Diatoms Si Uptake Capacity Drives Carbon Export In Coastal Upwelling Systems

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15 **Abstract**

Coastal upwelling systems account for approximately half of global ocean primary production and contribute
disproportionately to biologically driven carbon sequestration. Diatoms, silica–precipitating microalgae, constitute the
dominant phytoplankton in these productive regions, and their abundance and assemblage composition in the sedimentary
record is considered one of the best proxies for primary production. The study of the sedimentary diatom abundance (SDA)

20 and total organic carbon content (TOC) in the five most important coastal upwelling systems of the modern ocean (Iberia-
Canary, Benguela, Peru-Humboldt, California and Somalia-Oman) reveals a global-scale positive relationship between
diatom production and organic carbon burial. The analysis of SDA in conjunction with environmental variables of coastal
upwelling systems such as upwelling strength, satellite-derived net primary production and surface water nutrient
concentrations shows different relations between SDA and primary production on the regional scale. At the global-scale,

25 SDA appears modulated by the capacity of diatoms to take up silicic acid, which ultimately sets an upper limit to global
export production in these ocean regions.

1 Introduction

Coastal upwelling zones exist along the eastern boundary currents of the Atlantic and Pacific Oceans. In these areas, alongshore equatorward winds and the Coriolis effect force surface waters to diverge offshore, giving rise to the upwelling of nutrient-rich

5 deep waters into the surface. The five most important coastal upwelling systems of the modern ocean are associated with: (1) the Canary Current off northwest Africa including its extension to the Iberian Peninsula (Iberia-Canary); (2) the Benguela current along southwest Africa; (3) the Peru-Humboldt current off western south America (SE Pacific); (4) the California Current off western north America (NE Pacific) and the Somalia-Oman monsoon derived upwelling off the Arabian Peninsula (Barber and Smith, 1984; Hill et al., 1998). At present, 80 to 90% of oceanic primary production, which represents 50% of Earth's primary

10 production, occurs in the ±1% of the ocean characterized by coastal upwelling (Field et al., 1998; Hill et al., 1998).
The potential role of coastal upwelling systems on carbon uptake and export turns their dominant phytoplankton, the diatoms, into key players of marine planktonic food webs and the carbon cycle (Field et al., 1998). Diatoms require dissolved silica (as orthosilicic acid, H_4SiO_4), which they precipitate from seawater, to form their opal (amorphous hydrated Si) frustules (Lewin and Guillard, 1963) making coastal upwelling areas also a major Si sink (Tréguer and De La Rocha,

15 2013).

The prolific diatom-dominated blooms that respond to episodic inputs of nutrients are dominated by chain-forming marine species of the genus *Chaetoceros* Ehrenberg (Estrada and Blasco, 1985). Maximum fluxes of *Chaetoceros* coincide with intervals of increased nutrient availability in most coastal upwelling regions (California (Sancetta, 1995); Humboldt (Romero et al., 2001); Iberia-Canary (Wefer and G., 1993; Treppke et al., 1996b; Lange et al., 1994; Abrantes et al., 2002);

20 Benguela (Treppke et al., 1996a; Romero et al., 2002); Somalia-Oman (Koning et al., 2001; Nair et al., 1989) attesting for their great capacity for C export.
Although only a minor percentage (1–4%) of the initial diatom population gets preserved in the sediments (e.g. Takahashi et al., 1989; Sancetta, 1992; Abrantes et al., 2002), the positive relationship between abundance of diatom frustules and content of organic carbon in sediments beneath major upwelling systems ((*Iberia-Canary system* (Abrantes, 1988; Nave et al.,

25 2001)*; Benguela System* (Schuette and Schrader, 1981); *Peru-Humboldt system* (Abrantes, 2004)*, N California system* (Lopes et al., 2006)) suggests that estimates of sedimentary diatom abundance (#valves/g - SDA) is representative of C export production at coastal upwelling regions. In support of this relationship, time-series of organic carbon content and diatom abundance from Atlantic coastal upwelling sites indicate concomitant variations of the two productivity proxies (e.g. Muller and Suess, 1979; Abrantes, 2000). Conversely, other sequences from the NW and SW African margins show

30 contradictory results (e.g. Martinez et al., 1999; Caulet et al., 1992; Heinze and Wefer, 1992). A time-series located off the Oregon coast (Lopes et al., 2014), also shows disagreement between carbon and diatom-based estimates of primary productivity. In this record high abundances of small diatoms, which dominate highly productive ecosystems, co-occur with low concentrations of total organic carbon (TOC) in the sediments while higher carbon burial rates seem to be associated with the accumulation of large diatoms typical of unproductive environments.

35 It has long been recognized that both the physical and chemical processes as well as the biological response in coastal upwelling have a non-linear and complex relationship (Barber and Smith, 1981). Furthermore, intra- and inter-regional variability is known to be extensive through space and time, demanding dynamical and fine-scale biological modeling to faithfully understand those complex interactions. Here we analyze an extensive dataset of sedimentary diatom abundance (SDA for 703 sites) and organic carbon content (TOC for 200 sites) in concert with mean annual values of net primary

40 production; upwelling index; and seawater nutrient concentrations extracted from long time-series and global climatologies to assess the main factors controlling SDA. Our study relies on two main arguments: 1) it is possible to make generalizations about the functioning of coastal upwelling ecosystems (Barber and Smith, 1981); and 2) the sediments retain the imprint of the different processes that, on average, determine the physical, chemical and biological properties of coastal upwelling

ecosystems

2 Materials and Methods

The used data set comprises of 703 sediment samples recovered from the five most important coastal upwelling areas of the

5   modern ocean, collected by different institutions and sampling processes (box-, multi- and in some cases piston- coring devices since the 1970's). For the analysis, the topmost sediment (0-1 or -2 cm) was used (Figure 1; Data available at PANGEA). Calibration between the diatom data produced by different researchers followed the process described by Abrantes et al., (2005), and counting principles defined by Schrader and Gersonde (1978). Obtained values are given as number of valves / g of dry-sediment (#valves/g) and show 4 orders of magnitude in variability, between 10^5 and 10^9.

10   Considering that cell growth is exponential, and to avoid the effect of extreme values and preserve minor variability within each order of magnitude, the data is plotted as its natural log (ln).

Organic Carbon content (TOC - %w) for the Galicia, Portuguese Margin, NW Africa – Canary, SE and NE Pacific was measured following the methodology in use at the IPMA sedimentology and micropalentology laboratory. Three replicates of 2 mg subsamples of each dried and homogenized sediment sample are measured, before and after

15   combustion, on a CHNS-932 LECO elemental analyzer. The relative precision of repeated measurements of both samples and standards was 0.03 w%.

Upwelling indices were determined according to the National Oceanic and Atmospheric Administration (NOAA) procedure (Bakun, 1973) http://las.pfeg.noaa.gov/las/doc/global_upwell.html. Geostrophic winds were calculated from the FNMOC 6-hourly pressure analysis (1º grid) and further used to calculate wind stress and Ekman transport. Finally, the Ekman transport

20   is rotated to get the offshore component (provided that the orientation of the coast is known), and a monthly upwelling index was obtained for each site location from 1969 to 2013.

Net Primary Production (NPP) data was provided by the Oregon State University Ocean Productivity Center (http://www.science.oregonstate.edu/ocean.productivity/) as mean annual and seasonal values for the available 10-year dataset (2003-2013). NPP is determined by the Vertically Generalized Production Model (VGPM) and is a function of

25   chlorophyll, available light, and the photosynthetic efficiency (Behrenfeld and Falkowski, 1997).

The *World Ocean Atlas* 2013 (WOA13) is the source for *in situ* measured phosphate, silicate, and nitrate in µMl[-1] at standard depth levels and for annual, seasonal, and monthly composite periods (Garcia et al., 2014). Surface values correspond to the 10 m water depth and bottom data comprises the closest available value for each sample site water depth.

To address the long-term global relationship between SDA and all the environmental variables, escaping the temporal

30   variability (seasonal and annual) within and between regions, we used the annual mean value estimated from the number of years of available data. Regressions between SDA and each variable annual mean were calculated and the corresponding plot generated for the entire dataset as well as for the sites confined to the main upwelling zone of each system. The latitudinal boundaries for each main upwelling area were set to include seasonal upwelling regions and followed Rykaczewski et al., (2015).

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3 Results And Discussion

3.1 Sedimentary Organic Carbon Content (TOC) and Diatom Abundance (SDA)

Our dataset allows evaluation of the relationship between SDA and TOC per geographic region and globally (200 sites; Table 1 and Figure 2). No relationship exists for the Canary upwelling System (Galicia to Canaries), the Benguela and the

40   Peru-Humboldt systems, but a positive and significant relationship was found for the California system (NW Pacific) ($R^2 = 0.98$, $p=0.01$, n=5). When the entire existing dataset is considered, a significant positive relation is obtained ($R^2 = 0.40$, $p=0.01$, n=200). These results suggest that small-scale regional conditions are likely to determine different SDA and TOC accumulation loci. Diatoms give a detailed picture of the centers of maximum annual primary production generated during

the upwelling season (Abrantes and Moita, 1999; Nelson et al., 1995). TOC is indicative of the mean annual production (independent of the generating process), and a stronger SDA-TOC relationship occurs in centers of preferential accumulation of fine-grained sediments, such as off large river mouths (e.g. Abrantes, 1988; Abrantes et al., 2004; Reimers and Suess, 1983). On a global scale, the covariance between SDA and TOC is likely to reflect the higher annual contribution of diatoms

5 to total carbon export in the high-Si coastal upwelling systems.

When dealing with sediment components, however, one has to verify to what extent can sedimentary processes alter the sediment record. Both diatom and organic carbon burial success depend on, (1) the sealing effect provided by the rate of contribution of other particles to the bulk sediment, that is, sediment accumulation rate (MAR); and, (2) early diagenetic processes on the seafloor (Broecker and Peng, 1982).

3.1.1 Sealing effect

MAR corresponds to the amount of sediment deposited by unit of area and time, is expressed in g cm^{-2} ky^{-1}, can only be calculated if knowing the age of the sediments and it is subject to errors that can be caused by faulty age models, or processes like sediment focusing by bottom currents. Such problems can only be circumvented through the combined use of

15 MAR estimation from excess ^{230}Th determinations (Lyle et al., 2014). For our sites, little or no ^{230}Th data is available, and dated cores are scarce and punctual, reducing the original data set to 28 sites (SI Table 2). We used this data to investigate the possible influence of MAR variability on diatom accumulation rate (DAR) according to:

DAR (# valves cm^{-2} ky^{-1}) = Diatom abundance (SDA - #valves/g) * MAR (g cm^{-2} ky^{-1})

where MAR (g cm^{-2} ky^{-1}) is calculated multiplying the sedimentation rate (SR, cm/yr) by the sediment dry bulk density

20 (g/cm^3).

Sediment dry bulk density is also not available for the majority of the dated cores, but one can consider its variability between 0.7 and 2 g/cm^3 (authors laboratory data for thousands of samples). SR was determined on the basis of the two topmost published radiocarbon dates for each site (SI Table 2). Both DAR and MAR were estimated using the minimum, mean and maximum dry bulk density (0.7, 1.4 and 2 g/cm^3 - SI Figure 1A, B). The results reveal that SDA is not dependent

25 on MAR (R^2=0.01), but DAR values are mainly controlled by diatom abundance (R^2=0.90).

When the same exercise is preformed for TOC concentrations, the data set gets reduced to 10 sites which is not representative of all 5 areas and displays no relation to either MAR (R^2=0.18 at p=0.1 and n=10), or to TOC accumulation rate (R^2=0.62 at p=0.1 and n=10).

30 **3.1.2 Diatom and TOC diagenetic effects at the sea floor**

Diatom dissolution on the seafloor, although influenced by factors such as pH, temperature, organic matter and metal ions associated with the frustule surface, is mainly determined by the degree of Si saturation in the medium, that is, the concentration of silicic acid in the bottom waters (e.g. Lewin and Guillard, 1963; Hurd and Takahashi, 1982; Van Cappellen et al., 2002; Van Bennekom and Berger, 1984).

35 No relation between SDA and concentration of silicic acid in deep waters was found at the regional level (SI Figure 2). Throughout the world's oceans, the pathway of thermohaline deep water circulation generates inter-basin differences in the concentration of silicic acid, which increases as deep waters flow from the Atlantic Ocean to the Southern and Pacific basins (Rageneau et al., 2000). The comparison of bottom [H$_4$SiO$_4$] to SDA at our sites displays the two expected clusters that separate the lower silicate of the Atlantic *vs.* the higher silicate of the Pacific (Figure 3). Furthermore, the mean SDA (ln

40 transformed) values for the two clusters are statistically different (t test: T= -20.481, p<0.001, mean Atlantic=5.606 +- 0.072 and mean Pacific/Indian = 6.696 +- 0.076), but a large overlap within the diatom abundance of the two clusters is also evident. These results indicate that despite the diatom losses related to sea-floor [Si(OH)$_4^-$], the preserved sediment diatom signal carries generalized information that overrides the result of dissolution effects.

As to TOC, the preservation of the organic material that escapes water-column degradation and reaches the bottom, is dependent on the type of organic matter, bioturbation level and bottom water oxygenation (Canfield, 1994; Emerson, 1985; Zonneveld et al., 2010). Aside from the long-standing debate regarding the kinetics of organic matter decomposition at different bottom-water O_2 concentration, Canfield (1994) showed that in regions with high rates of organic carbon deposition

5   (typical of continental margins), differences in preservation are weakly dependent on bottom water O_2 concentrations.

3.2 Upwelling Intensity and SDA

In the modern subtropical ocean coastal upwelling is mostly seasonal (Spring-Summer) but in the more tropical latitudes of a few locations such as off Cape Blanc (Canary system), Walvis-Bay (Benguela system), off Peru (Humboldt system) it is

10   perennial. Inter-annual atmospheric and oceanic variations can cause latitudinal extension and retraction in the seasonal spatial coverage of each system as well as in the offshore extension of upwelling filaments. The best-known and dramatic inter-annual variations in coastal upwelling derived primary production occurs in the Humboldt-Peru system, caused by the El Niño-Southern Oscillation (ENSO) Cycle (Barber and Kogelschatz, 1990; Philander, 1990).

To investigate the possible effect of upwelling strength on sediment diatom abundance, we used the 47-year time-series of

15   the annually averaged upwelling index estimated for each sample site following the method of Bakun (1973). A method that can generate errors for sites located close to the equator or within 1 degree off the coast, that is, the inner-shore areas which are the most influenced by the coastal upwelling process, and where a large number of our sites are located (519 in total – SI Figure 3). An alternative approach would be the use of local wind datasets, but problems arise from the fact that different areas have dissimilar data sets both in terms of time length as in the index calculation approach. As such, we decided to use

20   the NOAA dataset after exclusion of very large values. The results (SI Figure 4; Table 1) reveal that independently of using all the sites or just the main upwelling areas, the only significant relationships are observed for the Southern Hemispheric systems (Benguela and Humboldt – Table 1). As a whole, the physics (although essential), does not appear as the primary factor determining diatom bloom size and its sediment record.

25   ### 3.3 Primary production and SDA

On the global scale, the restricted coastal upwelling areas are always highly associated to the spatial distribution of primary production, independently of the methodological approach (Berger, 1989; Gregg and Conkright, 2008; Field et al., 1998). There is also evidence for a good agreement between net primary production (NPP) and sediment diatom abundance, at the regional level (e.g. Figures 1E and 8 in Abrantes et al., 2005 and Figure 6 in Lopes et al., 2005). The relationship between

30   the sediment diatom abundance data and NPP at each of this study sites is presented in figure 4A. Although the general positive relationship between SDA and NPP, a significant correlation is only observed for the Canary system region with perennial upwelling conditions (Table 1). However, a close inspection of figure 4A reveals that potentially three different correlation lines can be defined through data from all different geographic locations. A result that reflects a combination of intra-regional differences and inter-regional similarities in the SDA-NPP relationship, but hampers the possibility of defining

35   a single equation at the global level.

3.4 Nutrient Availability and SDA

The variables evaluated so far revealed that SDA, contrarily to what has been found at the regional level, is not solely influenced by upwelling strength or ecosystem productivity. Sedimentary processes do not also appear to be a major

40   determinant of SDA. Thus, we explored the role of nutrient availability in regulating SDA under the premise that nutrient supply ratios can select for specific phytoplankton groups (Raymont, 1980; Platt et al., 1992; Barber and Kogelschatz, 1990). In coastal upwelling areas the type and amount of nutrients delivered to the ocean surface depends on the upwelling intensity (discussed above) since it determines the water mass source depth. Upwelled waters are in general, central waters of sub-

polar and sub-tropical origin in different mixing proportions. On a global scale, the previously mentioned inter-ocean fractionation also causes different nutrient concentrations to exist in the Atlantic and the Pacific coastal upwelling source waters. Similarly, intra-ocean circulation determines nutrient differences at the hemispheric level, in particular for silicate concentrations (Broecker and Peng, 1982; Sarmiento et al., 2003).

5   In coastal upwelling areas, diatoms dominate the biomass of phytoplankton communities. Their obligatory requirement for silicic acid makes it a limiting nutrient for diatom growth (Brzezinski and Nelson, 1996; Lima et al., 2014). Mesocosm experiments revealed that marine diatoms dominate phytoplankton communities when the concentration of silicic acid exceeds 2μM whenever other nutrients are in excess (Egge and Aksnes, 1992). Further analyses have shown that diatom productivity is limited by the availability of silicic acid in broad regions of the global ocean (Dugdale and Wilkerson, 1998).

10 To evaluate the large-scale spatial and temporal relation between surface water macronutrient contents and SDA we used mean annual $[NO_3^-]$, $[PO_4^{2-}]$ and $[Si(OH)_4^-]$ from the WOA13 database (Table 1 and SI figure 5 and figure 4B). SDA has significant positive relationships to $[NO_3^-]$ and $[PO_4^{2-}]$ on the Humboldt (0.44 and 0.52 respectively, at p=0.1 and n=162) and the Somalia-Oman systems (0.79 and 0.67 at p=0.1 and n=23), but not at the global level, as it is clear from SI figure 5. When the data set is restricted to the main upwelling areas the positive relationship between SDA and nitrate becomes

15 positive and significant (0.39 at p=0.1 and n=400), consistent with the effect of nitrate on diatom standing stocks. Between SDA and $[Si(OH)_4^-]$ we found a statistically significant relationship for the Canary, Humboldt and Somalia-Oman systems (0.52, 0.49 and 0.74 respectively –see Table 1). The relationship was also significant for the Benguela system (0.41 at p=0.1 and n=32) when only the main upwelling areas are considered (Table 1; Figure 4B). Figure 4B and SI Figure 6A represent the relationship found between SDA and silicate for the main upwelling sites and the total dataset respectively, and

20 show the same but a reduction in data scattering when only the main upwelling areas are considered (figure 4B). In detail, it reveals a steep slope near the low silicate concentrations ($\leq$ 2 μM) defined by the NE Atlantic regions (Galicia to the Canary Islands region – 29ºN). An increase towards the asymptote is defined by the data from the Canary (Cape Blanc), Benguela and Humboldt systems, and the sites from the Somalia-Oman and California regions, the Si-richest within the modern coastal upwelling systems, establish the maximum diatom abundances. This pattern is retained when treating the Atlantic

25 and Pacific Ocean datasets independently (SI Fig. 6 B, C), which confirms that the inter-hemispheric difference in preservation potential is not the main cause behind the global SDA pattern.

These results led us to explore the possible link between SDA and $[Si(OH)_4^-]$ in the surface waters using a theoretical framework focused on cell physiology. Our strategy assumes that the observed SDA reflects surface ocean diatom productivity and export fluxes. The concentration of silicic acid in upwelled waters can potentially increase SDA in two

30 ways: 1) increasing diatom productivity (and hence diatom numerical abundance) and, 2) increasing the thickness and sinking rate of diatom frustules. Our model considers that the physiological response of marine diatoms to surface waters silicic acid availability represents a long-term (tens to hundreds of years) control on coastal upwelling SDA. It has been shown that not only does diatom productivity increase with increasing silicic acid concentrations (Dugdale and Wilkerson, 1998), but also that diatoms have a higher Si[OH]₄ uptake rate for higher silicic acid ambient concentrations (Dugdale et al.,

35 2011). Thus, we speculate that it is silicic acid concentration that sets the upper limit to diatom growth rate, which, in turn, is imposed by the physiological capacity of individual cells to take up and use silicic acid.

The dynamics of silicic acid uptake by diatoms has been a matter of continuous debate (Dugdale, 1967; Thamatrakoln and Hildebrand, 2008), but it is traditionally parameterized by a Michaelis-Menten model, defined by two parameters, the maximum uptake rate and the half saturation constant (i.e. the concentration of nutrient at which the population reaches half

40 of the maximum uptake rate), (Del Amo and Brzezinski, 1999). We applied the mathematical expression used to model nutrient uptake kinetics to our SDA data at the regional, oceanic, hemispheric and global scale:

$V = V_{max} [S] / (K_s + [S])$

where V_{MAX} is considered to be the maximum diatom abundance value ($Diat_{MAX}$) defined by the best line fit (log) to the data; [S] the concentration of silicic acid; ($Si_{surfMAX}$) and Ks the half saturation constant defined as $Diat_{MAX}/2$ ($Diat_S$) (e.g. Fig.5).

The results obtained are presented in SI table 1, where the parameter V represents the expected sediment diatom abundance

5 at a given silicic acid concentration in the surface ocean waters. V values are in the order of 10^8 for a silicic acid concentration $\pm 7\mu M\ l^{-1}$ in the Pacific and Indian upwelling areas, as well as for all 5 areas together. For the Southern Hemisphere coastal upwelling systems the values were in the order of 10^7 for the same $[Si(OH)_4^-] \pm 7\mu M\ l^{-1}$. The parameter V in the Atlantic Ocean is one order of magnitude lower than in the Southern Hemisphere systems and two orders of magnitude lower than in the Pacific Ocean or all the 5 areas together. Similarly, a $[Si(OH)_4^-]$ yield-dose of $1\mu M\ l^{-1}$ in the

10 Atlantic and North Hemisphere (excluding the Somalia-Oman system), suggests that in these oceanic regions marine diatoms are outcompeted by non-siliceous phytoplankton in agreement with observations in mesocosm experiments (Egge and Aksnes, 1992).

4 Conclusions

15 In summary, our results indicate that SDA is not dependent on sedimentation rate nor is it solely a function of the bottom water silicate concentration. On decadal to centennial time scales, nitrate and silicic acid concentrations in surface waters contribute to define the global SDA pattern. However, the ability of marine diatoms to take up silicic acid sets an upper limit to SDA that strongly influences the potential of coastal upwelling areas for C sequestration.

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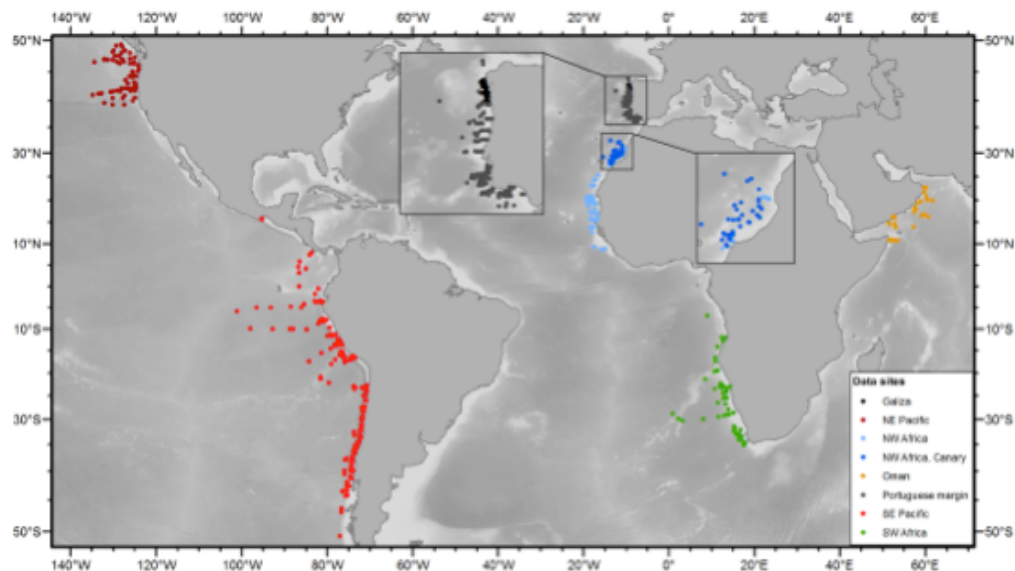
Figure 1: Geographic distribution of the total data set sites considered in this study. Map in WGS84 and Mercator projection. Different colors represented different upwelling systems.
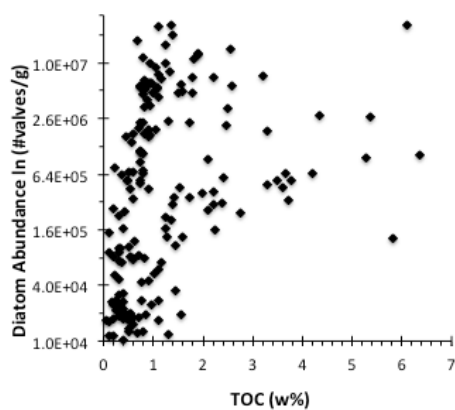
Figure 2: Relationship between total marine diatom abundance ln (# valves /g) and total organic carbon content (W%) for the Canary (Galicia to Canary), Humboldt (SE Pacific) and California systems (NE Pacific).
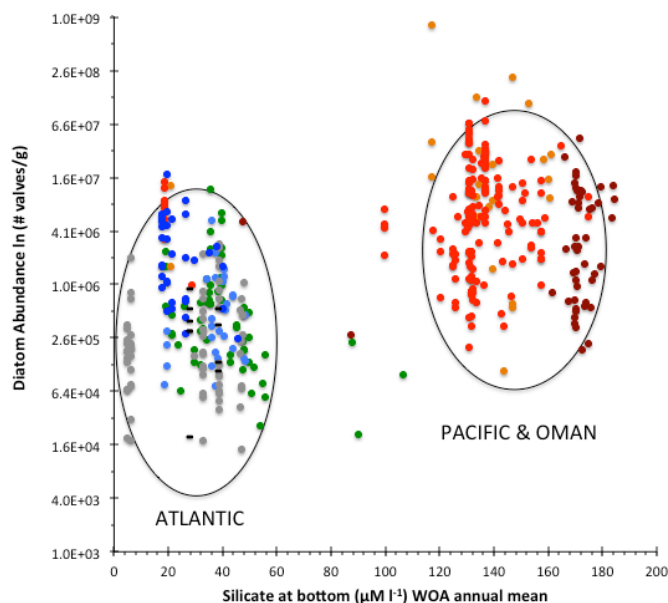
Figure 3: Relationship between total marine diatom abundance ln (# valves /g) and bottom water [Si(OH)$_4^-$] in µM from WOA 2009 database. Color scheme as in Figure 1.
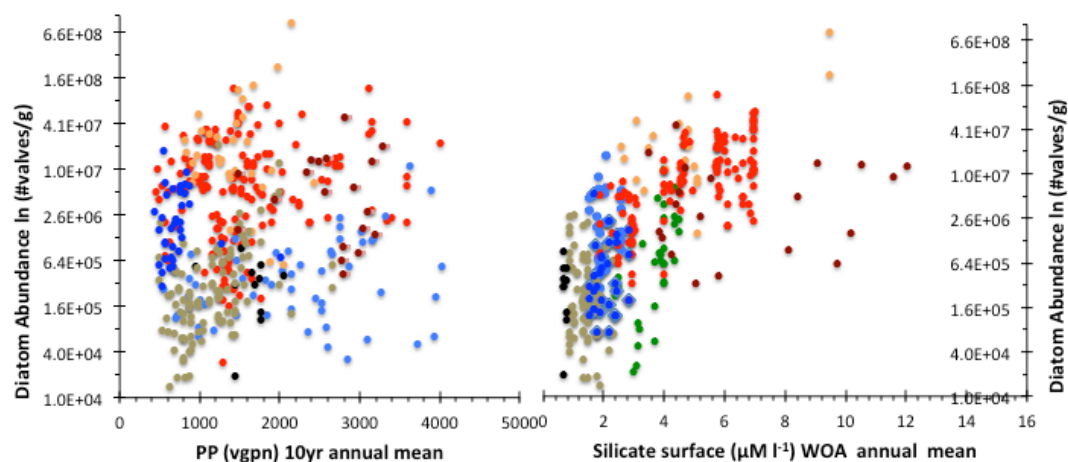
Figure 4: Relationship between total marine diatom abundance ln (# valves /g) to: A. NPP generated from SeaWiFS chlorophyll distributions according to the Vertically Generalized Production Model (VGPM) (Behrenfeld and Falkowski, 1997 for sites located

10 **on main upwelling areas; B. surface water [Si(OH)$_4^-$] in µM, from WOA 2013 database. Sites located on main upwelling areas. Color scheme as in Figure 1.**
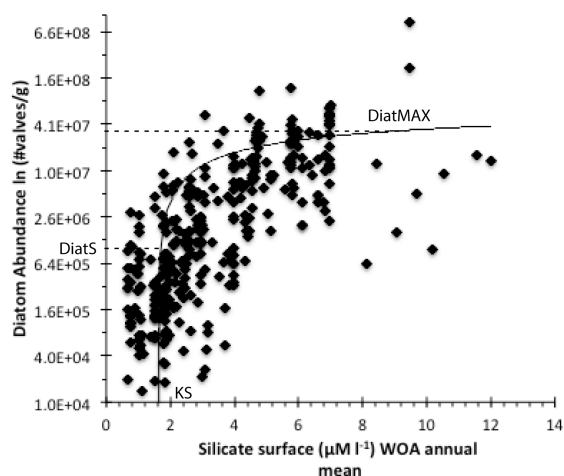
Figure 5: Translation of Michaelis-Menten model, which defines the relationship between population abundance and [Nutrient] to the long-term SDA dataset. That relationship is expressed by the mathematical equation $V = V_{max}\,[N]\,/\,(K_s + [N])$ where (V) is the algal population growth rate, (V_{max}) the maximum diatom abundance in the sediments ($Diat_{MAX}$) at threshold $[N = Si_{surfMAX}]$ above

5 **which population abundance remains constant; $[N - Si_{surfS}]$ is silicate concentration on upwelled surface waters, and (Ks) is silicate concentration at $Diat_{MAX}/2$**

Parameters	Time series	Galiza / Portuguese-Canary System	Portuguese Margin / Portuguese-Canary System	NWAfrica Canary / Portuguese-Canary System	NW Africa / Canary System	SW Africa / Benguela System	SE Pacific / Humboldt System	NE Pacific / California System	Oman / Indian Monsson	TOTAL
n		11	119	37	21	61	176	62	26	513
Upidex	43yr ann mean	0.09	0.14	0.00	-0.01	**0.34**	**0.41**	-0.12	-0.16	0.04
n		-	-	-	-	28	116	20	-	378
Upidex Tup	43yr ann mean	-	-	-	-	**0.35**	**0.41**	-0.16	-	0.13
n		11	111	37	50	62	207	63	33	573
NPP	10yr ann mean	-0.19	0.22	-0.03	0.10	0.24	0.18	-0.05	0.36	0.09
n		-	-	-	-	38	166	19	-	463
NPP Tup	10yr ann mean	-	-	-	-	**0.64**	0.15	0.14	-	0.09
n		10	61	34	35	62	162	37	23	422
Sil b	(site water depth)	-0.24	0.16	-0.27	0.19	-0.05	0.07	0.03	-0.03	0.15
n		-	-	-	-	32	116	21	-	338
Sil b Tup	(site water depth)	-	-	-	-	-0.27	0.07	0.14	-	0.19
n		10	61	34	50	52	162	37	23	429
Si surf	(10 m)	-0.24	-0.21	0.12	**0.52**	-0.08	**0.49**	0.03	**0.74**	0.27
n		-	-	-	-	32	116	21	-	353
Si surf Tup	(10 m)	-	-	-	-	**0.41**	**0.51**	-0.05	-	**0.31**
n		10	73	34	50	62	162	43	23	400
P		0.24	**-0.35**	0.23	0.08	0.25	**0.52**	0.08	**0.67**	0.04
N		0.24	-0.24	-0.10	0.16	0.33	**0.44**	0.06	**0.79**	0.06
n		-	-	-	-	32	116	21	-	303
P Tup		-	-	-	-	0.30	**0.58**	0.04	-	0.16
N Tup		-	-	-	-	0.23	-0.21	0.09	-	**0.39**
n		11	85	30	na	na	43	5	na	174
TOC (W%)	(sediment)	0.51	0.08	0.31	na	na	0.15	***0.98***	na	***0.43***

p=.01; **p=.05**

Table 1: Pearson correlation between the total Sediment Diatom Abundance data set (SDA as ln (#valves/g) and ecological parameters (UPindex – 47 year annual mean upwelling index; NPP – 10 year annual mean Net Primary Production from VGPM; N - WOA13 [NO_3^-]; P – WOA13 [PO_4^{2-}]; Si_{surf} – WOA13 [$Si(OH)_4^-$]; Si_b – WOA09 [$Si(OH)_4^-$] at site depth; TOC – Sedimentary organic carbon content as W%) for each upwelling area and all the 5 areas. Upwelling considers the data points located under the main upwelling areas. Bold numbers indicate the highest significant correlations. Factors followed by (-) indicate negative factors, for which the signal of the correlation value has to be multiplied by -1.