1. Introduction

Marine phytoplankton form a taxonomically and functionally diverse group, where communities are structured by a variety of factors, including nutrient and light availability, predation and competition for resources (Litchman and Klausmeier, 2008). Environmental heterogeneity, thus, creates biogeographical patterns of abundance, composition, traits and diversity of phytoplankton communities in the global ocean (Barton et al., 2013; Follows et al., 2007; Hays et al., 2005). Phytoplankton communities within a biogeographical region are subject to similar environmental conditions, such as temperature (Bouman et al., 2003), nutrient concentration (Browning et al., 2014) and irradiance (Arrigo et al., 2010). These environmental factors, along with phytoplankton composition itself (Bouman et al., 2005), affect the overall photophysiological response and bulk primary productivity of the phytoplankton community.

Biogeography of phytoplankton communities and their photophysiological characteristics, consequently, impact the structure of marine ecosystems due to their functional community role in biogeochemical cycling and transfer of energy to higher trophic levels. For example, distinct phytoplankton assemblages have been reported to influence differently particulate (Martiny et al., 2013a, 2013b; Smith and Asper, 2001) and dissolved elemental stoichiometry (C:N:P)(Weber and Deutsch, 2010), the drawdown of gases (Arrigo, 1999; Tortell et al., 2002) and the efficiency of carbon export (Guidi et al., 2009; Le Moigne et al., 2015). Patterns of phytoplankton stoichiometry has been assumed to be consistent phylogenetically and within higher taxonomic levels (Ho et al., 2003; Quigg et al., 2003). Nonetheless, phytoplankton stoichiometry has been reported to vary according to nutrient supply ratios (Bertilsson et al., 2003; Rhee, 1978), as well as phenotypically within species across the same population (Finkel et al., 2006).

The sub-Arctic North Atlantic is a complex system with contrasting hydrography that structures plankton communities within distinct biogeographical provinces (Fragoso et al., 2016; Head et al., 2003; Li and Harrison, 2001; Platt et al., 2005; Sathyendranath et al., 2009, 1995). Biogeographical regions of the Labrador Sea shape phytoplankton community composition (Fragoso et al., 2016), bio-optical properties (Cota, 2003; Lutz et al., 2003; Platt et al., 2005; Sathyendranath et al., 2004; Stuart et al., 2000) and the seasonality of phytoplankton blooms (Frajka-Williams and Rhines, 2010; Lacour et al., 2015; Wu et al., 2008, 2007). Phytoplankton blooms, for example, occur first (April to early May) in the shelves due to haline-driven stratification driven by the input of Arctic-related waters, in addition to rapid sea ice melt in the Labrador Shelf near Canada (Frajka-Williams and Rhines, 2010; Wu et al., 2007). The central Labrador bloom occurs later in the season (late May to June) as result of thermal stratification (Frajka-Williams and Rhines, 2010). Fragoso et al. (2016) showed that the biogeography of phytoplankton communities in the Labrador Sea during spring and early summer is shaped by distinct species found Atlantic or Arctic waters, which may have distinct impact on the biogeochemical cycles and transfer of energy to upper trophic level. However, these authors focused in taxonomy and investigated only larger phytoplankton (> 4µm). The photophysiological and biochemical signatures, such as stoichiometry (C:N ratio) of these distinct spring phytoplankton communities occurring in distinct sectors of the Labrador Sea has not been previously investigated.

Quantification of marine phytoplankton community composition, for large numbers of samples, is challenging because small cells (< 5µm) are difficult to identify and count using light microscopy, in addition to being a time-consuming method. To overcome these problems, quantification and analyses of phytoplankton pigments by high performance liquid chromatography (HPLC) has been widely used to monitor phytoplankton community distributions over large temporal and spatial scales (e.g., Aiken et al., 2009; Peloquin et al., 2013; Platt et al., 2005). The interpretation of the pigment data is not always straightforward, since some pigments are shared by several algal groups and can change according to local nutrient and light conditions

(DiTullio et al., 2007; van Leeuwe and Stefels, 2007, 1998). The chemotaxonomic tool, CHEMTAX (CHEMical TAXonomy), provides a valuable approach to estimate phytoplankton class abundances when used in conjunction with microscopic information (Irigoien et al., 2004; Mackey et al., 1996; Wright et al., 1996). CHEMTAX has the advantage of providing more information about phytoplankton classes than individual diagnostic pigments or ratios and has been used widely to investigate phytoplankton biogeography on regional scales (Muylaert et al., 2006; Wright and Van den Enden, 2000) and globally (Swan et al., 2015).

The aim of this study is to provide a baseline description of the current distributions and biogeochemical traits of phytoplankton communities from distinct biogeographical regions of the Labrador Sea. For this purpose, we investigate the multi-year (2005-2014) distributions of late spring and early summer (May to June) phytoplankton communities in the various hydrographic settings across the shelves, slopes and deep basin of the Labrador Sea based on phytoplankton pigments. In addition, we examine the overall photophysiological and biogeochemical traits associated with these phytoplankton communities. We believe that the results presented here will provide important information about the current condition of phytoplankton communities in the Labrador Sea and improve our understanding of potential long-term changes in high-latitude oceans.

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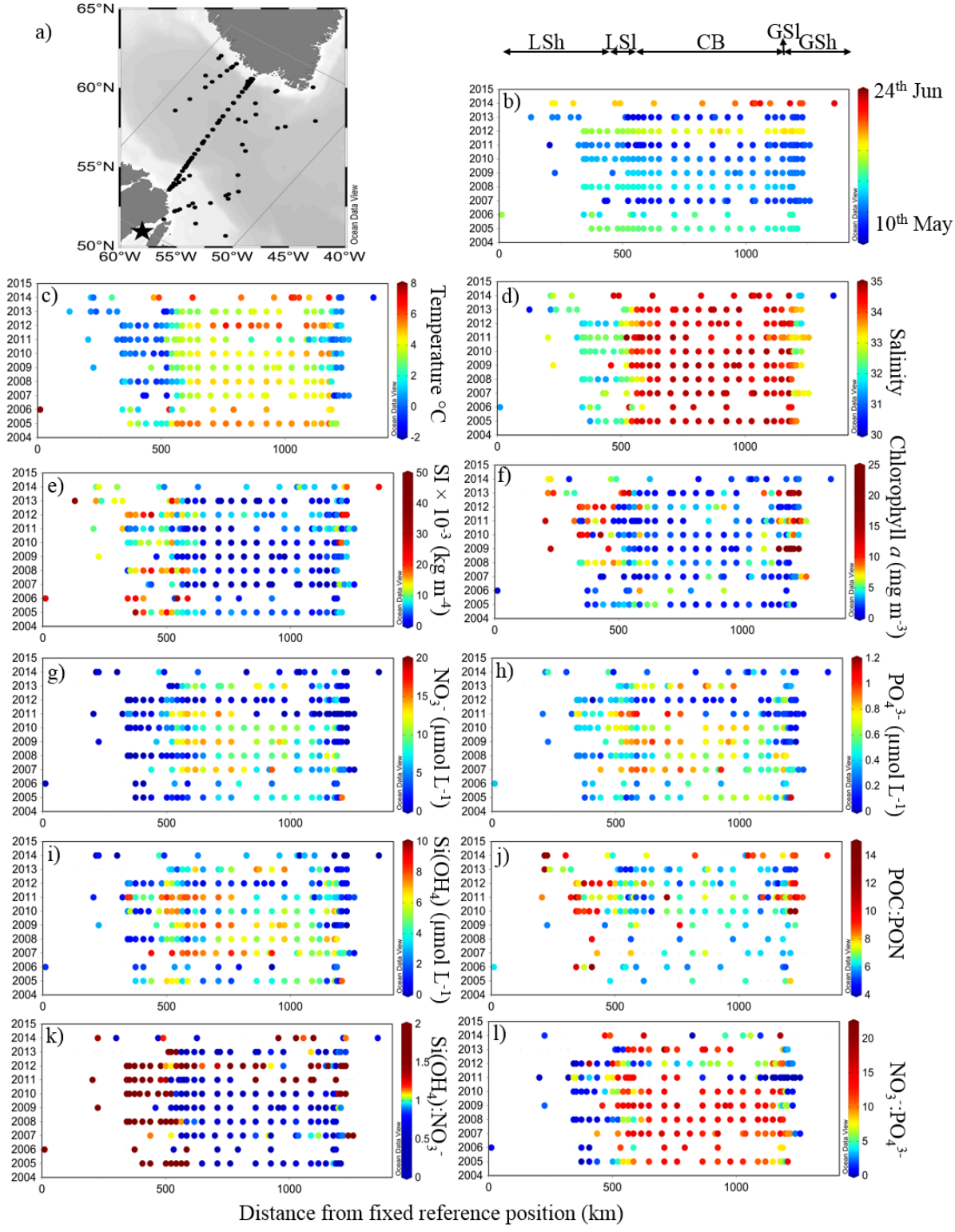

Figure 3 – Map with sampling stations and distances from a fixed reference position (Northeast Gulf of St Lawrence) in the x-axis shown by the star (a). Values are given at individual stations sampled between 2005 and 2014 (y-axis) for the following variables: date of sample collection (b), temperature (c), salinity (d), stratification index (SI) (e), chlorophyll *a* (f), nitrate (NO_3^-) (g), phosphate (PO_4^{3-}) (h), silicate ($Si(OH)_4$) concentrations (i), ratios of particulate organic carbon (POC) to particulate organic nitrogen (PON) (j), silicate to nitrate ($Si(OH)_4$:NO_3^-) ratios (k), and nitrate to phosphate (NO_3^-:PO_4^{3-}) ratios (l). LSh = Labrador Shelf, LSl = Labrador Slope, CB = Central Basin, GSl = Greenland Slope, GSh = Greenland Shelf.

Figure 4

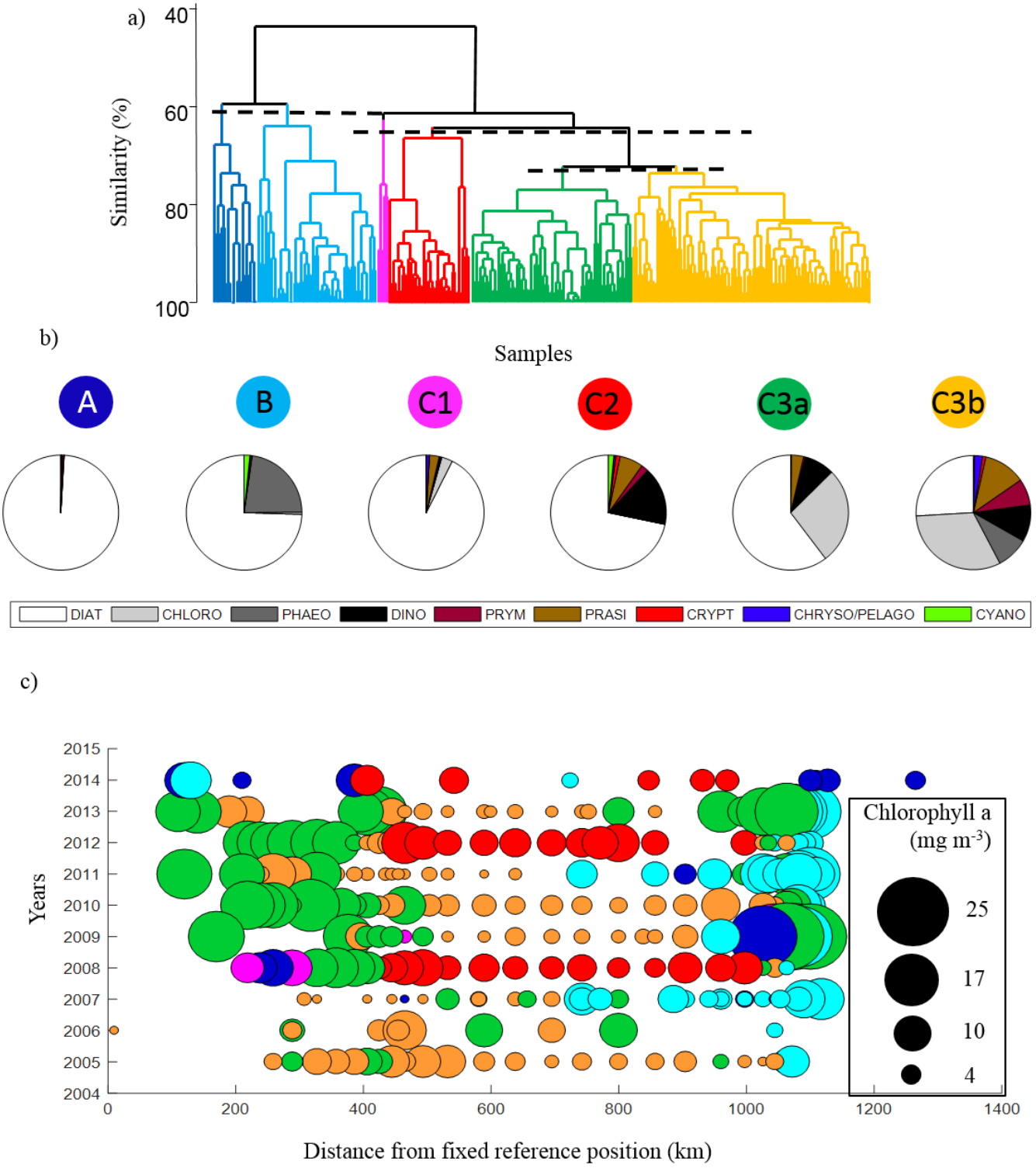

Figure 4. Dendrogram showing clustering of samples (a) and the proportion of chlorophyll *a* contributed by each phytoplankton class for each cluster (b). Spatial distribution of distinct phytoplankton communities (cluster groups) along the section, showing the distance from the star in Fig 3a) (c). Bubble size in (c) represents total chlorophyll *a* biomass.

4.2 Chemtax interpretation and groups distributions

Diatoms were the most abundant phytoplankton group found in the Labrador Sea, particularly at the shelves where they dominated almost 100% of the total phytoplankton community (Fig. 4a). Chlorophytes and prasinophytes were common in the center-western part (Fig. 4b,c), whereas *Phaeocystis* was abundant at the eastern part of the Labrador Sea (Fig. 4d). Dinoflagellates were abundant in the center region of the Labrador Sea (Fig. 4e). Other prymnesiophytes, including coccolithophores and *Chrysochromulina* were also common at the center part of the Labrador Sea (Fig. 4f). Overall, chrysophytes and pelagophytes were found in low abundance in the Labrador Sea, except at the center region of the Labrador Sea during 2011 (Fig. 4g). Cyanobacteria was more abundant at the Labrador Slope and Greenland Shelf and during some years (2005 and 2012) at the center Labrador Sea (Fig. 4f). Cryptophytes comprised less than 10% of total phytoplankton chlorophyll concentrations (data not shown).

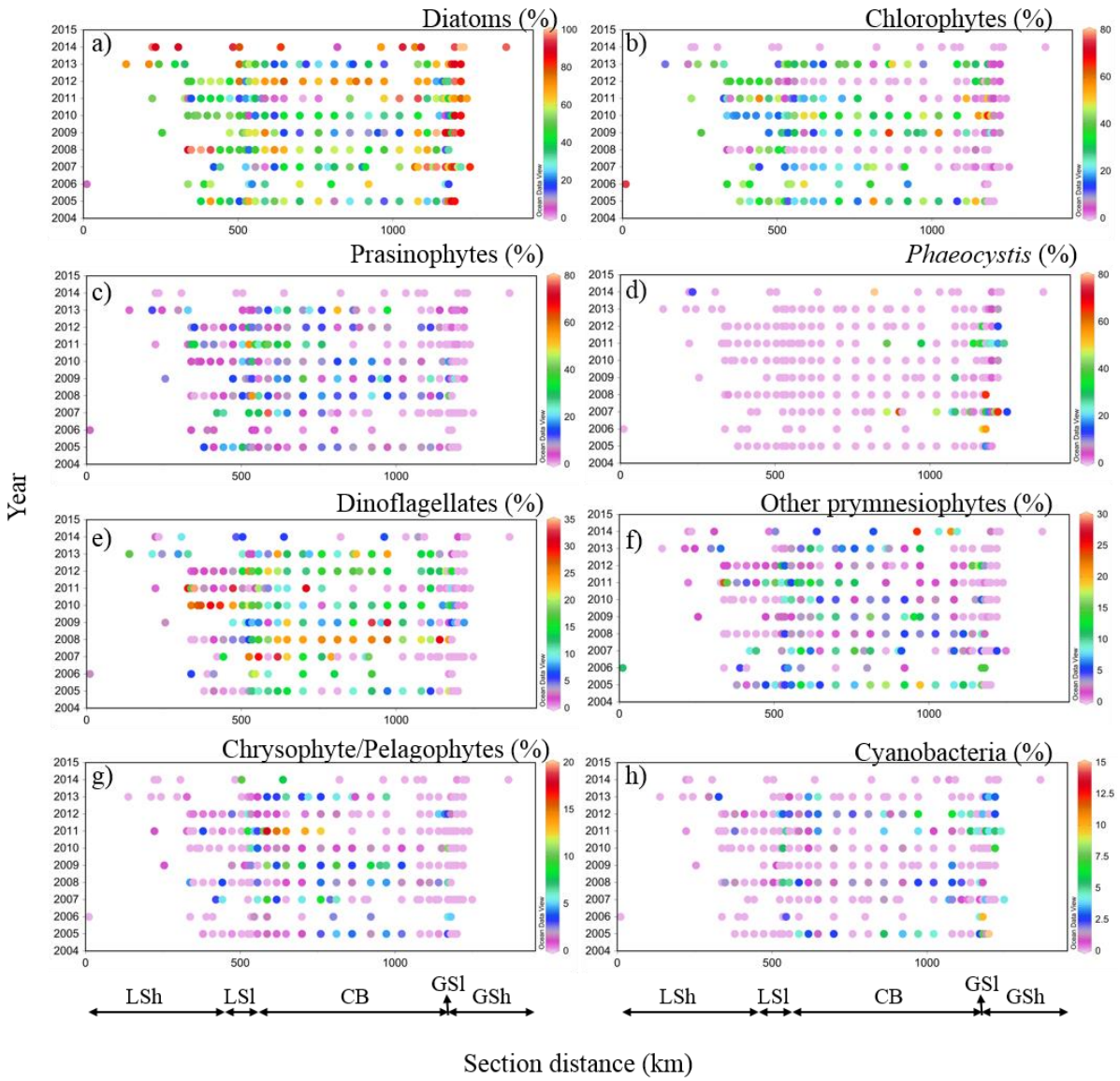

Figure 4 – Relative contribution (%) of chlorophyll a from distinct phytoplankton classes at each station from 2005 to 2014 along the section distance from Labrador coast represented in Figure 3a (star symbol in a). LSh = Labrador Shelf, LSl = Labrador Slope, CB = Center Basin, GSl = Greenland Slope, GSh = Greenland Shelf. Note the distinct scales for each group.

Table 4 – Results of the Redundancy Analyses (RDA) with the eigen-values, taxa-environmental correlations and percentages of variance explained used in the analysis (a). Automatic forward selection (a *posteriori* analysis) was used to determine the environmental variable(s) that best explain the variance of the data (b). The subset of environmental variable(s) that significantly explained phytoplankton distribution are referred to marginal effects (λ_1) when analysed individually, or conditional effects (λ_a) when analysed additively in the model (b). Explanatory variables are temperature (°C), salinity, nitrate (NO_3^-; µmol L^{-1}), phosphate (PO_4^{3-}; µmol L^{-1}), silicate ($Si(OH)_4$; µmol L^{-1}) and Stratification Index (SI) (kg m^{-4}). Significant p-values ($p < 0.05$) represents the variables that explain the variation in the analyses.

a) Axes	1	2	3	4	Total variance
Eigen-values	0.26	0.04	0.005	0	1
Taxa-environment correlations	0.68	0.4	0.321	0.25	
Cumulative percentage variance					
of species data	25.7	29.9	30.3	30.7	
of species-environment relation	83.5	97.2	98.8	99.8	
Sum of all eigenvalues					1
Sum of all canonical eigenvalues					0.31

b) Marginal Effects		Conditional Effects			
Variable	λ_1	Variable	λ_a	*P*	*F*
$Si(OH)_4$	0.2	$Si(OH)_4$	0.2	0.001	61.7
NO_3^-	0.19	Temperature	0.05	0.001	17.3
PO_4^{3-}	0.17	Salinity	0.02	0.002	6.94
Salinity	0.09	NO_3^-	0.01	0.016	4.31
Temperature	0.07	PO_4^{3-}	0.02	0.002	7.22
SI	0.06	SI	0.01	0.153	1.72

Table 5 – Average, standard deviations and number of observations (in parenthesis) of environmental and biological variables of each cluster group. MLD = mixed layer depth, SI= Stratification index, NO_3^- = nitrate, PO_4^{3-} = phosphate, $Si(OH)_4$ = silicate, DT= diatoxanthin, DD= diadinoxanthin, POC= particulate organic carbon, PON= particulate organic nitrogen, POC_{phyto} = phytoplankton-derived particulate organic carbon, α^B = initial slope of the photosynthesis-irradiance curve, P_m^B = maximum normalised photosynthesis, E_k = half-saturation irradiance, *Es* = saturation irradiance.

	Cluster A		Cluster B		Cluster C3a		Cluster C3b		Cluster C2		Cluster C1	
Temperature (°C)	2.8 ± 2.4	(17)	2.0 ± 1.8	(46)	1.6 ± 1.9	(62)	3.4 ± 1.9	(92)	4.8 ± 1.5	(32)	1.4 ± 1.7	(4)
Salinity	33.4 ± 1.5	(17)	33.7 ± 0.8	(46)	33.1 ± 1.2	(62)	34.1 ± 1.0	(92)	34.4 ± 0.5	(32)	33.0 ± 1.6	(4)
MLD (m)	32.2 ± 43.8	(17)	32.6 ± 23.4	(46)	31.2 ± 28.5	(62)	59 ± 71.1	(92)	29.8 ± 17.0	(32)	16.0 ± 4.2	(4)
SI x 10^{-3} (kg m^{-4})	9.1 ± 6.3	(17)	6.3 ± 5.7	(46)	10.7 ± 8.5	(62)	5.0 ± 6.8	(92)	6.1 ± 4.5	(31)	6.6 ± 8.5	(4)
NO_3^- (µmol L^{-1})	2.9 ± 4.7	(17)	2.7 ± 3.5	(46)	3.4 ± 4.3	(58)	8.4 ± 4.1	(83)	3.7 ± 3.9	(32)	3.8 ± 6.8	(4)
$Si(OH)_4$ (µmol L^{-1})	2.2 ± 2.7	(17)	2.8 ± 2.1	(46)	3.5 ± 2.4	(58)	5.4 ± 2.2	(83)	3.0 ± 2.2	(32)	2.3 ± 3.4	(4)
PO_4^{3-} (µmol L^{-1})	0.3 ± 0.3	(17)	0.3 ± 0.2	(45)	0.4 ± 0.2	(55)	0.7 ± 0.2	(79)	0.3 ± 0.2	(32)	0.4 ± 0.3	(4)
$Si(OH)_4$:NO_3^-	6.0 ± 11.8	(14)	3.6 ± 7.9	(37)	8.5 ± 18.2	(54)	1.1 ± 1.5	(82)	1.6 ± 1.8	(32)	3.9 ± 4.4	(4)
NO_3^-:PO_4^{3-}	8.2 ± 6.7	(11)	5.2 ± 5.0	(45)	5.9 ± 5.8	(55)	11.4 ± 4.1	(79)	8.7 ± 4.6	(32)	5.5 ± 7.1	(4)
Chlorophyll a (mgChl*a* m^{-3})	3.8 ± 4.7	(17)	5.5 ± 4.8	(45)	7.7 ± 5.6	(59)	2.0 ± 1.7	(91)	4.0 ± 1.8	(31)	8.8 ± 9.6	(4)
DT:(DT+DD)	0.01 ± 0.03	(16)	0.02 ± 0.05	(44)	0.04 ± 0.05	(62)	0.10 ± 0.10	(92)	0.08 ± 0.07	(32)	0.02 ± 0.04	(4)
(DD+DT):Chla	0.08 ± 0.07	(17)	0.03 ± 0.03	(46)	0.04 ± 0.02	(62)	0.07 ± 0.03	(92)	0.12 ± 0.03	(32)	0.07 ± 0.04	(4)
POC (mgC m^{-3})	245 ± 90	(4)	498 ± 198	(27)	533 ± 198	(45)	234 ± 145	(63)	512 ± 179	(15)	392 ± 418	(2)
PON (mgN m^{-3})	39 ± 16	(4)	65 ± 23	(27)	74 ± 30	(45)	37 ± 26	(64)	84 ± 33	(15)	42 ± 41	(2)
POC_{phyto} (%)	23.0 ± 5.2	(4)	49.2 ± 29.5	(26)	60.9 ± 25.6	(44)	33.3 ± 10.1	(64)	36.0 ± 11.4	(15)	37.8 ± 1.3	(2)
POC:PON	6.5 ± 1.2	(4)	7.8 ± 2.1	(27)	7.5 ± 2.1	(45)	6.6 ± 1.3	(64)	6.2 ± 0.9	(15)	8.6 ± 1.6	(2)
α^B (mgC mgChl*a*$^{-1}$ h^{-1} $W^{-1}m^2$) x10^{-2}	-		6.8 ± 6	(9)	9.2 ± 5	(10)	7.1 ± 4	(18)	7.1 ± 1.5	(4)	-	
P_m^B (mgC mgChl*a*$^{-1}$ h^{-1})	-		2.9 ± 1.1	(9)	2.3 ± 0.8	(10)	2.3 ± 0.6	(18)	3.2 ± 0.7	(4)	-	
E_k (Wm^{-2})	-		60 ± 33	(9)	29 ± 13	(10)	39 ± 14	(18)	46 ± 5	(4)	-	
Es (Wm^{-2})	-		62 ± 32	(9)	35 ± 18	(10)	43 ± 18	(18)	56 ± 8	(4)	-	
β (mgC mgChl*a*$^{-1}$ h^{-1} $W^{-1}m^2$) x10^{-4}	-		4 ± 7	(9)	16 ± 23	(10)	10 ± 16	(18)	29 ± 24	(4)	-	

Supplemental Material - Table S2. Range of environmental and biological variables of each cluster group. MLD = mixed layer depth, SI= Stratification index, NO_3^- = nitrate, PO_4^{3-} = phosphate, $Si(OH)_4$ = silicate, DT= diatoxanthin, DD= diadinoxanthin, POC= particulate organic carbon, PON= particulate organic nitrogen, POC_{phyto} = phytoplankton-derived particulate organic carbon, α^B = initial slope of the photosynthesis-irradiance curve, P_m^B = maximum normalised photosynthesis, E_k = half-saturation irradiance, *Es* = saturation irradiance.

	Cluster A	Cluster B	Cluster C3a	Cluster C3b	Cluster C2	Cluster C1
Temperature (°C)	- 1.1 - 6.7	- 1.1 - 5.7	- 1.2 - 5.6	- 1.4 - 7.9	0.9 - 6.8	- 0.6 - 3.4
Salinity	30.2 - 34.9	31.8 - 34.8	30.4 - 34.8	31.3 - 35	32.8 - 34.8	31.4 - 34.7
MLD (m)	14 - 196	11 - 105	11 - 156	11 - 531	11 - 64	12 - 21
SI x 10^{-3} (kg m^{-4})	0.03 - 24	0.1 - 27	0.008 - 40	0.008 - 32	0.5 - 19	1 - 19
NO_3^- (µmol L^{-1})	0 - 15.2	0 - 16.0	0 - 15.9	0 - 15.1	0.2 - 13.7	0.1 - 13.9
$Si(OH)_4$ (µmol L^{-1})	0 - 7.8	0.3 - 8.5	0 - 8.6	0.9 - 8.8	0.4 - 8.0	0.2 - 7.4
PO_4^{3-} (µmol L^{-1})	0.1 - 1.1	0.1 - 1.0	0 - 1.0	0.2 - 1.0	0.1 - 0.9	0.2 - 0.9
$Si(OH)_4$:NO_3^-	0.2 - 44.1	0.4 - 45.4	0 - 87.3	0.1 - 9.3	0.6 - 9.5	0.2 - 9.4
NO_3^-:PO_4^{3-}	0.3 - 19.1	0 - 15.9	0 - 17.3	0 - 20.8	1.1 - 16.2	0.2 - 15.4
Chlorophyll a (mgChl*a* m^{-3})	0.6 - 20.2	0.7 - 19.7	1.1 - 24.1	0.4 - 9.0	0.4 - 9.1	0.9 - 22.8
DT:(DT+DD)	0 - 0.1	0 - 0.2	0 - 0.2	0 - 0.4	0 - 0.3	0 - 0.1
(DD+DT):Chla	0 - 0.3	0 - 0.1	0 - 0.1	0 - 0.2	0.1 0.2	0 - 0.1
POC (mgC m^{-3})	119 - 331	178 - 952	160 - 960	55 - 658	211 - 796	97 - 688
PON (mgN m^{-3})	20 - 54	29 - 109	24 - 154	4 - 138	38 - 154	13 - 71
POC_{phyto} (%)	17.9 - 29.0	14.9 - 100*	8.0 - 100*	12.2 - 64.6	18.8 - 56.6	36.9 - 38.7
POC:PON	5.2 - 7.9	5 - 12.5	4.6 - 13.4	4.7 - 12.4	5.2 - 8.5	7.5 - 9.7
α^B (mgC mgChl*a*$^{-1}$ h^{-1} $W^{-1}m^2$) x10^{-2}	-	2 - 18	4 - 17	2 - 17	5 - 9	-
P_m^B (mgC mgChl*a*$^{-1}$ h^{-1})	-	1.0 - 4.7	1.2 - 4.0	0.9 - 3.2	2.5 - 4.0	-
E_k (Wm^{-2})	-	20 - 127	15 - 52	16 - 67	41 - 51	-
Es (Wm^{-2})	-	21 - 127	15 - 59	17 - 76	45 - 62	-
β (mgC. mgChl*a*$^{-1}$ h^{-1} $W^{-1}m^2$) x10^{-4}	-	0 - 16	0 - 75	0 - 49	5 - 60	-

* Values > 100% due to variability of the data was set to a maximum value of 100%.