nutrient-limited)
Present ocean
Future ocean
Mixed layer
Meso-pelagic layer
Bathy-pelagic layer
Sediment

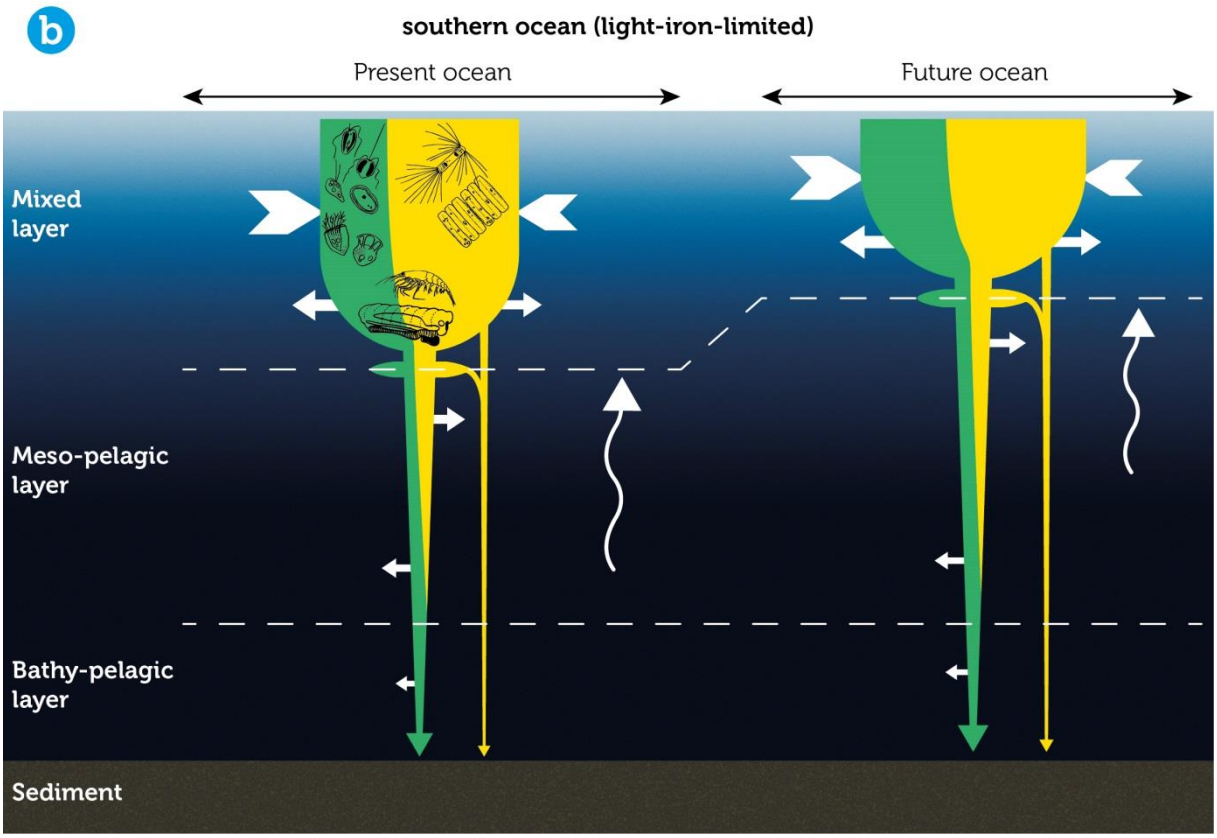

b
southern ocean (light-iron-limited)
Present ocean
Future ocean
Mixed layer
Meso-pelagic layer
Bathy-pelagic layer
Sediment

Figure 4, detailed caption: Schematic views on the role of diatoms in the biological carbon pump (BCP) in the present and future ocean. Superimposed are key players of primary and export production in the present ocean. The diatom pathway is in yellow, the non-diatom pathway in green. **a**-mid and low latitudes (nutrient-limited). *Present day ocean*. In the surface ocean <40% of photosynthetically generated organic carbon production (Field et al. 1998, ref. 9) is due to diatoms, the rest being generated by non-siliceous pico-, nano, and micro-phytoplankton. Conversely, around < 40% of the exported particulate organic carbon is transported through the siliceous pathway (Jin *et al.* 2006, ref. 11). Through the diatom pathway, specific environments (Kemp & Villareal 2013, ref. 15) e.g., niches of diatoms in gyres and fronts and filaments -see Figure 1- accumulation of diatoms in DCM as spores or as specialized adapted species, and severe nutrient/light limitation of the growth of diatoms in the surface layer can trigger massive sedimentation of particulate carbon that is able to reach the bathypelagic layer (i.e., the CO_2 sequestration layer). *Future ocean*. In a warm, stratified ocean, most models predict a decrease in primary and export production integrated over the low and mid-latitudes (Bopp *et al.* 2013, ref. 88), though due to re-arrangement of nutrient limitation, some regions may actually increase (Dutkiewicz *et al*. 2013, ref 29). However ocean acidification might enhance diatom growth (Dutkiewicz *et al*., 2015, ref 94), and in particular favour large-sized diatom species (Wu *et al.* 2014, ref. 95) that contribute significantly to export production through the siliceous pathway. The impacts of specific environments on the diatom pathway of the BCP are likely to be similar to those occurring in the present day ocean, although the proportion of fronts is also likely to change in the future. **b**- Southern Ocean (light- and iron-limited): *Present day ocean*. In the Southern Ocean primary production is generally limited by light and iron availability. Diatoms play a major role both in primary and in export production (e.g. Henson *et al.* 2012, ref. 75 ; Jin *et al*. 2006, ref. 11). The exported labile carbon transported by the diatom pathway is mostly recycled within the mesopelagic layer (Honjo *et al.* 2008, ref. 76). However, through frontal systems or "shade flora," evidence indicates that massive sedimentation (Quéguiner 2013, ref. 58) of organic carbon-rich siliceous matter can reach the bathypelagic layer and ultimately the sediments. *Future ocean*: In a warmer Southern Ocean diatoms might double their growth rates primarily in response to rising temperatures and iron-availability (Bopp *et al.* 2013, ref. 88; Hutchins & Boyd, 2016, ref. 97). Consequently, most model projections predict an increase in diatom abundance in the Southern Ocean (Dutkiewicz *et al.* 2013, ref. 29). Whether this will result in increased export production remains an open question.