# Phytoplankton biovolume is independent from the slope of the size spectrum in the oligotrophic Atlantic Ocean

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## ARTICLE INFO

## ABSTRACT

Modelling the size-abundance spectrum of phytoplankton has proven to be a very useful tool for the analysis of physical–biological coupling and the vertical flux of carbon in oceanic ecosystems at different scales. A frequent observation relates high phytoplankton biovolume in productive regions with flatter spectrum slope and the opposite in oligotrophic ecosystems. Rather than this, the relationship between high biovolume phytoplankton assemblages and flatter size-abundance spectra does not correspond with measurements of the phytoplankton community in the Atlantic Ocean open waters. As part of the Malaspina Circunnavegation Expedition, sixty seven sampling stations within the Atlantic Ocean covering six oceanographic provinces, at different seasons, produced a complete set of phytoplankton size-spectra whose slope and biovolume did not show any obvious interrelation. In these oligotrophic sites, small (procaryotes) and medium-size (nanoplankton) cells are responsible for the most part of biovolume, and their response to environmental conditions does not apply to changes in the size-abundance spectrum slope as expected in richer, large-cell dominated ecosystems.

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## 1. Introduction

Phytoplankton size structure is a key property strongly determining food-web organisation, energy flow and matter cycling in marine ecosystems. Phytoplankton physiological rates and ecological function, including metabolic rates, light and nutrients dynamics, sinking rates, trophic organization and the efficiency of organic carbon exportation into the deep ocean are directly related to the size structure of phytoplankton assemblages (Legendre and Le-Fevre, 1989; Chisholm, 1992; Legendre and Rassoulzadegan, 1996; Rodríguez et al., 2001; Platt et al., 2005; Falkowski and Oliver, 2007; Marañón, 2009; Finkel et al., 2010; Moreno-Ostos et al., 2011; Ward et al., 2012; Marañón et al., 2013; Marañón, 2015).

Studies on the phytoplankton size structure are usually based on size-abundance spectra, a valuable ataxonomic and integrative approach to analyze the structure of the complex and highly diverse phytoplankton community (Blanco et al., 1994; Dickie et al., 1987; Gaedke, 1992; Marañón, 2009; Rodríguez and Mullin, 1986). Mathematically, it consists in a two-dimensional plot showing the

phytoplankton abundance (e.g., cells mL$^{-1}$) distribution along a scale of cell volume (e.g., μm$^3$). A simple least-squares linear regression on the log-transformed values of abundance and cell size provides the two parameters that characterize the size spectrum, slope ($b$) and y-intercept ($a$). The integral of the mathematical function describing the size-abundance spectrum is the total phytoplankton biovolume (e.g. μm$^3$ mL$^{-1}$) (Blanco et al., 1994; Platt and Denman, 1977).

Both $a$ and $b$ parameters have been proposed as quantitative measures of aquatic ecosystem structure (Marañón et al., 2007; Rodríguez et al., 1998; Sprules and Munawar, 1986). The intercept $a$ seems to be related to total phytoplankton biovolume (Sprules and Munawar, 1986), while the slope of the linear model ($b$) is an indicator of the proportion of biovolumes between consecutive size classes (Blanco et al., 1994) providing information on the transfer efficiency along the spectrum (Gaedke, 1993). Phytoplankton size-abundance spectrum slope is also related to the ecosystem productivity. Thus, oligotrophic regions typically show steeper slopes ($-1.3$ to $-1.1$), while the slope become less negative ($-0.8$ to $-0.6$) in highly productive, coastal ecosystems (Cavender-Bares et al., 2001; Cermeño and Figueiras, 2008; Cermeño et al., 2006; Huete-Ortega et al., 2010, 2011, 2014; Marañón et al., 2007; Reul et al., 2005; Rodríguez et al., 1998).

This pattern has led to the common assumption that there is a relation between the value of the size-abundance spectrum slope and the phytoplankton community biovolume. Thus, communities with

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high phytoplankton biovolume (found in productive regions) usually exhibit size-abundance spectra with a less-negative (flatter) slope, this being due to the comparatively higher contribution of large-size cells to total biovolume. By contrast, low biovolume communites (usually found in low productivity regions) depict more-negative (steeper) slopes due to the comparatively higher contribution of small pico- and nanophytoplanktonic cells. As a consequence of this paradigm, $b$ could be considered as an adequate ecosystem indicator itself.

However, on theoretical, mathematical grounds, Gómez-Canchong et al. (2013) have demonstrated that total phytoplankton biovolume is, at the same time, directly related to $a$ and inversely related to the absolute value of $b$. Consequently, total biovolume could remain constant for different spectrum shapes if changes in one of the parameters were compensated by opposite changes in the other. They concluded that to characterize any aquatic ecosystem from its phytoplankton size structure at least two elements of the size-abundance spectrum triad (biovolume or abundance, $a$ and $b$) are indeed necessary. On the other side, the assumed relation between total biovolume and spectrum slopes derives from the comparison of phytoplankton communities from highly contrasting ecological conditions, such as coastal versus open ocean ecosystems. Does this relation between spectrum slope and total phytoplankton biovolume hold for less-contrasting ecosystems, such as those occupying open ocean waters?

In this article we examine the size-abundance spectra of phytoplankton along six biogeographical provinces (Longhurst, 2007) in the Atlantic Ocean. Our spectra cover a cell size (volume scale) range of eight orders of magnitude (from phototrophic picoplankton to microplankton). The main goal of this study is to analyze the relationship between size-abundance spectrum parameters and total phytoplankton biovolume in the open ocean. Our results will show that, in spite of sharp changes in cell abundance, total phytoplankton biovolume and spectrum slope are uncorrelated in the oligotrophic ocean.

## 2. Material and methods

### 2.1. Study area and general hydrography

Three oceanographic cruises were conducted in the Atlantic Ocean on board R/V Hespérides as part of the Malaspina Circunnavegation Expedition (Fig. 1). The cruises took place in December 2010–January 2011 (Malaspina Leg 1; Atlantic latitudinal cruise), January–February 2011 (Malaspina Leg 2; South Atlantic longitudinal cruise) and June–July 2011 (Malaspina Leg 7; North Atlantic longitudinal cruise). A total of 67 sites were visited, covering the following biogeographical provinces (Longhurst, 2007): Caribbean (CARB), North Atlantic Subtropical Gyral (NASE), North Atlantic Tropical Gryral (NATR), Western Tropical Atlantic (WTRA), South Atlantic Gyral (SATL) and Benguela Current Coastal (BENG). Some of them (NASE, NATR and SATL) were partially surveyed in two of the three cruises (NASE and NATR during Malaspina Legs 1 and 7; SATL during Malaspina Legs 1 and 2).

At each sampling station, vertical profiles of water temperature and fluorescence were obtained from the surface to 300 m depth using a Conductivity–Temperature–Depth probe (CTDSea-Bird 911) attached to a rosette sampler equipped with 24 Niskin bottles. The CTD fluorometer was calibrated against chlorophyll $a$ (chl $a$) concentration extracted from water samples and determined by fluorometric analysis. The upper mixed layer depth (UML) was defined as the depth at which the thermal gradient was higher than 0.1 °C m$^{-1}$ (Leppäranta and Myrberg, 2009; Ortega-Retuerta et al., 2010; Pérez et al., 2006).

### 2.2. Nutrient concentrations

Concentrations of nitrate were determined on-board on fresh samples using a Skalar autoanalyzer following the methods described in Moreno-Ostos (2012). The nitracline was defined as the depth at which nitrate concentration reached 1 μmol L$^{-1}$ (Robinson et al., 2006).
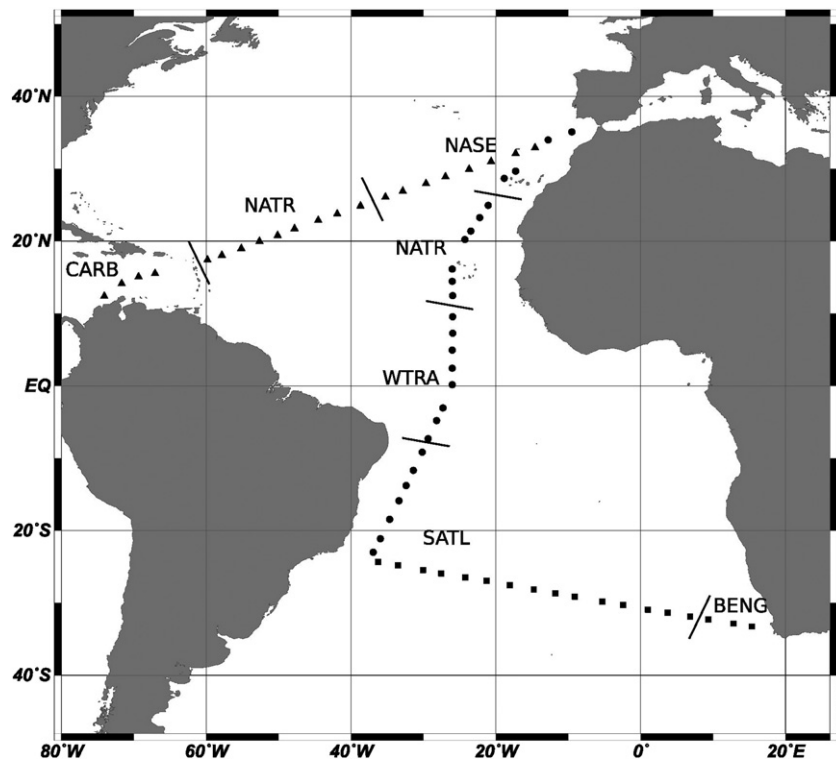


**Fig. 1.** Cruise tracks and location of the sampling stations. Circles, Malaspina Leg 1; Squares, Malaspina Leg 2; Triangles, Malaspina Leg 7. CARB: Caribbean province; NATR: North Atlantic Tropical Gyre province; NASE: North Atlantic Subtropical Gyral province; WTRA: Western Tropical Atlantic province; SATL: South Atlantic Gyral province; BENG: Benguela Current Coastal province.