

Mapping plankton biomass in the deep-ocean: an ecological provinces approach

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The distribution of epipelagic plankton biomass by size-fractions was studied during Malaspina-2010 expedition across the Indian, Pacific and Atlantic oceans. The objective was to characterize plankton biomass structure at large spatial scales in poorly explored areas of the ocean. Samples from 95 stations, representative of 3 of major ocean biomes and 12 ecological provinces, were fractionated in 5 size-classes (40 to 5000 μm) and biomass determined as dry weight. Mean plankton biomass was similar for all oceans and major biomes but varied significantly between provinces, being particularly high in the N Pacific Equatorial Countercurrent and in the Caribbean provinces. The differences were mainly due to increases in medium-sized plankton, while for most provinces the biomass was uniformly distributed across logarithmic size-classes. Total and size-class plankton biomass was negatively and non-linearly correlated with the mixing layer depth and with the depth of the chlorophyll maximum across provinces. In contrast only the biomass of the smaller plankton was positively and linearly correlated with sea surface temperature, while the biomass of other size-classes was positively affected by the thermal stratification gradient in the upper layer. The obtained relationships will improve our ability to monitor and model the ocean response to global change.

Keywords: plankton, biomass, deep-ocean, size-fractions, ecological provinces, Atlantic, Pacific, Indian

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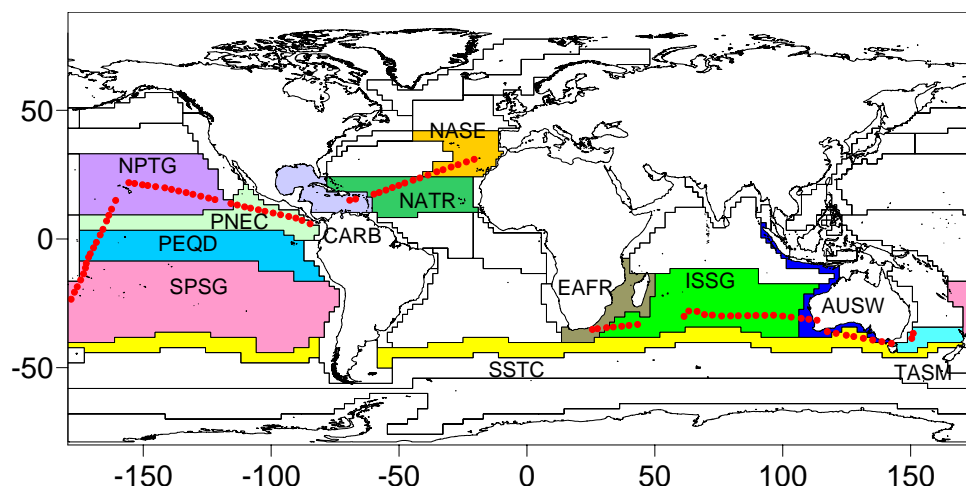


Figure 1. Location of plankton sampling stations (red dots) in the biogeochemical ocean provinces defined in Longhurst (2007).

Introduction

Despite the importance of the ocean in the response and regulation of global changes (Hoegh-Guldberg and Bruno, 2010), large regions of the deep ocean remain unexplored. Only the surface is regularly accessed by satellites, thus providing data on primary production and phytoplankton biomass (e.g. Behrenfeld et al., 2006). Information on most of the components of the food web is thus restricted to a few and sparse observations by cruises covering a small part of the unexplored regions, while most repeated cruises concentrate along established navigation routes (Reid et al., 2003; Isla et al., 2004; San Martin et al., 2006).

Information on the marine ecosystems for large regions may be provided by models. Ecosystem models allow to estimate biomass and abundance along the food web but for practical reasons the estimations are generally limited to a few components (Shin et al., 2010). Alternatively, models based on macroecological functions and body-size of organisms allow for biomass estimations on practically any organism (Lopez-Urrutia et al., 2006; Jennings et al., 2008). However, the implementation and testing of models require observations acquired in the ocean.

One way to overcome the impossibility of having observations on oceanic ecosystem components at all spatial and temporal scales relies in the common properties of ocean biomes and biogeochemical provinces (Longhurst, 2007). These large portions of the ocean are defined over the main geographic and hydrodynamic boundaries and allow for a synthesis of the main biological and biogeochemical processes of production and loss of organic matter and elements in a relatively small number of units. In this way, average values of productivity, biomass and seasonal changes are available for all regions of the ocean, including the deep ocean (Longhurst, 2007).

The objectives of this study are to characterize plankton biomass structure in deep ocean provinces and to determine empirical relationships predicting plankton biomass in the deep ocean.

Materials and methods

Plankton samples were collected during Malaspina-2010 expedition (Fig. 1). In this study only samples from 95 stations visited during legs 4 (February 2010) to 7 (July 2010) were employed. Samples were collected by vertical hauls of a bongo-type net (30 cm diameter, 40 μm mesh size) between 200 m depth and the surface during early morning hours. Plankton was size-fractionated using sieves of 200, 500, 1000, 2000 and 5000 μm , collected on pre-weighted glass-fiber filters and oven dried (60°C, 24 h) on board. Biomass was later determined in the laboratory as dry weight (± 0.01 mg). Hydrographic information was obtained from CTD-rosette casts at the same stations and chlorophyll-a was determined from acetic extracts of phytoplankton collected at up to 8 discrete depths in the photic layer (>0.1% of surface

Table 1. Biogeochemical ocean provinces and biomes, as defined in Longhurst (2007), sampled in this study.

Code	Province	Biome
EAFR	E. Africa Coastal Province	Coastal
ISSG	Indian S. Subtropical Gyre Province	Trades
AUSW	Australia-Indonesia Coastal Province	Coastal
SSTC	S. Subtropical Convergence Province	Westerlies
TASM	Tasman Sea Province	Westerlies
SPSG	S. Pacific Subtropical Gyre Province	Trades
PEQD	Pacific Equatorial Divergence Province	Trades
PNEC	N. Pacific Equatorial Countercurrent Province	Trades
NPTG	N. Pacific Tropical Gyre Province	Trades
CARB	Caribbean Province	Trades
NATR	N. Atlantic Tropical Gyral Province	Trades
NASE	N. Atlantic Subtropical Gyral Province (East)	Westerlies

photosynthetically active irradiance). Details of the sampling and analytical methods employed can be found in Moreno-Ostos (2012). The difference in temperature between the surface and 50 m depth was used as an index of stratification of the upper ocean.

In addition to in situ measurements, mean values of primary production, surface chlorophyll, mixing layer and euphotic depth, and stratification for each sampled biogeochemical province were obtained from Longhurst (2007).

Results and discussion

Mean biomass distribution

Our study covered 12 provinces in 3 ocean basins and were distributed over all biomes, except the polar biome (Table 1). A preliminary analysis indicated no significant differences between mean values of total plankton biomass (i.e. the sum of biomass in all size-fractions) between biomes or oceans (ANOVA, $P > 0.05$). Mean plankton biomass was also very similar among provinces

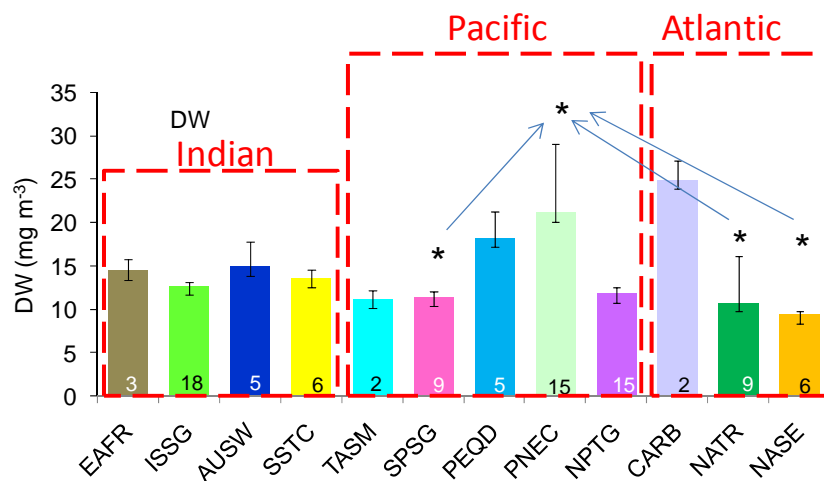


Figure 2. Mean (\pm se) plankton biomass (mg DW m^{-3}) in the biogeochemical ocean provinces defined in Longhurst (2007) and major oceans. The numbers at each bar indicate the number of

(Fig. 2) but in this case some differences appeared due to the values found in the North Pacific Equatorial Countercurrent Province (PNEC, Dunnett-C test, $P < 0.05$). Although temporal variability (e.g. seasonality) may explain some of these differences, the similarity in mean biomass of plankton in the upper ocean, particularly in the central regions, is consistent with an steady state of the ecosystems, with primary production inputs balanced by consumer and export losses (Platt and Denman, 1977; Rodriguez and Mullin, 1986).

Biomass by size classes

There was an even distribution of biomass by the chosen size classes in most provinces (Fig. 3). This implies an approximately equal amount of biomass in logarithmic individual body carbon classes, as predicted by pelagic size spectrum theory (Platt and Denman, 1977; Kerr and Dickie, 2001), and reported for most of the oligotrophic deep ocean (e.g. Rodriguez and Mullin, 1986; Piontkovski et al., 2003; San Martín et al., 2005). Only in some provinces there are an excess of biomass in some classes, as in the Caribbean that showed maximum biomass in large mesozooplankton (500-1000 μm), suggesting temporal deviations from the steady state. The use of a single net to capture a relatively large range of plankton sizes in this study may have negatively affected the collection of macrozooplankton ($>1000 \mu\text{m}$) that may have avoided the net. This may be the case of samples collected in the Atlantic where biomass decreased with increasing sizes (Fig. 3). However, most samples from the other basins did not show such decrease, suggesting that there were increases of small plankton in the Atlantic instead. Similarly there may have been losses of large zooplankton

because the sampling was performed during daylight when some macrozooplankton is expected to be in deep water layers (Gallienne et al., 2001), but other detailed vertical studies in the deep ocean have found a remarkably constant and low biomass of large zooplankton in the upper 400 m (Koppelman, and Weikert, 1992).

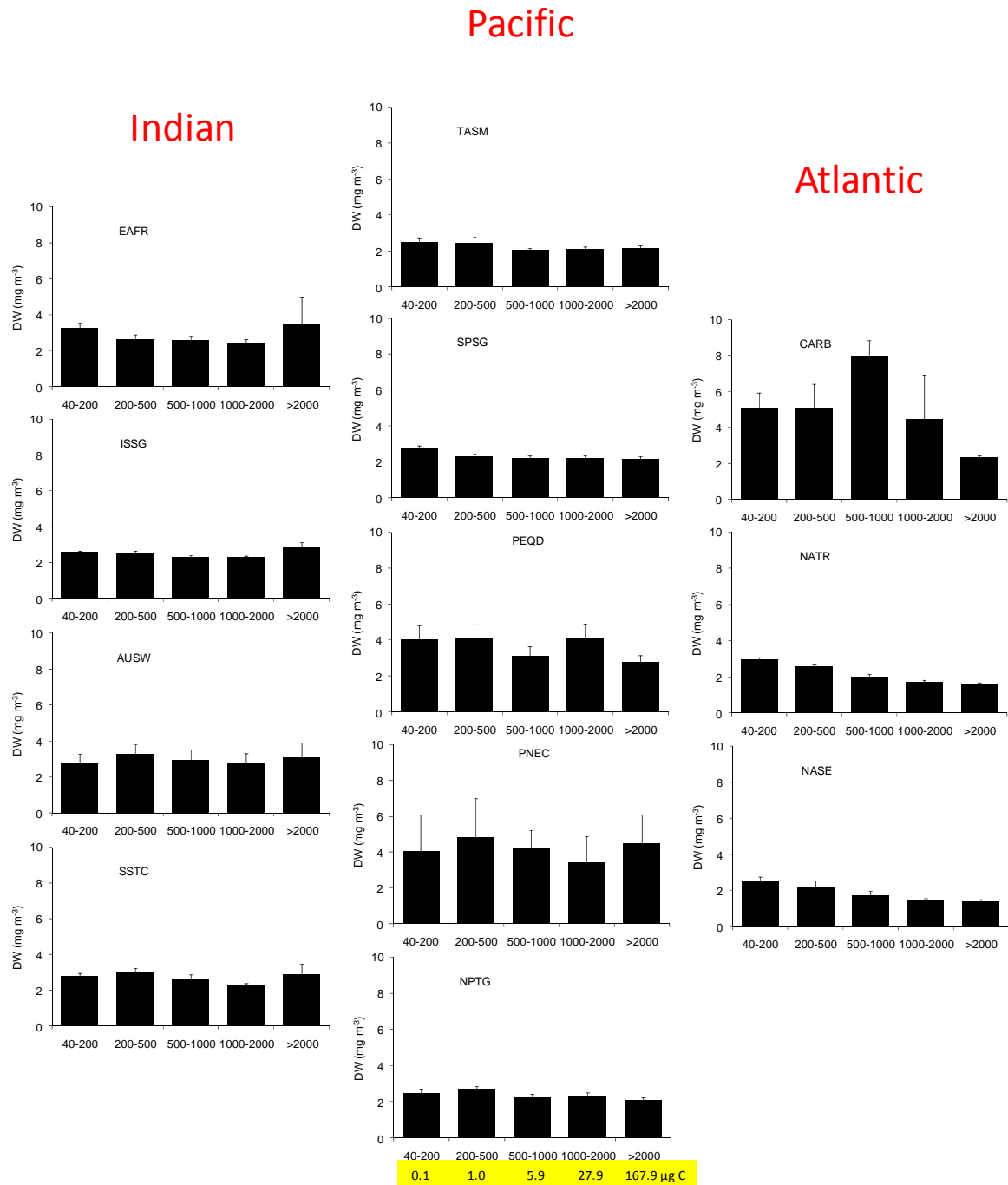


Figure 3. Mean (\pm se) plankton biomass (mg DW m^{-3}) by size-classes (μm) in the biogeochemical ocean provinces defined in Longhurst (2007) and major oceans. The median value of individual carbon biomass for each class is indicated in the yellow box.

Empirical relationships between biomass and oceanographic variables

Notwithstanding they were mostly located in deep waters, the sampled provinces were characterized by a large range of vertical oceanographic structure and consequently primary production and biomass (Table 2). These values allowed for exploring their relationships with plankton biomass and producing empirical predictive functions.

Table 2. Mean values of oceanographic variables characterising the biogeochemical provinces, as defined in Longhurst (2007) and those measured in this study. PP: primary production ($\text{mg C m}^{-2} \text{d}^{-1}$), Chla_0 : surface chlorophyll-a from satellite (mg Chla m^{-2}), Chla_i : photic depth integrated chlorophyll-a from in situ samples (mg Chla m^{-2}), z_e : photic zone depth (m), MLD: mixing layer depth (m), DCM: depth of chlorophyll maximum (m), SST: sea surface temperature ($^{\circ}\text{C}$), T_{50} : temperature at 50 m ($^{\circ}\text{C}$), T_{0-200} : mean temperature of the layer 0-200 m ($^{\circ}\text{C}$), T_{0-50} : temperature difference between 0 and 50 m ($^{\circ}\text{C}$).

Province	Mean values (Longhurst, 2007)							Mean values <i>in situ</i>					
	PP	Chla_0	z_e	MLD	SST	T_{50}	T_{0-50}	Chla_i	z_e	DCM	SST	T_{0-200}	T_{0-50}
EAFR	0.52	2.92	49.5	34.7	24.04	22.78	1.26	32.19	121.00	71.33	24.80	18.80	1.96
ISSG	0.19	2.08	63.3	41.7	23.03	22.10	0.93	13.24	169.59	111.78	23.63	18.83	1.69
AUSW	0.55	5.42	46.8	43.0	23.45	22.63	0.81	15.72	145.20	85.20	22.31	18.16	1.48
SSTC	0.37	8.67	50.0	87.9	13.96	13.34	0.62	16.72	133.00	58.50	16.96	13.90	0.07
TASM	0.45	9.92	40.0	67.9	17.82	17.09	0.73	25.63	129.00	65.00	21.45	18.35	0.19
SPSG	0.24	3.21	62.9	49.2	22.83	22.10	0.72	17.06	156.25	92.00	27.22	24.69	0.12
PEQD	0.31	6.13	55.8	32.9	26.01	24.37	1.63	18.35	134.75	59.60	27.96	25.24	0.07
PNEC	0.29	4.29	53.3	22.5	27.56	24.25	3.31	23.33	133.93	41.67	28.03	17.98	5.89
NPTG	0.16	1.38	68.8	43.8	23.71	22.72	0.99	21.38	171.83	119.00	23.72	20.58	0.35
CARB	0.52	6.58	44.2	23.0	26.94	25.84	1.10	17.89	135.00	78.00	28.96	25.40	0.71
NATR	0.29	3.63	55.2	36.2	25.56	24.56	1.00	15.77	186.25	131.89	27.15	23.89	1.38
NASE	0.33	3.88	55.0	61.3	19.62	18.45	1.17	12.96	162.00	120.50	22.59	20.37	0.86

Mean values of biomass by province were not significantly correlated with either mean reported primary production or surface chlorophyll (Table 3). However there was a positive correlation between biomass in the 40-200 μm size class and temperature which can be described by a linear function (Fig. 4) implying enhanced biomass of small plankton at high temperatures. This relationship is consistent with the prediction of smaller body sizes with warming by macroecological theories (Lopez-Urrutia et al., 2006). The strongest negative correlations were found between mean biomass in several size

classes and the depth of the mixing layer (Table 3). In the case of total biomass this relationship can be described by a negative power function indicating a rapid decrease of biomass as the mixing layer deepens but a stabilization of

Table 3. Correlations (Pearson's r) between mean values of plankton biomass (mg DW m^{-3}) by size classes and oceanographic variables characterising the biogeochemical provinces. province: mean values from Longhurst (2007), *in situ*: mean values measured in this study. Yellow shading indicate significant values ($P < 0.05$). Variable names as in Table 2.

		DW ₄₀₋₂₀₀	DW ₂₀₀₋₅₀₀	DW ₅₀₀₋₁₀₀₀	DW ₁₀₀₀₋₂₀₀₀	DW ₂₀₀₀₋₅₀₀₀	DW _{total}
province	PP	0.337	0.267	0.406	0.283	0.180	0.359
	Chla_0	0.175	0.238	0.224	0.226	0.005	0.213
	z_e	-0.328	-0.308	-0.378	-0.244	-0.144	-0.343
	MLD	-0.655	-0.584	-0.517	-0.588	-0.329	-0.607
	SST	0.623	0.562	0.469	0.563	0.268	0.562
	T_{50}	0.581	0.490	0.459	0.533	0.162	0.509
	T_{0-50}	0.515	0.633	0.280	0.425	0.659	0.538
<i>in situ</i>	SST	0.664	0.518	0.480	0.544	0.088	0.522
	DCM	-0.483	-0.587	-0.366	-0.580	-0.729	-0.595
	T_{0-200}	0.442	0.217	0.323	0.368	-0.432	0.227
	T_{0-50}	0.302	0.440	0.190	0.171	0.722	0.388
	Int. Chla	0.134	0.083	0.033	0.114	0.442	0.160
	z_e	-0.439	-0.446	-0.373	-0.503	-0.582	-0.518

this decrease at depths larger than 50 m (Fig. 4). Other studies have also reported the inverse relationship between mesozooplankton biomass and the depth of the thermocline (Isla et al., 2004; San Martín et al., 2006). In addition, positive correlations were found between thermal stratification in the upper 50 m and biomass of some classes, particularly of macrozooplankton. However, this relationship is caused by the large biomass and stratification found at PNEC, while there was no significant correlation when values for this province were removed (Fig. 4). Similar correlations and relationships were found when using mean values of environmental variables measured in situ during the Malaspina cruises (Table 3).

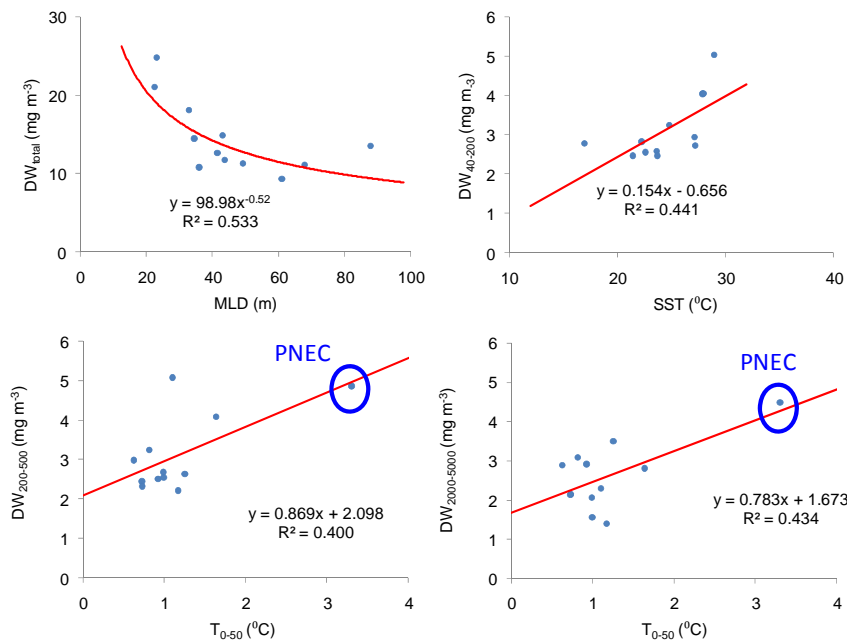


Figure 4. Example of significant relationships between mean values of plankton biomass and oceanographic variables averaged by biogeochemical province. The red lines and the equations indicate a significant regression function ($P < 0.05$). R^2 : determination coefficient. Blue circles indicate the value for PNEC province. Variable names as in Table 2.

A larger number of significant correlations were found when using concurrent measurements of environmental variables and plankton biomass (Table 4). The detailed analysis of these relationships, however, revealed that generally non linear functions provided the best fits and that samples obtained at PNEC provided most of the variability (Fig. 5). These results suggest that

the sampling of PNEC included a larger range of ecosystem states than for the other provinces, as it included stations located at both geographic limits of the province, thus producing relationships

between biomass and environmental variables similar to those observed at scales of the whole ocean including all provinces. For instance, the increase of biomass with temperature and thermal stratification or the negative relationship between biomass and the depth of the euphotic zone (Fig. 5)

mimic those found using mean provincial values (Fig. 4). In any case, the correlation coefficients were generally larger when using mean values than when using in situ values at each station, despite the lower number of data points in the former.

While the decrease in plankton biomass with the deepening of

Table 4. Correlations (Pearson's r) between values of plankton biomass (mg DW m^{-3}) by size classes and oceanographic variables measured concurrently. Yellow shading indicate significant values ($P < 0.05$). Variable names as in Table 2.

	DW ₄₀₋₂₀₀	DW ₂₀₀₋₅₀₀	DW ₅₀₀₋₁₀₀₀	DW ₁₀₀₀₋₂₀₀₀	DW ₂₀₀₀₋₅₀₀₀	DW _{total}
SST	0.327	0.255	0.289	0.246	0.113	0.277
T ₅₀	0.140	-0.001	-0.059	0.086	-0.321	-0.085
T ₀₋₅₀	0.196	0.283	0.412	0.175	0.542	0.426
DCM	-0.471	-0.505	-0.491	-0.535	-0.495	-0.608
T ₀₋₂₀₀	0.099	-0.082	-0.081	0.007	-0.286	-0.124
Int. Chla	0.217	0.238	0.170	0.226	0.181	0.247
z _e	-0.311	-0.341	-0.327	-0.354	-0.317	-0.399

the mixing layer is consistent with the decrease in primary production in regions with low supply of nutrients from deep layers, the increase in plankton biomass with temperature and thermal stratification is contrary to the expected decrease in plankton with global warming (e.g. Behrenfeld et al., 2006). These findings imply a low dependence between trophic transfer along the size spectrum and primary production, suggesting that oligotrophic ecosystems of the tropical and subtropical ocean are very efficient in the transfer of biomass up the food web despite their low primary production values (San Martin et al., 2005). This interpretation is supported by the equivalence of biomass values along the size classes (implying flat slopes of the biomass size spectrum) in most provinces and the absence of significant correlations with primary production or chlorophyll values.

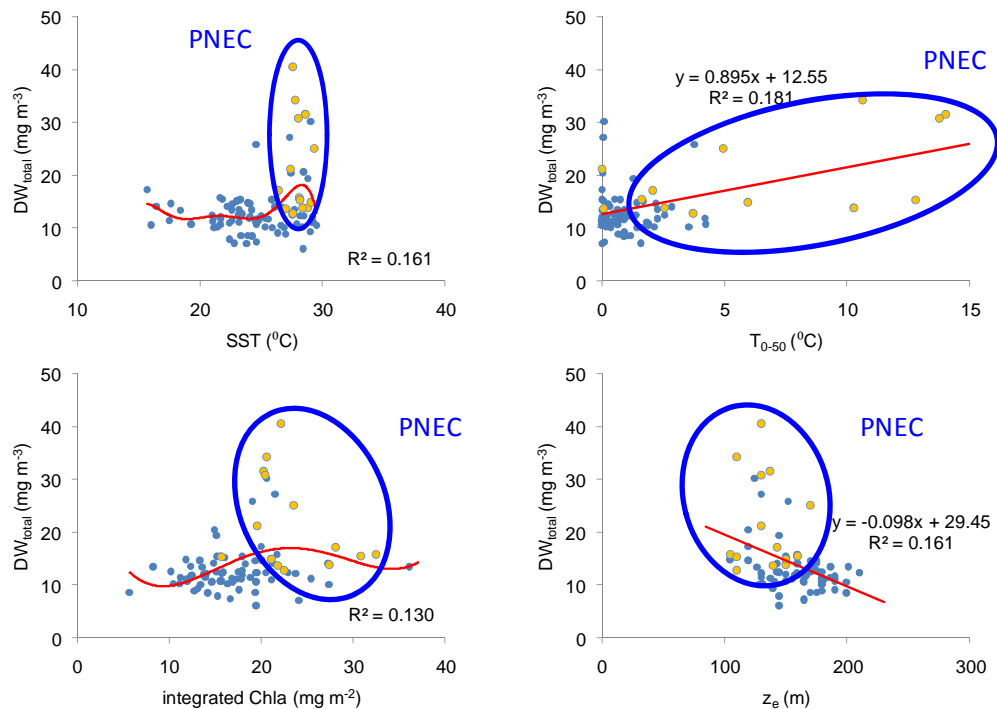


Figure 5. Example of significant relationships between values of plankton biomass and oceanographic variables measured concurrently. The red lines and the equations indicate a significant regression function ($P < 0.05$). R^2 : determination coefficient. Blue circles and orange dots indicate samples from PNEC province. Variable names as in Table 2.

Conclusions

Low plankton biomass ($10-15\ mg\ DW\ m^{-3}$) was found in most deep ocean subtropical and tropical provinces (except PNEC). This biomass was almost constant along logarithmic classes of individual body size in most provinces, suggesting steady state in the plankton.

Mean plankton biomass by province was not directly correlated with mean values of primary production or surface chlorophyll. Instead, a negative correlation was found between biomass and the depth of the upper mixing layer or the depth of the chlorophyll maximum, which resulted the best predictors of biomass. Also at province level, small plankton biomass increased with SST and biomass of other classes increased with stratification.

Local plankton biomass was correlated with integrated chlorophyll for some classes but all classes were negatively correlated with the depth of the chlorophyll maximum or the depth of the euphotic zone, best predictors of biomass. At local scale the biomass increases with SST and stratification were due to the variability observed at PNEC.

These results contribute to the global database of plankton biomass and will allow for the estimation of biomass in unexplored regions

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