



# Predicting marine phytoplankton community size structure from empirical relationships with remotely-sensed variables

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Predicting marine phytoplankton community size structure from empirical relationships with remotely-sensed variables

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For Peer Review

## Abstract

The size composition of primary producers has a potential influence on the length of marine food chains and carbon sinking rates, thus on the proportion of primary production that is removed from the upper layers and available to higher trophic levels. While total rates of primary production are widely reported, it is also necessary to account for the size composition of primary producers when developing food web models that predict consumer biomass and production. Empirical measurement of size composition over large space and time scales is not feasible, so one approach is to predict size composition from environmental variables that are measured and reported on relevant scales. Here, we describe relationships between the environment and the size composition of phytoplankton communities, using a collation of empirical measurements of size composition from sites that include polar, tropical and upwelling environments. The size composition of the phytoplankton communities can be predicted using two remotely-sensed variables, Chl *a* concentration and sea surface temperature. Applying such relationships in combination allows prediction of the slope and location of phytoplankton size spectra and estimation of the percentage of different sized phytoplankton groups in communities.

**Keywords:** Primary production, community, phytoplankton, trophic level, transfer efficiency, size composition, picoplankton, nanoplankton, microplankton.

## Introduction

Global primary production by marine phytoplankton is around  $5 \times 10^{10}$  tonnes C  $y^{-1}$  (Carr et al. 2006) but there are large regional variations in the proportion of this production being removed from the upper layer through sinking and therefore available to higher trophic levels. This is due to variations in absolute productivity among regions, with 50% of production estimated to come from 27% of ocean area (Longhurst et al. 1995), and to regional differences in phytoplankton community structure. Regionally, the factors that affect the availability of phytoplankton to a given size class of consumers are their (i) spatial and temporal distribution, (ii) palatability, (iii) abundance, and (iv) size composition (due to morphological constraints of consumers and because cell individual sinking rates are related to size (Smayda 1971)).

Marine pelagic food chains are strongly size-based, with larger predators eating smaller prey. This size-based predation is predominantly responsible for the transfer of energy from phytoplankton to

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progressively larger animals and total production falls with body mass as trophic level rises (Sheldon et al. 1972). Mean ratios between predator and prey body mass (predator-prey mass ratio PPMR) are relatively constant in marine ecosystems (Barnes et al. 2010). Consequently, when primary producers are smaller, there are, on average, more steps in a food chain to a predator of given size. Further, since mean annual trophic transfer efficiency at each step is also relatively constant (Barnes et al. 2010), production by consumers of a given body size will be a smaller proportion of primary production in regions where the primary producers are smaller. Such an effect has been shown in lakes (Sprules and Munawar 1986), although it has not yet been reported in large-scale observations in marine systems (San Martin et al. 2006b).

With knowledge of PPMR and the factors that influence trophic transfer efficiency, estimates of primary production can be used to predict production at higher trophic levels (Dickie 1976). For global scale analyses of the transfer of energy from phytoplankton to higher trophic levels it is often convenient to use primary production estimates based on satellite measurements of surface chlorophyll concentration provided by the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) global time series (McClain et al. 2004). Some progress has been made with estimating phytoplankton cell sizes by linking phytoplankton absorption to phytoplankton size classes using a single variable, the optical absorption by phytoplankton at 443 nm, which can be derived from the inversion of ocean colour data (Hirata et al. 2008) but a complementary approach is to identify general relationships between remotely-sensed environmental variables and the size composition of phytoplankton communities.

Here, we seek to identify relationships between the observed size composition of phytoplankton communities and remotely-sensed environmental variables. Our aim is purely to use readily available remotely-sensed environmental variables such as surface chlorophyll and sea surface temperature to enable estimations of phytoplankton size parameters for input to models. To provide a comprehensive description of the size and relative abundance of cells we used 4 descriptors of community structure: (1) mean mass ( $\log_{10}$ ), (2) the variance of mass ( $\log_{10}$ ), (3) the slope of size spectra (relationship between the logarithm of total abundance by cell mass class and the logarithm of cell mass, with individuals binned to cell mass classes irrespective of species identity (Sheldon and Parsons 1967)) and (4) the range of cell masses that encompass a given proportion of total biomass or production. This information is necessary to predict phytoplankton production by size class in inputs to size-based models of production at higher trophic levels (Jennings et al. 2008; Blanchard et al. 2009).

## Method

Abundance and species composition were determined for phytoplankton in 361 water samples collected at twelve sites: five transects from 48° N to 50° S in the Atlantic Ocean (hereafter AMT1-5,  $n = 125$ , taken at 7 m (second samples at each site, taken at the deep Chl *a* maximum were excluded from this analysis), the Benguela upwelling ( $n = 54$ ), mesocosms in the Bergen fjord ( $n = 46$ ), the Irminger Sea ( $n = 59$ ), Long Island Sound ( $n = 7$ ), the North Sea ( $n = 44$ ), the Norwegian Sea ( $n = 19$ ) and the Oregon upwelling ( $n = 7$ ). In all locations samples were taken in subsurface but see Irigoien et al. (Irigoien et al. 2005) for details. Sub-samples (100 ml) were settled (Utermöhl technique (Lund et al. 1958)) and individuals counted at the species level with an inverted microscope. Heterotrophic species were excluded from the analysis. Picoplankton was measured using flow cytometry (see Irigoien et al (Irigoien et al. 2004) for details). Biomass was calculated as the product of numerical abundance and cell mass. More details of sample positions, collection, processing and composition are provided by Irigoien et al. (Irigoien et al. 2004; Irigoien et al. 2005).

To assess the proportion of phytoplankton biomass (B) or production (P) that was attributable to cells in specified mass (M) ranges, we investigated expressing cumulative B or P as a function of M by attempting to fit various forms. All samples were successfully fitted by:

$$B = 100 (1 - \exp(-pM^q)) \quad \text{Equation 1}$$

The fitted relationships were used to predict the M ranges that contributed to 10%, 25%, 50%, 75%, 80% and 90% of total B or P (Fig. 1). For example,

$$M_{80\%} = (-\ln(0.2)/p)^{1/q} \quad \text{Equation 2}$$

Since P was not measured directly, we calculated the net production rate (R) of individuals from M, accounting for photosynthetic active radiation (PAR) following López-Urrutia et al. (López-Urrutia et al. 2006):

$$\ln R = \ln(Nc) + \alpha \times \ln(M) - E \times (1/kT) + \ln\left(\frac{PAR}{PAR + K_m}\right) \quad \text{Equation 3}$$

1 where  $N_c$  is the normalization constant ( $\ln(N_c) = -11.28$ );  $\alpha$  is the allometric exponent ( $\alpha = 1.05$ );  $E$  is  
2 the activation energy for photosynthetic reactions ( $E = 0.29$ ); and  $PAR/(PAR + K_m)$  is the Michelis-  
3 Menten photosynthetic light response where  $PAR$  is the photosynthetically available radiation at the  
4 sample site and  $K_m$  is the half-saturation constant ( $K_m = 1.51$ ) that represents the amount of quanta  
5 at which half the maximum photosynthetic activity is reached.  $R$  is expressed as metabolic rate in  
6 mmol of  $O_2\ d^{-1}$  and  $M$  is expressed in  $pg\ C$ ,  $T$  is the absolute temperature and  $PAR$  is irradiance in  
7 mol photons (Einsteins)  $m^{-2}\ d^{-1}$  (2003  $PAR$  values for each sample site were taken from  
8 <http://oceandata.sci.gsfc.nasa.gov/SeaWiFS/Mapped/Annual/par/>). Rate in mmol of  $O_2\ d^{-1}$  was  
9 converted to rate in  $pg\ C\ year^{-1}$  (molar mass of  $C = 12.01$ ):

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20  $Rate\ in\ pg\ C\ year^{-1} = R / 12.01 \times 365 \times 10^{12}$  Equation 4  
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24 Biomass of each species of phytoplankton in each sample was calculated by multiplying the  
25 abundance by species mean  $M$ . Attempts to fit Pareto distributions to estimate the slopes of size-  
26 spectra (Vidondo et al. 1997) were unsuccessful since the data consisted of abundance by mean  
27 species' cell mass rather than individual mass measurements. Instead, traditional normalized  
28 biomass size spectra were defined by assigning each species to a  $\log_2$  integer scale size class based  
29 on the mean cell size of the species. Total abundance of individuals at mass was then calculated by  
30 summing the numbers of individuals of all species in each size class. Biomass in each size class was  
31 normalized by dividing the biomass in that class by the width of the class. The size spectrum slope  
32 and intercept were calculated for each sample at each site after removing very small and very large  
33 classes so that all contiguous classes contained non-zero abundance. To ensure that slope and  
34 intercept were independent, mid-point heights of the spectra were zeroised (Daan et al. 2005). All  
35 data manipulation and analyses were performed using R (R Development Core Team 2007).  
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47 To provide a long-term description of the environment at the sampling sites we estimated mean  
48 annual sea surface temperature (SST), surface chlorophyll a concentration (Chl a) and primary  
49 production (PP) at each site. SST data were derived from the Moderate-resolution Imaging  
50 Spectroradiometer (MODIS) aboard the NASA satellites. Monthly SST averages for 2003 were  
51 extracted through the Jet Propulsion Laboratory physical oceanography DAAC web portal  
52 (<http://poet.jpl.nasa.gov/>) and averaged to give a mean annual value at a scale of  $36\ km^2$ . Estimates  
53 of Chl a were taken from Sea-viewing Wide Field-of-view Sensor (SeaWiFS) data  
54 (<http://orca.science.oregonstate.edu/1080.by.2160.monthly.hdf.chl.seawifs.php>) by calculating an  
55 annual mean value for each sampling location from data extracted for each month in 2003. Where  
56 no value was available for a given month at a particular location then the value from the nearest  
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available location for that month was used. PP was computed from a wavelength- and depth-resolved model (Mélin 2003), building on the approach of Longhurst et al. (Longhurst et al. 1995). The main biological input to the models was the surface concentration of chlorophyll a pigment provided by SeaWiFS (see above). All changes from the implementation of Longhurst et al. (Longhurst et al. 1995) are detailed in Mélin (Mélin 2003). Outputs were calculated on a 36km grid. Annual primary production was obtained by averaging positive values ( $\text{mg C m}^{-2}\text{d}^{-1}$ ) over the number of available months, except at high latitudes where it was normalized to 12 (as ocean colour has no good coverage of wintertime high latitudes, owing to the presence of cloud cover and sea ice). The mean annual values were assigned to each station location. When station locations had to be matched to point locations rather than onto a grid, we attempted the match in the following order; (1) number of degrees to one decimal place for both latitude and longitude, (2) number of degrees to one decimal place for latitude, rounded whole number of degrees for longitude, (3) rounded whole number of degrees for latitude and number of degrees with one decimal place for longitude, (4) rounded whole number of degrees for both latitude and longitude. All were successfully matched (split between the 4 priorities 0%, 8%, 5% and 87% respectively).

For some comparisons, cell size had to be converted between equivalent spherical diameter (ESD) and M. For example, a phytoplankton cell with ESD  $2\mu\text{m}$  has carbon content of approximately  $0.8\text{pg}$  ( $-0.08$  on the  $\log_{10}$  pg scale used in our Figures) using the conversion

$$\text{pg C year}^{-1} = 0.216 \times \text{volume}^{0.939} \mu\text{m}^{-3} \quad \text{Equation 5}$$

reported for taxonomically diverse protist plankton (Menden-Deuer and Lessard 2000).

Relationships were explored between the remotely-sensed environmental variables primary production, sea surface temperature and chlorophyll a and (a) cell mass that accounted for 50% of total phytoplankton biomass (i.e. 50% on cumulative biomass curve) (hereafter  $M_{B50}$ ), (b) cell mass range that included 80% of total biomass (range of cell masses from 10% to 90% of biomass on cumulative biomass curve) ( $M_{B90-10}$ ), (c) cell mass that accounted for 50% of total phytoplankton production (i.e. 50% on cumulative production curve) ( $M_{P50}$ ), (d) cell mass range that included 80% of total production ( $M_{P90-10}$ ), (e) size spectra slope and (f) size spectra mid-point height. Prior to performing ANOVA, where necessary the data were log-transformed to achieve normality and equality of variance.



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2 To identify the remotely-sensed environmental variables that best predicted the properties of the  
3 phytoplankton communities we randomly divided the data into equal-sized ‘training’ and  
4 ‘predicting’ data sets (Tian et al. 2007). We fitted linear models to the cases in the training set and  
5 then evaluated how well these models predicted the properties of the phytoplankton communities in  
6 the predicting set. The training set models were of the form:  
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$$Y(t) = f(X(t); \theta) + \text{error}$$
 Equation 6  
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16 where the  $Y(t)$  variable was related to a function of a subset of the environmental variables  $X(t)$  and  
17 the parameters  $\theta$  were estimated by least squares. The models were assumed to be normally  
18 distributed with mean zero and constant variance. The effect of each variable as a predictor was  
19 tested individually; then each was tested as the second variable along with the variable previously  
20 identified as the best predictor.  
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27 The performance of the training set models was evaluated using the prediction data set and we  
28 described performance with the following summary statistic (Tian et al. 2007):  
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$$D = |Y(p) - Z(p); \hat{\theta}|$$
 Equation 7  
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36 Where  $Y(p)$  are the  $Y$  values in the prediction data set and  $Z(p)$  contains the predicted values of  $Y(p)$   
37 based on the training data set model with its estimated parameter vector  $\hat{\theta}$ . This statistic can be  
38 interpreted as prediction error.  
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43 We report the mean values of  $D$  from 1000 calculations based on different random choices of the  
44 training and prediction data sets. This approach ensures that our results are not affected by the  
45 selection of training and prediction data sets. We refer to the mean  $D$  as  $\bar{D}$  and use it to evaluate  
46 our models (rather than a summary of the fit of the model) because we want to use our model for  
47 prediction (models with the best fit often include more variables than those that give the best  
48 prediction). We then investigate the explanatory power of the best prediction model by fitting the  
49 model to the whole dataset.  
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57 Applying these relationships in combination allows prediction of the slope, intercept and location of  
58 phytoplankton size spectra with respect to  $M$ . The location of the cell mass range is calculated so  
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that that the integrated biomass to either side of the mid-point is equal. Thus the value for mass at 10% ( $M_{B10}$ ) is calculated as:

$$M_{B10} = M_{B50} \{ (10^{(b+1) \log_{10}(M_{B90-10})} + 1) / 2 \}^{-1/(b+1)} \quad \text{Equation 8}$$

where  $M_{B50}$  is mid-point mass,  $b$  is slope and  $\log_{10}(M_{B90-10})$  is  $(\log_{10}(M_{B90}) - \log_{10}(M_{B10}))$ , the values predicted by the models. The derivation is shown in the Supplementary Material.  $M_{B90}$  is then calculated as:

$$M_{B90} = 10^{(\log_{10}(M_{B10}) + \log_{10}(M_{B90-10}))} \quad \text{Equation 9}$$

A statistical model that adequately fitted the very variable tails of the cumulative distribution was not found, and so to ensure the integrated B was equal to 100% of cumulative B the values of  $M_{B0}$  and  $M_{B100}$  were estimated by plotting  $M_{B10}$ ,  $M_{B50}$  and  $M_{B90}$  and fitting a second order polynomial relationship.

The percentage contribution of a particular size class to total community biomass or production can then be calculated for a given sea surface temperature and chlorophyll a concentration. The derivations of the equations are shown in the Supplementary Material.

## Results

Mean cell mass ranged from 243pg of C (AMT3) to 4740pg of C (Bergen fjord) and variance was lowest on AMT1 and highest in the Bergen fjord (Table 1).  $M_{B50}$  ranged from 1.6pg C (AMT3) to 1209pg C (Long Island Sound) and  $M_{B90-10}$  ranged from 6.2pg C (AMT1) to 4476pg C (AMT4) (Table 1).  $M_{P50}$  ranged from 3.0pg C (AMT3) to 1340pg C (Long Island Sound) and  $M_{P90-10}$  ranged from 8.9pg C (AMT1) to 4070pg C (Bergen fjord) (Table 1).

Across all sites the mean size spectra slope was  $-1.19$ , ranging from  $-1.66$  in the Norwegian Sea to  $-0.74$  in Long Island Sound. Mean mid-point height ( $\log_2$  C pg) was 22.11 ranging from 20.54 on AMT5 to 23.41 in the Benguela. The fits of all size spectra slopes were significant at the 0.1 level except Long Island Sound ( $p=0.14$ ) and mean  $r^2$  was 0.63 (Table 2).

There was a positive linear relationship between  $M_{B50}$  ( $\log_{10}$ ) and both of the variables primary production ( $\log_{10}$ ) and chlorophyll a ( $\log_{10}$ ) and an inverse linear relationship between  $M_{B50}$  ( $\log_{10}$ )

1 and sea surface temperature. There was an inverse linear relationship between  $M_{B90-10}$  ( $\log_{10}$ ) and  
2 both of the variables primary production ( $\log_{10}$ ) and chlorophyll a ( $\log_{10}$ ) (Fig. 2 and Supplementary  
3 Table 1). There was a positive linear relationship between  $M_{B90-10}$  ( $\log_{10}$ ) and sea surface  
4 temperature but the p-value for the intercept was not significant (Fig. 2 and Supplementary Table  
5 1). These biomass relationships were consistent with those for production (Fig. 3 and  
6 Supplementary Table 1).  
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14 There were significant positive linear relationships between size spectra slope and both the  
15 variables primary production ( $\log_{10}$ ) and chlorophyll a ( $\log_{10}$ ) and an inverse relationship between  
16 slope and sea surface temperature (Fig. 4 and Supplementary Table 1). The linear relationships  
17 between size spectra mid-point height and primary production ( $\log_{10}$ ) and chlorophyll a ( $\log_{10}$ ) were  
18 also significant and positive and again there was an inverse relationship with sea surface  
19 temperature (Fig. 4 and Supplementary Table 1).  
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27 **Prediction results**  
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30 Prediction models are only useful for application on large space and time scales when the  
31 explanatory variables are readily available so we only investigated prediction using primary  
32 production, sea surface temperature and chlorophyll estimates that can be easily derived from  
33 remote sensing.  
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39 Chl a and SST together successfully predicted  $M_{B50}$ ,  $M_{B90-10}$ ,  $M_{P50}$ ,  $M_{P90-10}$  and the slope of the size  
40 spectrum, with all prediction models being significant at  $p < 0.001$ . No environmental variables  
41 predicted the intercept of the size spectrum any better than by just taking the mean value. However,  
42 to enable an estimate to be made, we report a single variable model using Chl a (this gave as good a  
43 result as using SST or PP or any combination of the three variables) and this single variable  
44 prediction model was also significant at  $p < 0.001$ . The prediction equations are given in Table 3 and  
45 the statistical results are given in Supplementary Table 2.  
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53 Applying these relationships in combination allows prediction of the slope, height and location of  
54 the phytoplankton size spectra over relevant size ranges (Fig. 5) and the make-up of communities  
55 by size class (see Supplementary Material). For example, where sea surface temperature is 15°C and  
56 chlorophyll a concentration is 1.0 mg m<sup>-3</sup> there is total biomass of 47  $\log_{10}$  pg C, of which 24% is  
57 picoplankton (ESD < 2µm), 76% is nanoplankton (ESD > 2 but < 20µm) and there is no microplankton  
58 (ESD > 20µm).  
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## Discussion

The analyses reveal that relationships between the size composition of phytoplankton communities and the environment can be used to predict mean cell mass, the slopes of size spectra and the range of cell masses that encompass a given proportion of total biomass or production. Since predictions are based on temperature and chlorophyll estimates that are available at high resolution and over large spatial scales, for example from remote sensing, they can be used to predict community size structure at the same scales. Such predictions provide necessary inputs to models that seek to link primary production to production at higher trophic levels.

Chlorophyll concentration varies due to a variety of physical and chemical factors. Irradiance over the mixed layer depth, surface nitrate, sea-surface temperature, and latitude and longitude together can predict 83% of the variation in log chlorophyll in the North Atlantic (Irwin and Finkel 2008). We are not here investigating the mechanisms leading to the correlation between phytoplankton size composition and chlorophyll; instead we accept the practical value of the relationship pending research that identifies mechanistic relationships. Tight correlations between temperature, chlorophyll a and nitrate concentrations are known suggesting that the environmental factors are highly intertwined and strongly regulate the phytoplankton average cell size (Chen and Liu 2010).

Picophytoplankton made up 50% of the biomass at chlorophyll a concentrations less than  $0.25 \text{ mg m}^{-3}$  and at temperatures over  $20.4^\circ\text{C}$ . At this temperature, 50% of production was from cells up to  $2.5\mu\text{m}$ . The relationship to chlorophyll is consistent with the findings of Agawin et al. (Agawin et al. 2000) who reported that picophytoplankton dominated ( $\geq 50\%$ ) where chlorophyll a concentration was lower than  $0.3 \text{ mg m}^{-3}$  but they reported picophytoplankton dominating in waters over  $26^\circ\text{C}$  compared to our estimate of  $20.4^\circ\text{C}$ . Using our prediction models, which use both temperature and chlorophyll a concentration, we estimate that at  $26^\circ\text{C}$  and  $0.3 \text{ mg m}^{-3}$  chlorophyll concentration, phytoplankton cells up to  $1.3\mu\text{m}$  diameter ( $0.24 \text{ pg C}$ ) make up 50% of the biomass (see Fig. 5c) and up to  $1.2\mu\text{m}$  diameter ( $0.20 \text{ pg C}$ ) make up 50% of the production.

Slopes of phytoplankton size spectra are predicted to be steeper when total biomass is low and at higher temperatures. If the size-spectrum slope is  $-1$ , then the trend is for all size classes to have equal biomass; if the slope is greater than  $-1$  then biomass tends to increase with increasing cell mass; if the abundance-mass slope is less than  $-1$  then biomass decreases with increasing cell mass. Modellers have often assumed slopes of either  $-0.75$  or  $-1.0$  when describing the size structure of

the phytoplankton community but the model: " $Slope = -0.007 SST (^{\circ}C) + 0.114 \log_{10} (Chl\ a\ (mg\ m^{-3})) - 1.049$ " suggests a mean slope of  $-1.05$  at  $3^{\circ}C$  but  $-1.20$  at  $25^{\circ}C$  (for an intermediate level of  $Chl\ a$  of  $1.5\ mg\ m^{-3}$ ). There are relatively few empirical estimates of size-spectrum slope for phytoplankton communities with which to compare our estimates, as most estimates are for communities that include zooplankton. However, those available provide qualitative support for our results. For example, Marañón et al. (Marañón et al. 2007) reported that unproductive ecosystems were characterized by more negative slopes ( $-1.3$  to  $-1.1$ ) than productive ones ( $-0.8$  and  $-0.6$ ), but the slopes were rather shallower than reported in our study in which 10 of the 12 sites had a slope steeper (more negative) than  $-1$  and 3 sites steeper than  $-1.3$ . San Martin et al. (San Martin et al. 2006a) also found that the slopes of biomass size spectra for the picoplankton and microplankton size ranges were positively related to biomass (but the pattern disappeared with the addition of mesozooplankton). They did not report relationships with temperature.

Size spectrum slopes as steep as  $-1.39$  have been reported for pure phytoplankton (Huete-Ortega et al. 2010). These values, like ours, are much steeper than the value of  $-0.75$  that is theoretically predicted to result from the allocation of energy among competing individuals (Belgrano et al. 2002). Our values are also steeper than the slope of  $-0.78$  (Li 2002) and slopes ranging from  $-0.74$  to  $-1.06$  (Cermeño and Figueiras 2008) reported for phytoplankton. Differences in slope could be attributed to sampling artefacts or ecological processes. Smaller plankton are not effectively sampled by some gears, are not so well preserved after sampling and can be under-sampled during microscopic identification so we expect that any bias in the data will lead to the under representation of small cells and lower rather than higher estimates of slope (Harris et al. 2000). Of necessity, deriving a size spectrum by pooling the abundance of cells with a mean mass that fall in that size class will introduce bias. Biases introduced by working with mean mass in studies of relationships between abundance and body mass are greatest when working with species that have indeterminate growth and when the range of body sizes considered is narrow (Jennings et al. 2007). These biases will be minimal for phytoplankton that have limited and determinate growth and a range in mean mass that spans over 5 orders of magnitude. Another factor that may have biased slope estimates is the exclusion of sizes at the extremes of the distribution. However, we excluded small and large species using the same rules. Since sampling and analytical artefacts are unlikely to explain why slopes are relatively negative, there may be an influence of ecological processes. For example, consumer density increases with temperature, leading to increased grazing pressure (O'Connor et al. 2009) thus the slopes may increase as a result of greater predation rates on larger phytoplankton or uniform predation rates that have a greater impact on larger phytoplankton owing to their slower turnover times.

Our analyses do not determine cause and effect and are primarily intended to predict the size composition of phytoplankton communities from readily available large scale and high-resolution remote sensing data to support parameterisation of food web models. However, direct linkages between temperature and the size composition of phytoplankton communities have been proposed (López-Urrutia 2008). He suggests that large cells may dominate in colder systems owing to the different temperature dependence of heterotrophic and autotrophic rates. In colder areas heterotrophs may not grow fast enough to control autotrophs while in warmer areas large phytoplankton cells are likely to have relatively longer division times than smaller ones and may not be able to attain high levels of abundance given the high abundance of heterotrophic predators. We also expect community structure to be influenced by nutrient supply and the colder seas (as represented in the database) often correspond to areas with more nutrients (e.g. upwellings and coastal areas) than the warmer ones (e.g. oligotrophic subtropical gyres).

Other methods are being developed to predict the size composition of phytoplankton communities at high spatial resolution over large spatial scales. For example, Uitz et al. (Uitz et al. 2006; Uitz et al. 2008) have determined size-spectra of phytoplankton communities from near-surface chlorophyll a concentration using accessory pigments as markers for pico, nano and micro-plankton to infer the column-integrated phytoplankton biomass, its vertical distribution, and ultimately the community composition by quantifying on a global scale the phytoplankton biomass associated with each of the three algal assemblages. However pigment analysis based on high-performance liquid chromatography although a widely used method for studying phytoplankton community composition does not provide any information on size structure in each group (Chen and Liu 2010).

Our approach can be used to allocate phytoplankton biomass and primary production to cell mass classes and thus improve the description of the primary producer community in size based models that have been used to link primary production and production at higher trophic levels. This is useful because estimates of phytoplankton production from NPZD (Nutrient Phytoplankton Zooplankton Detritus) models and remote sensing rarely provide information on the size composition of the phytoplankton community alone. At a sea surface temperature of 5°C, our predictions suggest that the phytoplankton cell size at 50% of biomass ranges from 31 to 47 pg C, at 15°C it ranges from 5.4 to 8.1 pg C and at 25°C it ranges from 0.9 to 1.4 pg C for intermediate chlorophyll a concentrations from 1 to 1.5 mg m<sup>-3</sup>. At a sea surface temperature of 5°C the phytoplankton cell size at 50% of production ranges from 3.3 to 4.8 pg C, at 15°C from 0.9 to 1.3 pg C and at 25°C from 0.2 to 0.3 pg C over the same range of chlorophyll a concentrations. The



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range of cell sizes that make up the majority of the community (the mid 80% of biomass/production) is smaller at more productive sites but wider at warmer temperatures. One consequence of the dominance of smaller primary producers in less productive waters is that food chains will be longer. The ratio between the sizes of consumers and their prey (reported as the predator-prey mass ratio, PPMR) does not depend on production or temperature (Barnes et al. 2010), so the mean trophic level of a given size class of consumers would be expected to be higher in low productivity areas such as ocean gyres. Since smaller primary producers are linked to lower primary production and PPMR and transfer efficiency may be unrelated to the environment, production at higher trophic levels is disproportionately low when primary productivity is low.

In addition to predicting fluxes of energy to higher trophic levels and the biomass of consumer communities based on measurements of primary production and temperature, our predictive relationships may also be valuable for predicting how the composition of phytoplankton communities may change in relation to environmental change. For example, Morán et al. (Morán et al. 2009) have reported consistent relationships among temperature, cell size and picophytoplankton abundance and speculate that the size of cells in phytoplankton assemblages will gradually decrease as temperatures rise. Li et al. (Li et al. 2009) concur that a reduction in community average cell size because of an increase in the abundance of individuals belonging to small-sized species may be a common response to increasing sea temperatures. There is evidence that reduced body size is the third universal ecological response to global warming besides the shift of species ranges toward higher altitudes and latitudes and the seasonal shifts in life-cycle events (Daufresne et al. 2009). Such influences need to be considered in models that seek to predict how future changes in primary production and temperature will affect production at higher trophic levels.

**Conclusions**

The size composition of primary producers is an essential input to enable estimations of food chain length, consumer biomass and production in any given location. We have described relationships between the environment and the size composition of phytoplankton communities using environmental variables that are easily estimated from ocean colour satellite measurements. Estimates of consumer biomass, production and trophic level depend on the length of food chains that support this biomass, a consequence of predator-prey size relationships and the size composition of primary producers. As mean predator-prey size ratios in marine ecosystems do not depend on temperature or primary production, the size composition of the phytoplankton

community has an overriding influence on food chain length which, in turn can be used to further explore fish production, fisheries catch potential and the bioaccumulation of contaminants.

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Figure 1: A graphical summary of the definitions of cell mass ranges that account for various proportions of biomass and production.  $M_{B50}$  ( $M_{P50}$ ) is the cell mass at which 50% of biomass (production) is reached.  $M_{B90-10}$  ( $M_{P90-10}$ ) is the range of cell masses that make up the mid 80% (i.e.  $\log_{10}(\text{cell mass at 90\%}) - \log_{10}(\text{cell mass at 10\%})$  of biomass (production)).

Figure 2: Relationships between (a)  $M_{B50}$ , the mass of phytoplankton cells that account for 50% of total biomass and (b)  $M_{B90-10}$ , the range of phytoplankton cell masses that account for the mid 80% of total biomass and remotely-sensed estimates of primary production, sea surface temperature and chlorophyll a at 12 sites.

Figure 3: Relationships between (a)  $M_{P50}$ , the mass of phytoplankton cells that account for 50% of total production and (b)  $M_{P90-10}$ , the range of phytoplankton cell mass that account for the mid 80% of total production and remotely-sensed estimates of primary production, sea surface temperature and chlorophyll a at 12 sites

Figure 4: Relationships between (a) size spectra slopes and (b) size spectra mid-point heights and remotely-sensed estimates of primary production, sea surface temperature and chlorophyll a at 12 sites.

Figure 5: Size spectra predictions for (a) a range of sea surface temperatures at an intermediate chlorophyll a level of  $1\text{ mg m}^{-3}$ ; (b) a range of chlorophyll a levels at  $10^{\circ}\text{C}$  and (c) a range of sea surface temperatures and a range of chlorophyll a levels. • show position of  $M_{B50}$ , the mass of phytoplankton cells that account for 50% of total biomass. See text for explanation for mid-point prediction comparison with Agawin et al. (2000).

Table 1: Phytoplankton cell mass (pg C) statistics from 12 sites that include polar, tropical and upwelling environments.

Table 2: Properties and statistical analysis of normalised biomass size spectra from 12 sites that include polar, tropical and upwelling environments.

Table 3: Equations for predicting phytoplankton cell sizes from remotely-sensed variables.

Table 1

|                                                                   | %  | AMT1 | AMT2  | AMT3  | AMT4  | AMT5  | Benguela | Bergen fjord | Irminger | Long Island Sound | North Sea | Norwegian Sea | Oregon upwelling |
|-------------------------------------------------------------------|----|------|-------|-------|-------|-------|----------|--------------|----------|-------------------|-----------|---------------|------------------|
| Mean cell mass                                                    |    | 253  | 279   | 243   | 316   | 246   | 912      | 4740         | 381      | 742               | 788       | 267           | 702              |
| 1 standard deviation                                              |    | 670  | 1150  | 817   | 941   | 954   | 4844     | 99418        | 1083     | 2133              | 3379      | 1052          | 1728             |
| 1 standard error                                                  |    | 5.5  | 9.9   | 6.6   | 7.3   | 7.5   | 28       | 635          | 6.4      | 33                | 25        | 14            | 24               |
| Smallest cell mass                                                |    | 0.1  | 0.1   | 0.01  | 0.01  | 0.01  | 0.1      | 1.0          | 0.2      | 1.0               | 1.0       | 1.0           | 0.2              |
| Largest cell mass                                                 |    | 8206 | 27123 | 10686 | 15221 | 27123 | 49930    | 2799208      | 14709    | 27123             | 143195    | 7000          | 14709            |
| Cell mass that accounts for % of total biomass                    | 10 | 19   | 0.31  | 0.06  | 0.03  | 0.22  | 5.3      | 4.9          | 3.4      | 175               | 20        | 2.2           | 4.6              |
|                                                                   | 25 | 25   | 1.8   | 0.30  | 0.19  | 0.6   | 20       | 15           | 6.4      | 466               | 41        | 5.3           | 15               |
|                                                                   | 50 | 35   | 10    | 1.6   | 1.8   | 3.8   | 165      | 117          | 19       | 1209              | 123       | 12            | 81               |
|                                                                   | 75 | 54   | 47    | 11    | 17    | 35    | 1324     | 961          | 81       | 2722              | 496       | 24            | 505              |
|                                                                   | 80 | 64   | 69    | 18    | 30    | 60    | 2181     | 1558         | 122      | 3265              | 708       | 28            | 789              |
|                                                                   | 90 | 118  | 184   | 71    | 132   | 229   | 8051     | 5174         | 361      | 5109              | 1769      | 41            | 2419             |
| Cell mass range that accounts for the mid 80% of total biomass    |    | 6.2  | 590   | 1098  | 4476  | 1049  | 1509     | 1050         | 107      | 29                | 90        | 19            | 529              |
| Cell mass that accounts for % of total production                 | 10 | 19   | 0.81  | 0.15  | 0.35  | 0.58  | 7.2      | 6.0          | 3.8      | 225               | 24        | 2.6           | 5.6              |
|                                                                   | 25 | 25   | 3.1   | 0.59  | 0.61  | 1.3   | 35       | 26           | 7.4      | 564               | 52        | 6.0           | 22               |
|                                                                   | 50 | 36   | 14    | 3.0   | 3.2   | 7.4   | 265      | 208          | 24       | 1340              | 161       | 13            | 118              |
|                                                                   | 75 | 63   | 61    | 19    | 33    | 53    | 2056     | 2590         | 124      | 2766              | 627       | 25            | 641              |
|                                                                   | 80 | 78   | 89    | 30    | 58    | 85    | 3470     | 4895         | 190      | 3252              | 881       | 29            | 951              |
|                                                                   | 90 | 165  | 247   | 101   | 258   | 269   | 25325    | 24322        | 590      | 4848              | 2093      | 41            | 2526             |
| Cell mass range that accounts for the mid 80% of total production |    | 8.9  | 305   | 657   | 745   | 463   | 3506     | 4070         | 155      | 22                | 88        | 16            | 453              |

Table 2

|                                                              | AMT1  | AMT2  | AMT3  | AMT4  | AMT5  | Benguela | Bergen fjord | Irminger | Long<br>Island<br>Sound | North<br>Sea | Norwegian<br>Sea | Oregon<br>upwelling |
|--------------------------------------------------------------|-------|-------|-------|-------|-------|----------|--------------|----------|-------------------------|--------------|------------------|---------------------|
| No. samples                                                  | 25    | 25    | 25    | 26    | 24    | 54       | 46           | 59       | 7                       | 44           | 19               | 7                   |
| Mean slope                                                   | -1.18 | -1.32 | -1.36 | -1.28 | -1.22 | -1.16    | -0.94        | -1.08    | -0.74                   | -1.10        | -1.66            | -1.21               |
| Mean mid-point<br>zeroised height<br>(log <sub>2</sub> pg C) | 21.38 | 21.91 | 21.78 | 21.37 | 20.54 | 23.41    | 22.56        | 22.48    | 23.24                   | 21.11        | 22.35            | 23.22               |
| Mean r squared                                               | 0.64  | 0.68  | 0.75  | 0.71  | 0.67  | 0.62     | 0.49         | 0.65     | 0.38                    | 0.50         | 0.78             | 0.71                |
| Mean p-value                                                 | 0.018 | 0.014 | 0.005 | 0.009 | 0.016 | 0.017    | 0.058        | 0.015    | 0.143                   | 0.067        | 0.004            | 0.021               |
| Slope coefficient<br>of variation                            | 0.19  | 0.17  | 0.13  | 0.18  | 0.19  | 0.26     | 0.27         | 0.15     | 0.49                    | 0.45         | 0.13             | 0.28                |
| Mid-point zeroised<br>height coefficient<br>of variation     | 0.06  | 0.05  | 0.07  | 0.06  | 0.07  | 0.09     | 0.03         | 0.06     | 0.08                    | 0.07         | 0.07             | 0.07                |
| R squared<br>coefficient of<br>variation                     | 0.28  | 0.18  | 0.11  | 0.17  | 0.24  | 0.24     | 0.39         | 0.22     | 0.63                    | 0.38         | 0.09             | 0.34                |

Table 3

|                     | Predicted Value                                                         | SST (°C)<br>multiplier | Log <sub>10</sub> (Chl a (mg<br>m <sup>-3</sup> )) multiplier | Constant |
|---------------------|-------------------------------------------------------------------------|------------------------|---------------------------------------------------------------|----------|
| M <sub>B50</sub>    | Log <sub>10</sub> (cell size (pg C) for 50% of<br>biomass)              | -0.076                 | 0.999                                                         | 1.873    |
| M <sub>B90-10</sub> | Log <sub>10</sub> (cell size range (pg C) for mid 80%<br>of biomass)    | 0.184                  | - 1.082                                                       | 0.447    |
| M <sub>P50</sub>    | Log <sub>10</sub> (cell size (pg C) for 50% of<br>production)           | -0.058                 | 0.909                                                         | 1.813    |
| M <sub>P90-10</sub> | Log <sub>10</sub> (cell size range (pg C) for mid 80%<br>of production) | 0.142                  | -0.837                                                        | 0.906    |
| Slope               | Slope of the size spectrum                                              | -0.007                 | 0.114                                                         | - 1.049  |
| Intercept           | Log <sub>2</sub> (intercept of the size spectrum)                       | 0                      | 0.816                                                         | 29.802   |

Figure 1

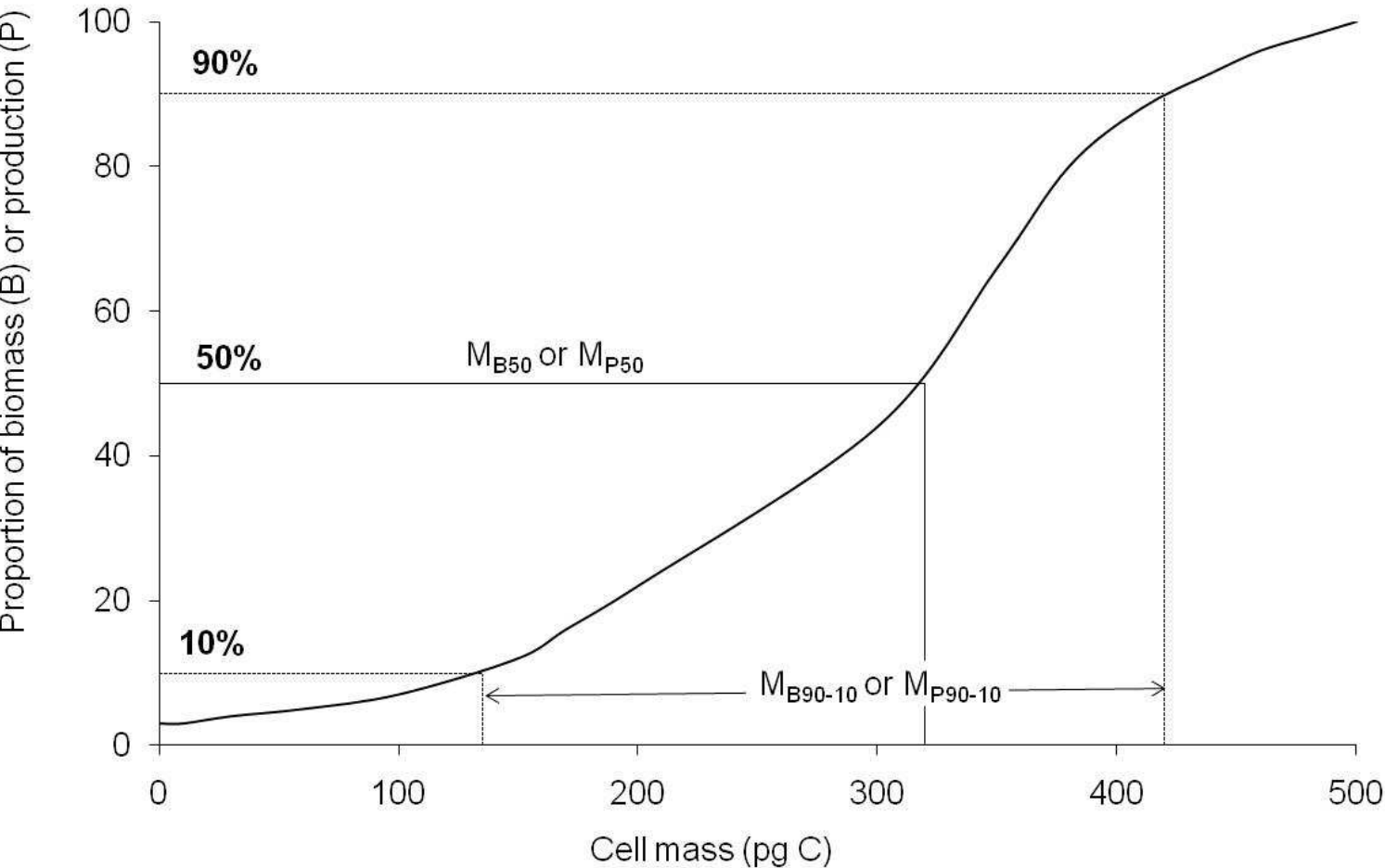




Figure 2

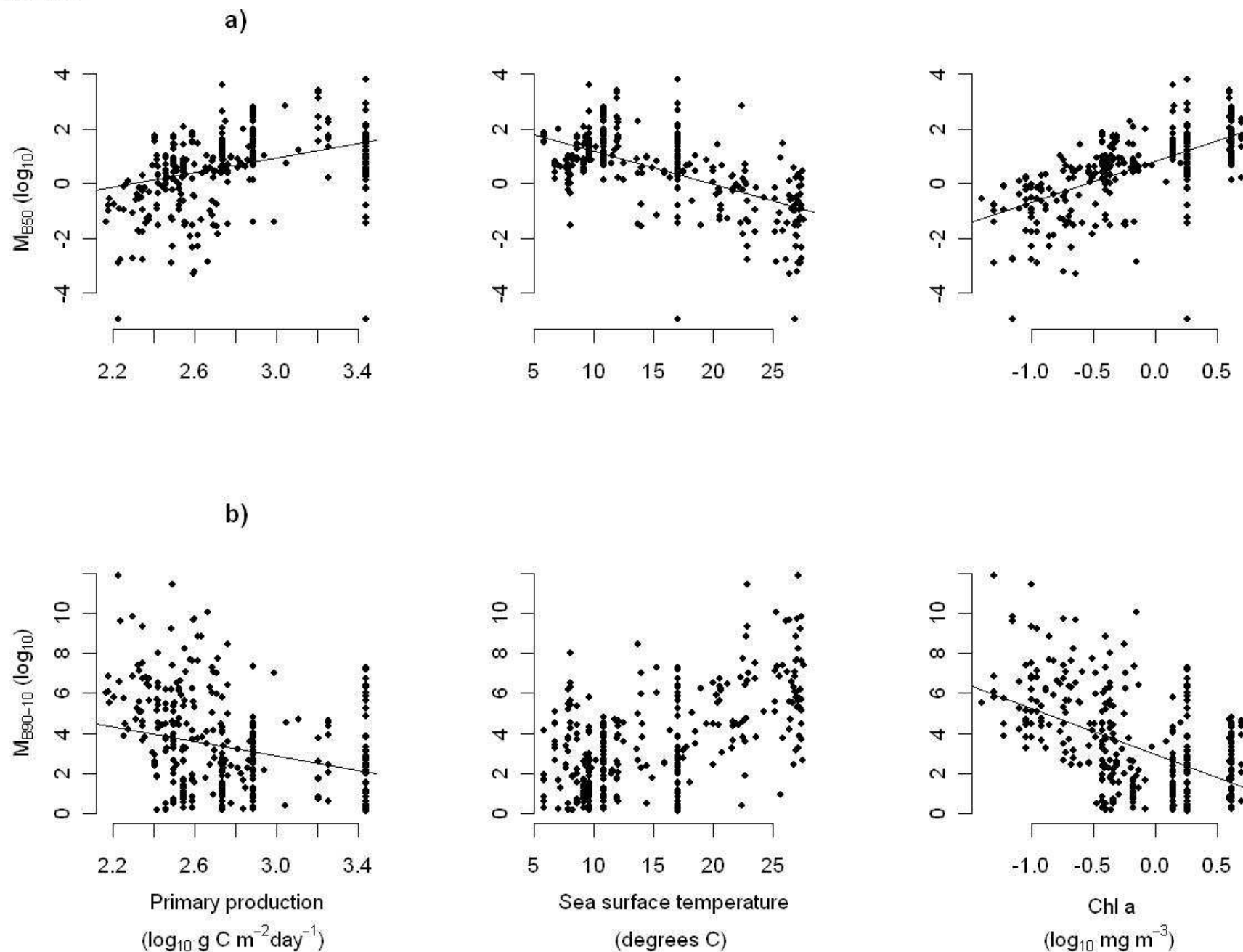


Figure 3

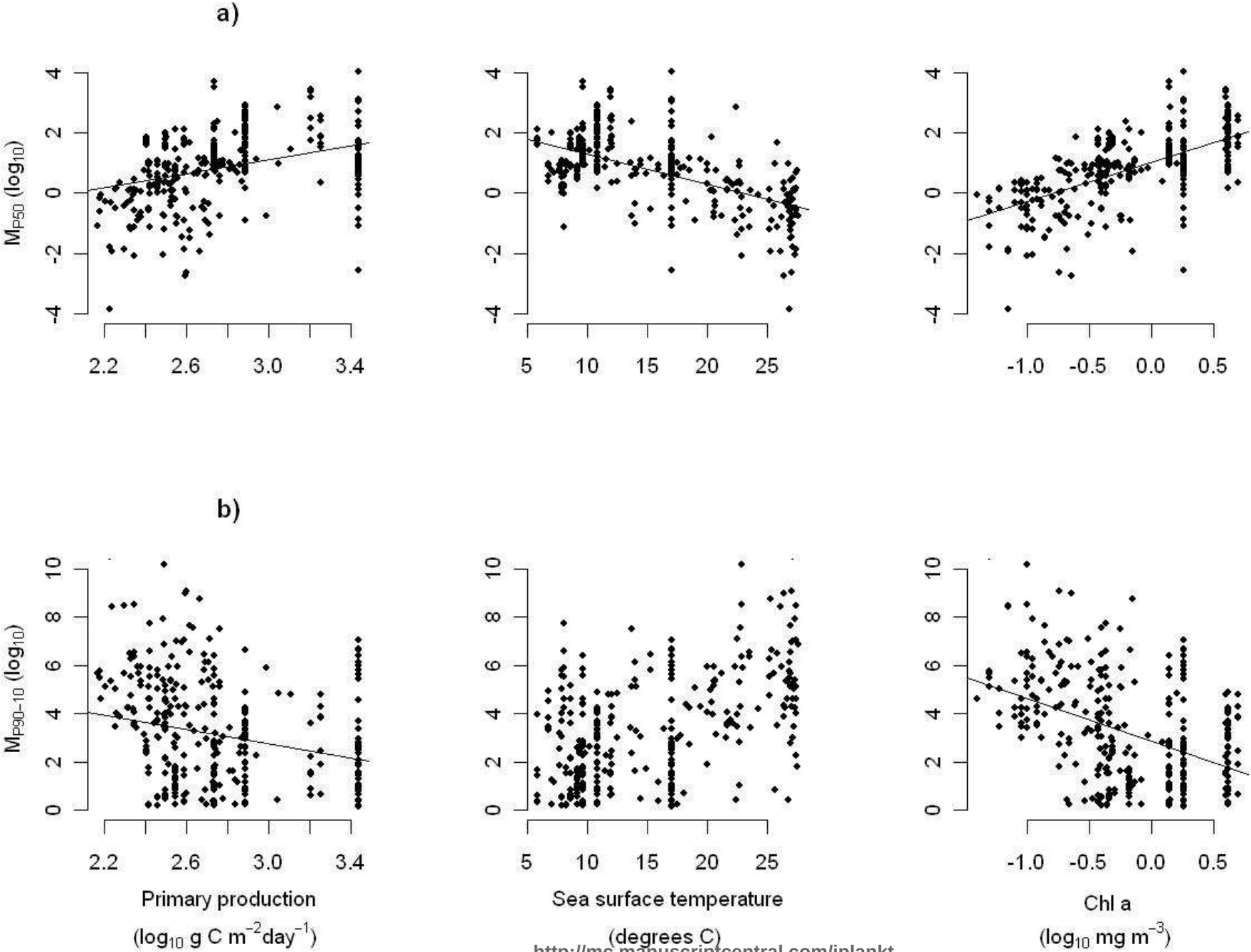
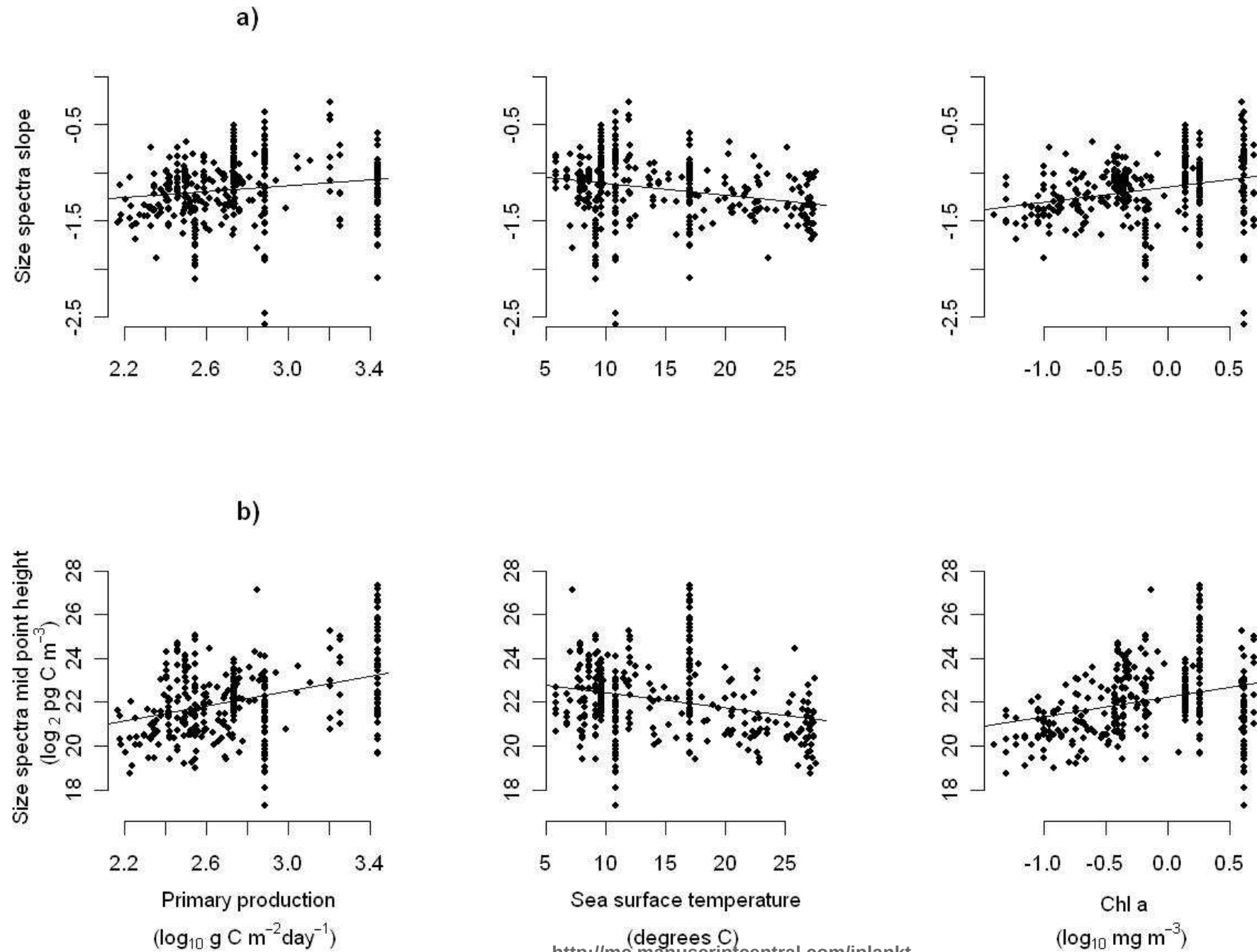
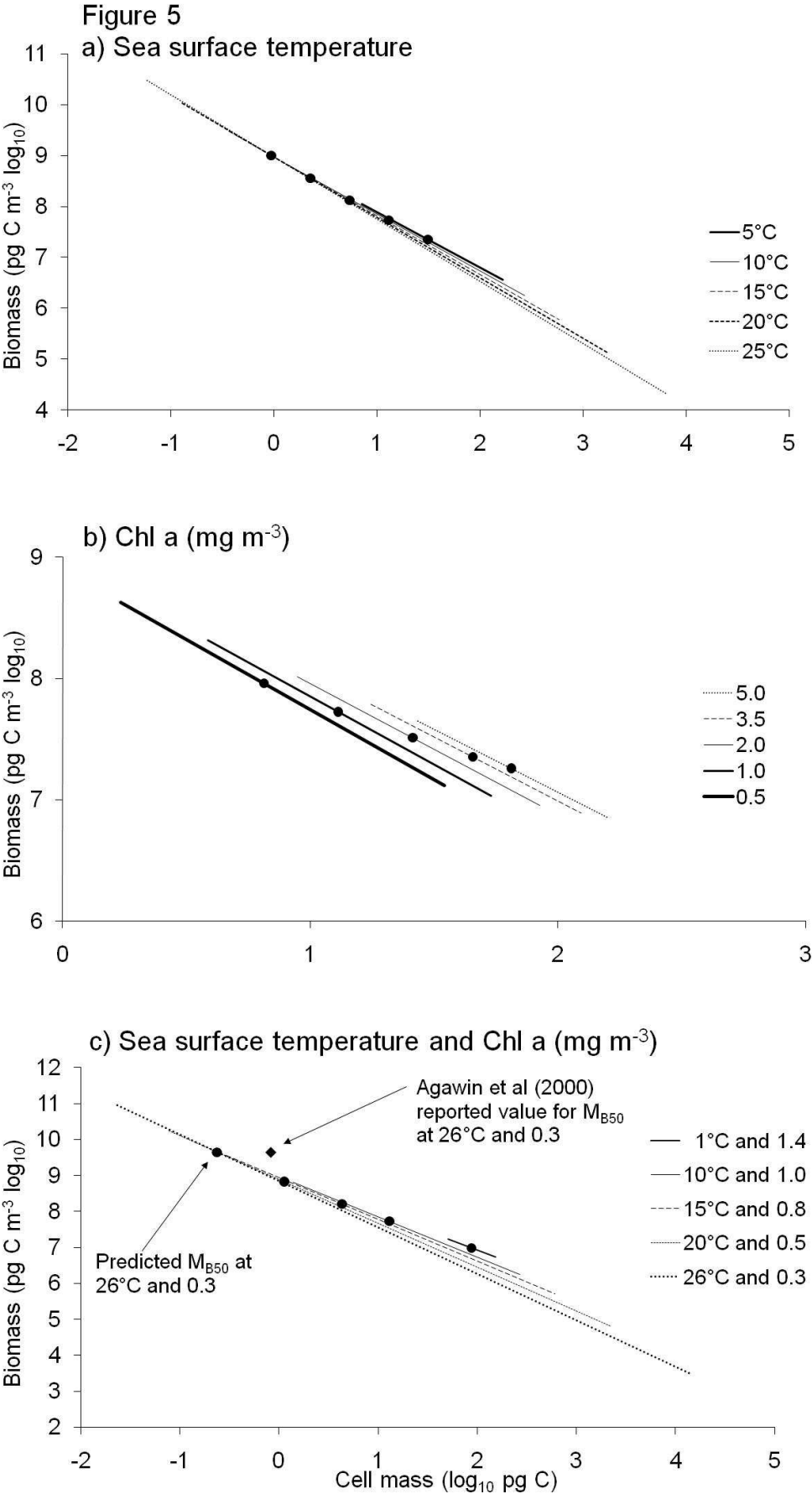


Figure 4





Supplementary Table 1: Analysis of variance statistics for linear relationships between remotely-sensed estimates of environmental variables and the phytoplankton cell masses that account for 50% of total biomass/production, the range that accounts for 80% of total biomass/production and the slope and mid-point height of size spectra of phytoplankton.

|                     | Predicted Value                                                                                                                       | Environmental variable                                                        | F-stat | DF    | P-value | Slope  | Slope P-value | Intercept | Intercept P-value | R <sup>2</sup> |
|---------------------|---------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------|--------|-------|---------|--------|---------------|-----------|-------------------|----------------|
| M <sub>B50</sub>    | Cell mass (log <sub>10</sub> pg C) that accounts for 50% of total biomass (log <sub>10</sub> )                                        | Primary production (log <sub>10</sub> g C m <sup>-2</sup> day <sup>-1</sup> ) | 55.71  | 1,359 | <0.001  | 1.331  | <0.001        | -3.063    | <0.001            | 0.13           |
|                     |                                                                                                                                       | Sea surface temperature (°C)                                                  | 217.1  | 1,359 | <0.001  | -0.121 | <0.001        | 2.388     | <0.001            | 0.38           |
|                     |                                                                                                                                       | Chlorophyll a (log <sub>10</sub> mg m <sup>-3</sup> )                         | 235.1  | 1,359 | <0.001  | 1.501  | <0.001        | 0.834     | <0.001            | 0.39           |
| M <sub>B90-10</sub> | Cell mass (log <sub>10</sub> pg C) that accounts for the mid 80% of total biomass (log <sub>10</sub> (90%) – log <sub>10</sub> (10%)) | Primary production (log <sub>10</sub> g C m <sup>-2</sup> day <sup>-1</sup> ) | 21.13  | 1,359 | <0.001  | -1.810 | <0.001        | 8.304     | <0.001            | 0.05           |
|                     |                                                                                                                                       | Sea surface temperature (°C)                                                  | 162.5  | 1,359 | <0.001  | 0.232  | <0.001        | -0.109    | 0.709             | 0.31           |
|                     |                                                                                                                                       | Chlorophyll a (log <sub>10</sub> mg m <sup>-3</sup> )                         | 93.95  | 1,359 | <0.001  | -2.299 | <0.001        | 2.965     | <0.001            | 0.21           |
| M <sub>P50</sub>    | Cell mass (log <sub>10</sub> pg C) that accounts for 50% of total production (log <sub>10</sub> )                                     | Primary production (log <sub>10</sub> g C m <sup>-2</sup> day <sup>-1</sup> ) | 56.86  | 1,359 | <0.001  | 1.166  | <0.001        | -2.392    | <0.001            | 0.13           |
|                     |                                                                                                                                       | Sea surface temperature (°C)                                                  | 179.5  | 1,359 | <0.001  | -0.099 | <0.001        | 2.280     | <0.001            | 0.33           |
|                     |                                                                                                                                       | Chlorophyll a (log <sub>10</sub> mg m <sup>-3</sup> )                         | 227.7  | 1,359 | <0.001  | 1.292  | <0.001        | 1.021     | <0.001            | 0.39           |
| M <sub>P90-10</sub> | Cell mass (log <sub>10</sub> pg C) that accounts for the mid 80% of total                                                             | Primary production (log <sub>10</sub> g C m <sup>-2</sup> day <sup>-1</sup> ) | 16.78  | 1,359 | <0.001  | -1.477 | <0.001        | 7.192     | <0.001            | 0.04           |
|                     |                                                                                                                                       | Sea surface temperature (°C)                                                  | 103.8  | 1,359 | <0.001  | 0.179  | <0.001        | 0.475     | 0.094             | 0.22           |

|           |                                                                         |                                                                               |       |       |        |        |        |        |        |      |
|-----------|-------------------------------------------------------------------------|-------------------------------------------------------------------------------|-------|-------|--------|--------|--------|--------|--------|------|
|           | production<br>(log <sub>10</sub> (90%) –<br>log <sub>10</sub> (10%))    | Chlorophyll a (log <sub>10</sub> mg m <sup>-3</sup> )                         | 63.06 | 1,359 | <0.001 | -1.776 | <0.001 | 2.850  | <0.001 | 0.15 |
| Slope     | Size spectrum slope                                                     | Primary production (log <sub>10</sub> g C m <sup>-2</sup> day <sup>-1</sup> ) | 9.207 | 1,359 | 0.003  | 0.147  | 0.003  | -1.576 | <0.001 | 0.02 |
|           |                                                                         | Sea surface temperature (°C)                                                  | 22.86 | 1,359 | <0.001 | -0.012 | <0.001 | -0.990 | <0.001 | 0.06 |
|           |                                                                         | Chlorophyll a (log <sub>10</sub> mg m <sup>-3</sup> )                         | 27.03 | 1,359 | <0.001 | 0.161  | <0.001 | -1.147 | <0.001 | 0.07 |
| Intercept | Size spectrum<br>intercept (log <sub>2</sub> cells<br>m <sup>-3</sup> ) | Primary production (log <sub>10</sub> g C m <sup>-2</sup> day <sup>-1</sup> ) | 54.16 | 1,359 | <0.001 | 1.714  | <0.001 | 17.378 | <0.001 | 0.13 |
|           |                                                                         | Sea surface temperature (°C)                                                  | 29.21 | 1,359 | <0.001 | -0.070 | <0.001 | 23.146 | <0.001 | 0.07 |
|           |                                                                         | Chlorophyll a (log <sub>10</sub> mg m <sup>-3</sup> )                         | 32.53 | 1,359 | <0.001 | 0.897  | <0.001 | 22.244 | <0.001 | 0.08 |

Supplementary Table 2: Prediction statistics for remotely-sensed environmental variables used to predict phytoplankton cell sizes.

| M <sub>B50</sub>                                                    |                     |                | M <sub>P50</sub>                                                    |                     |                |
|---------------------------------------------------------------------|---------------------|----------------|---------------------------------------------------------------------|---------------------|----------------|
| Explanatory Variables                                               |                     | $\overline{D}$ | Explanatory Variables                                               |                     | $\overline{D}$ |
| Mean                                                                |                     | 0.93           | Mean                                                                |                     | 0.80           |
| Primary production (log <sub>10</sub> )                             |                     | 0.88           | Primary production (log <sub>10</sub> )                             |                     | 0.77           |
| Sea surface temperature                                             |                     | 0.74           | Sea surface temperature                                             |                     | 0.69           |
| Chl a (log <sub>10</sub> )                                          |                     | 0.72           | Chl a (log <sub>10</sub> )                                          |                     | 0.65           |
| Chl a (log <sub>10</sub> ), primary production (log <sub>10</sub> ) |                     | 0.71           | Chl a (log <sub>10</sub> ), primary production (log <sub>10</sub> ) |                     | 0.64           |
| Chl a (log <sub>10</sub> ), sea surface temperature                 |                     | 0.66           | Chl a (log <sub>10</sub> ), sea surface temperature                 |                     | 0.61           |
| Prediction models                                                   |                     |                |                                                                     |                     |                |
| Variables                                                           | SST + Chl a (log10) |                | Variables                                                           | SST + Chl a (log10) |                |
| F-statistic                                                         | 178.8               |                | F-statistic                                                         | 157.6               |                |
| Degrees of freedom                                                  | 2,358               |                | Degrees of freedom                                                  | 2,358               |                |
| Multipliers (SST, log <sub>10</sub> Chl a)                          | -0.076              | 0.999          | Multipliers (SST, log <sub>10</sub> Chl a)                          | -0.058              | 0.909          |
| Intercept                                                           | 1.873               |                | Intercept                                                           | 1.813               |                |
| P-value                                                             | <0.001              |                | P-value                                                             | <0.001              |                |
| Adjusted R-squared                                                  | 0.50                |                | Adjusted R-squared                                                  | 0.47                |                |
| M <sub>B90-10</sub>                                                 |                     |                | M <sub>P90-10</sub>                                                 |                     |                |
| Explanatory Variables                                               |                     | $\overline{D}$ | Explanatory Variables                                               |                     | $\overline{D}$ |
| Mean                                                                |                     | 2.12           | Mean                                                                |                     | 1.94           |
| Primary production (log <sub>10</sub> )                             |                     | 2.01           | Primary production (log <sub>10</sub> )                             |                     | 1.85           |
| Sea surface temperature                                             |                     | 1.69           | Sea surface temperature                                             |                     | 1.66           |
| Chl a (log <sub>10</sub> )                                          |                     | 1.84           | Chl a (log <sub>10</sub> )                                          |                     | 1.74           |
| Sea surface temperature, primary production (log <sub>10</sub> )    |                     | 1.67           | Sea surface temperature, primary production (log <sub>10</sub> )    |                     | 1.63           |
| Sea surface temperature, Chl a (log <sub>10</sub> )                 |                     | 1.67           | Sea surface temperature, Chl a (log <sub>10</sub> )                 |                     | 1.65           |
| Prediction models                                                   |                     |                |                                                                     |                     |                |
| Variables                                                           | SST + Chl a (log10) |                | Variables                                                           | SST + Chl a (log10) |                |
| F-statistic                                                         | 93.82               |                | F-statistic                                                         | 58.88               |                |
| Degrees of freedom                                                  | 2,358               |                | Degrees of freedom                                                  | 2,358               |                |
| Multipliers (SST, log <sub>10</sub> Chl a)                          | 0.184               | -1.082         | Multipliers (SST, log <sub>10</sub> Chl a)                          | 0.142               | -0.837         |



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|--------------------|--------|--------------------|--------|
| Intercept          | 0.447  | Intercept          | 0.906  |
| P-value            | <0.001 | P-value            | <0.001 |
| Adjusted R-squared | 0.34   | Adjusted R-squared | 0.24   |

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Supplementary Table 3: Prediction statistics for remotely-sensed environmental variables used to predict slope and intercept of phytoplankton size spectra.

| Size spectra slope                                          |                             |           | Size spectra intercept                                    |                       |
|-------------------------------------------------------------|-----------------------------|-----------|-----------------------------------------------------------|-----------------------|
| Explanatory Variables                                       |                             | $\bar{D}$ | Explanatory Variables                                     | $\bar{D}$             |
| Mean                                                        |                             | 0.26      | Mean                                                      | 1.70                  |
| Primary production ( $\log_{10}$ )                          |                             | 0.25      | Primary production ( $\log_{10}$ )                        | 1.70                  |
| Sea surface temperature                                     |                             | 0.24      | Sea surface temperature                                   | 1.70                  |
| Chl a ( $\log_{10}$ )                                       |                             | 0.24      | Chl a ( $\log_{10}$ )                                     | 1.71                  |
| Sea surface temperature, primary production ( $\log_{10}$ ) |                             | 0.24      | Chl a ( $\log_{10}$ ), primary production ( $\log_{10}$ ) | 1.71                  |
| Sea surface temperature, Chl a ( $\log_{10}$ )              |                             | 0.23      | Chl a ( $\log_{10}$ ), sea surface temperature            | 1.72                  |
| Prediction models                                           |                             |           |                                                           |                       |
| Variables                                                   | SST + Chl a ( $\log_{10}$ ) |           | Variable                                                  | Chl a ( $\log_{10}$ ) |
| F-statistic                                                 | 16.48                       |           | F-statistic                                               | 13.52                 |
| Degrees of freedom                                          | 2,358                       |           | Degrees of freedom                                        | 1,359                 |
| Multipliers (SST, $\log_{10}$ Chl a)                        | -0.007                      | 0.114     | Multiplier ( $\log_{10}$ Chl a)                           | 0.816                 |
| Intercept                                                   | -1.049                      |           | Intercept                                                 | 29.802                |
| P-value                                                     | <0.001                      |           | P-value                                                   | <0.001                |
| Adjusted R-squared                                          | 0.08                        |           | Adjusted R-squared                                        | 0.03                  |

## Supplementary Material

### Calculation of biomass in defined cell size classes

The empirical models derived in the main paper are used to predict the slope ( $b$ ) and intercept of the size spectrum, location of size spectrum midpoint ( $M_{B50}$ ) and endpoints ( $M_{B10}$  and  $M_{B90}$ ).  $M_{B50}$  is defined as  $M$  at 50% cumulative biomass based on the relationship between cumulative  $B$  and  $M$ .  $M_{B10}$  and  $M_{B90}$  are similarly defined for 10% and 90% respectively. All points are derived by fitting the relationship  $B = 100 (1 - \exp(-pM^q))$  to data then rearranging and substituting to estimate  $M$  as  $M = (-\ln(1-x/100)/p)^{1/q}$  where  $x$  is the relevant percentage.

The prediction equations were:

$$\text{Slope}(b) = -0.007 \text{ SST } (^{\circ}\text{C}) + 0.114 \log_{10} \text{ Chl } a (\text{mg m}^{-3}) - 1.049$$

$$\text{Log}_2(\text{intercept}) = 0.816 \log_{10} \text{ Chl } a (\text{mg m}^{-3}) + 29.802$$

$$\text{Log}_{10}(M_{B90-10}) = 0.184 \text{ SST } (^{\circ}\text{C}) - 1.082 \log_{10} \text{ Chl } a (\text{mg m}^{-3}) + 0.447$$

$$\text{Log}_{10}(M_{B50}) = -0.076 \text{ SST } (^{\circ}\text{C}) + 0.999 \log_{10} \text{ Chl } a (\text{mg m}^{-3}) + 1.873$$

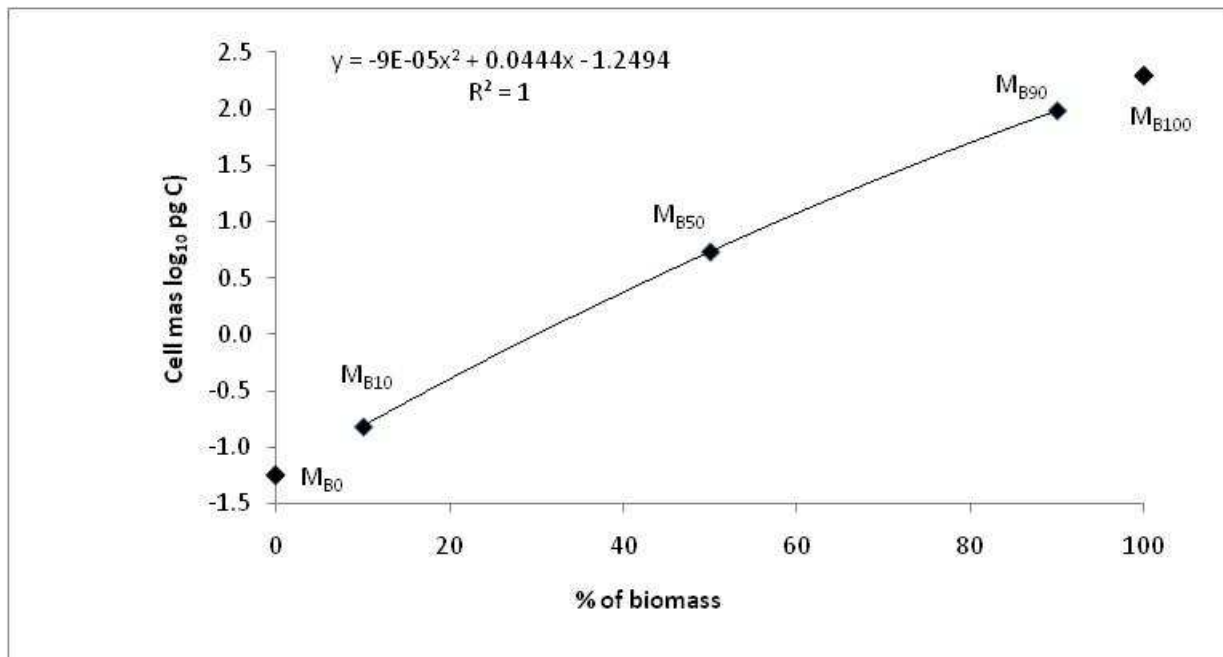
The location of the cell mass range is calculated so that that the integrated biomass to either side of the mid-point is equal. Thus the value for mass at 10% ( $M_{B10}$ ) is calculated as:

$$M_{B10} = M_{B50} \{ (10^{(b+1) \log_{10}(M_{B90-10})} + 1) / 2 \}^{-1/(b+1)}$$

And 90% ( $M_{B90}$ ):

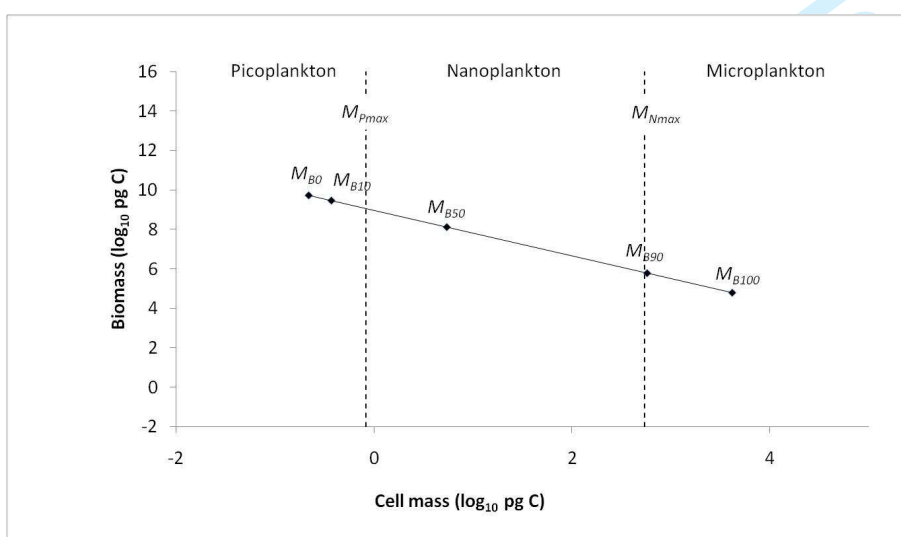
$$M_{B90} = 10^{(\log_{10}(M_{B10}) + \log_{10}(M_{B90-10}))}$$

A statistical model that adequately fitted the very variable tails of the cumulative distribution was not found, and so to ensure the integrated  $B$  was equal to 100% of cumulative  $B$  the values of  $M_{B0}$  and  $M_{B100}$  were estimated by plotting  $M_{B10}$ ,  $M_{B50}$  and  $M_{B90}$  and fitting a second order polynomial relationship (Supplementary Fig. 1).



Supplementary Figure 1: Example plot of  $M_{B10}$ ,  $M_{B50}$  and  $M_{B90}$  with a fitted second order polynomial relationship to enable estimation of  $M_{B0}$  and  $M_{B100}$ .

If the mass class boundaries between picoplankton and nanoplankton, and between nanoplankton and microplankton, are defined as  $M_{Pmax}$  ( $=M_{Nmin}$ ) and  $M_{Nmax}$  ( $=M_{Mmin}$ ) respectively then when (1)  $M_{B0} < M_{Pmax}$  and  $M_{B100} > M_{Nmax}$  then picoplankton, nanoplankton and microplankton are all present. When (2)  $M_{B0} > M_{Pmax}$  and  $M_{B100} > M_{Nmax}$  then nanoplankton and microplankton are present. When (3)  $M_{B0} < M_{Pmax}$  and  $M_{B100} < M_{Nmax}$  then picoplankton and nanoplankton are present and when (4)  $M_{B0} > M_{Pmax}$  and  $M_{B100} < M_{Nmax}$  then only nanoplankton are present (Supplementary Fig. 2).



Supplementary Figure 2: Example of the relationships between  $M_{B0}$ ,  $M_{B10}$ ,  $M_{B50}$ ,  $M_{B90}$  and  $M_{B100}$  for a hypothetical size spectrum. The biomass of phytoplankton in picoplankton, nanoplankton and

microplankton size classes is defined as the integrated biomass between  $M_{B0}$  and  $M_{B100}$  that falls within class boundaries (broken lines denote mass class boundaries  $M_{Pmax}$  ( $=M_{Nmin}$ ) and  $M_{Nmax}$  ( $=M_{Mmin}$ )).

So, to calculate the biomass of each size class that is present as a percentage of total biomass, the following approaches are adopted in each of these cases: (1), calculate the biomass of picoplankton, nanoplankton and microplankton as a proportion of total biomass, (2) picoplankton are not present, so calculate the biomass of nanoplankton and microplankton as a proportion of total biomass, (3) microplankton are not present, so calculate the biomass of nanoplankton and picoplankton as a proportion of total biomass and (4) only nanoplankton are present, so they must constitute 100% of total biomass.

For biomass, calculate the area under the curve  $y = mx + c$  between  $x_1$  and  $x_n$ :

$$\int_{x_1}^{x_n} (mx + c) dx = \left[ \frac{1}{2} mx^2 + cx \right]_{x_1}^{x_n} = \frac{1}{2} mx_n^2 + cx_n - \frac{1}{2} mx_1^2 - cx_1$$

Total biomass is found between  $M_{B0}$  and  $M_{B100}$ ; biomass in the picoplankton group is found between  $M_{B0}$  and  $M_{Pmax}$ , biomass in the nanoplankton group is found between  $M_{Pmax}$  and  $M_{Nmax}$  and biomass in the microplankton group is found between  $M_{Nmax}$  and  $M_{B100}$ .

For example, where sea surface temperature is 15°C and chlorophyll a concentration is 1.0 mg m<sup>-3</sup> there is total biomass of 47 log<sub>10</sub> pg C, of which 24% is picoplankton, 76% is nanoplankton and there is no microplankton.