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Production and respiration control the marine microbial metabolic balance in the eastern North Atlantic subtropical gyre

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ABSTRACT

Two main contrasted hypotheses have arisen during the last decades about the factors controlling the planktonic net metabolic balance in oligotrophic waters: gross primary production controls net community production vs. variability of net community production is also influenced by changes in microbial respiration. This work discusses both hypotheses analyzing the variability of metabolic rates along a gradient from the margin to the centre of the North Atlantic oligotrophic gyre, i.e. from relatively productive to more oligotrophic conditions. Net community production (NCP) was close to zero (between -3.34 and -11.77 mmol O_2 m^{-2} d^{-1}) at the margin of the gyre and tended towards net heterotrophy (-44.03 mmol O_2 m^{-2} d^{-1}) to the centre of the gyre as both gross primary production (GPP) and community respiration (CR) decreased. The strong relationships found between nutrient availability and both NCP and GPP suggest that factors controlling GPP are prevalent in determining NCP variability in this biogeographic region. However implementation of existing models to predict NCP from the measured GPP indicates that the precise estimation of NCP in different oligotrophic systems requires consideration of the magnitude and variability of microbial respiration rates.

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1. Introduction

An intense debate about the trophic status of open ocean oligotrophic ecosystems has been addressed during the last decades. Since del Giorgio et al. (1997) found that bacterial respiration exceeds phytoplankton net production in unproductive marine ecosystems, many studies have focused on clarifying the magnitude and trends of net microbial plankton metabolism in the open ocean. Most investigations based on the *in vitro* change in dissolved oxygen after controlled incubations, have systematically reported net heterotrophy to prevail in low production systems (Duarte and Agustí, 1998; Duarte et al., 2001; Gist et al., 2009; González et al., 2001; Morán et al., 2004; Robinson et al., 2002; Serret et al., 2001; Williams et al., 2004); although using similar *in vitro* methods, other studies found net autotrophic or balanced metabolism (Karl et al., 2003; Riser and Johnson, 2008; Serret et al., 2006; Williams and Purdie, 1991).

Regional to global ΔO_2 gross primary production (GPP) and community respiration (CR) databases have been used to validate theoretical models (López-Urrutia et al., 2006; Rivkin and Legendre, 2001 for example) and to derive generalizations and empirical models (del Giorgio and Duarte, 2002; Duarte and Regaudie-de-Gioux, 2009), whose predictive power has been empirically tested (Serret et al., 2009). However neither generalizations nor predictions derived from different databases, regions of the ocean, or by different authors, agree and as a result a new debate arose about what kind of information empirical GPP:CR relationships provide about factors controlling the functional relation of GPP with CR, and ultimately the net community metabolism of the microbial plankton communities in oligotrophic oceans.

Several works have reported a relative constancy in respiration rates against more variable primary production rates (Duarte et al., 2001; González et al., 2001; Morán et al., 2004), what derives in strong relations between the GPP/CR ratio and GPP (Duarte et al., 2001; González et al., 2001, 2002) that are interpreted as indicative of a control of the microbial metabolic balance by factors controlling GPP (Arístegui and Harrison, 2002; González et al., 2002). According to this view, some authors interpret net heterotrophy observations in open ocean systems

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as the result of universal thresholds of GPP that points out to the prevalence of heterotrophy whenever primary production is low (Duarte and Regaudie-de-Gioux, 2009). Other authors, while supporting the prevailing role of autotrophic processes, highlight the importance of the temporal decoupling of GPP and CR, so that pulses of GPP during autotrophic events would allow the maintenance of net heterotrophy (Williams et al., 2004). The first hypothesis would lead to the conclusion that low production habitats are systematically net heterotrophic, thus requiring an explanation to the source of allochthonous organic matter sustaining the prevalence of CR in open ocean oligotrophic provinces. In the later hypothesis, the excess CR is supported by previous local GPP, so that net autotrophy would prevail regionally in the long-term, even in oligotrophic provinces; this hypothesis in turn requires an explanation to the processes supporting such high episodic primary production rates in these unproductive areas. In any case, both hypotheses coincide in considering that the main controlling factor of NCP is GPP; consequently the variability of NCP in these provinces would be related to nutrient limitation due to stratification derived from the vertical thermohaline structure (Gist et al., 2009; González et al., 2002; Marañón and Holligan, 1999; Mc Andrew et al., 2007).

Other works have found that the balance between GPP and CR does not only depend on the total amount of photosynthesis. The observation of both positive and negative NCP in similarly oligotrophic low production systems (Serret et al., 2002) leads to the hypothesis that respiration, and not only GPP variability, plays an important role on the emergence of geographic and seasonal patterns of the metabolic balance (Biddanda et al., 2001; del Giorgio and Williams, 2005; Serret et al., 2006). According to this view, no universal GPP:CR relation or thresholds may exist because the factors controlling GPP (nutrients limitation) and CR (organic matter availability) do not always co-vary, especially in oligotrophic regions, so GPP:CR relations become system-dependant (Serret et al., 2009). Net heterotrophy in low production conditions would be either a result of the delayed consumption of organic matter previously produced locally (e.g., Serret et al., 1999), or the result of the consumption of allochthonous organic matter, mainly in dissolved form (DOM) (e.g., Robinson et al., 2002). In the first case the long-term community metabolism would be controlled by autotrophic processes within the system, while in the latter, trophic dynamics would be donor-controlled and geographic patterns of community metabolism would be associated to the spatial distribution of allochthonous DOM.

With the aim to elucidate the relative importance of the factors controlling the microbial NCP in oligotrophic waters, a quasi-longitudinal transect from the margin of the North Atlantic Oligotrophic Gyre to the centre was sampled in autumn 2006. We expected to find a gradient towards more oligotrophic conditions, thus enabling to study the variation of the balance between GPP and CR related to nutrient availability. Moreover, moving away from the main source of dissolved organic matter into the region, the highly productive eastern coastal upwelling system (Álvarez-Salgado et al., 2007; Hansell et al., 2004), the zonal section would also contribute to assess the influence of changes in CR variation on the microbial metabolic balance.

In addition to the spatial analyses of observations, NCP predictions from two contrasting published empirical models based on GPP (Duarte et al., 2001; Serret et al., 2009) have been compared with our data as a tool to ascertain the relevance of autotrophy in determining the net community metabolism.

Summarizing, we aim to test two of the contrasted hypotheses described above:

1- Production control hypothesis: Primary production is more variable than respiration. Regional production thresholds determine the microbial community net metabolic balance (Arístegui and Harrison, 2002; Duarte et al., 2001, Duarte and Regaudie-de-Gioux, 2009) and, therefore, NCP can be reliably predicted from GPP based empirical models. If this hypothesis is correct, GPP and consequently, NCP should tend to decrease as primary production decreased.
2- Production and respiration control hypothesis: Respiration can be as variable as production and then the metabolic balance

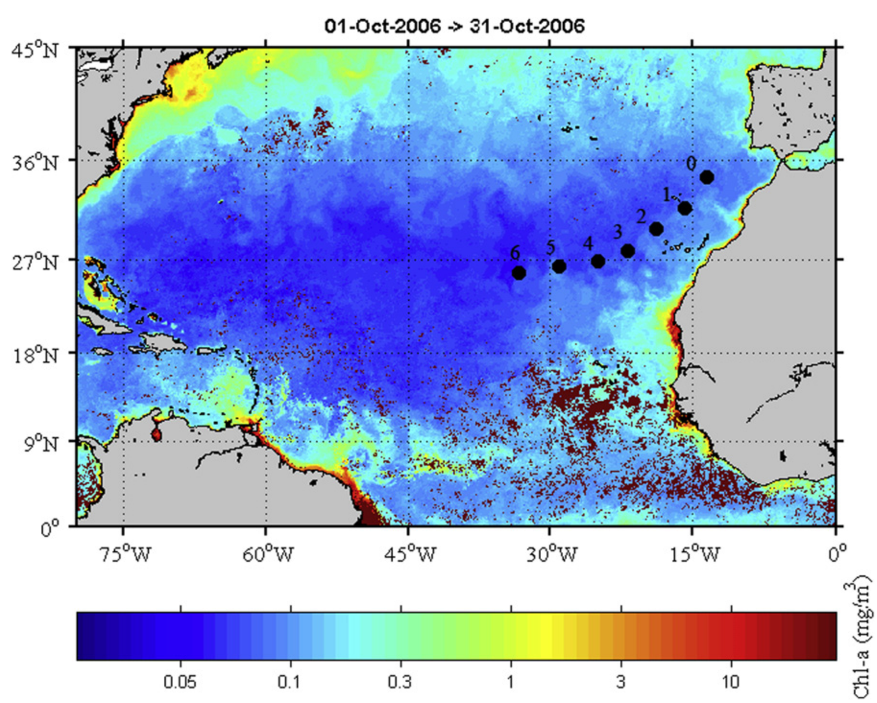

Fig. 1. Map of monthly averaged surface chlorophyll concentration (mg m^{-3}) in October 2006. Data were obtained from the ocean colour website (http://oceancolor.gsfc.nasa.gov/; Feldman and McClain, 2006) level-3 products (Modis-aqua mission) with 9 km resolution. White crosses signal the location of the stations sampled.

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