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Seasonal and spatial variability in plankton production and respiration in the Subtropical Gyres of the Atlantic Ocean

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ABSTRACT

Euphotic zone plankton production (*P*) and respiration (*R*) were determined from the *in vitro* flux of dissolved oxygen during six latitudinal transects of the Atlantic Ocean, as part of the Atlantic Meridional Transect (AMT) programme. The transects traversed the North and South Atlantic Subtropical Gyres (N gyre, 18–38°N; S gyre, 11–35°S) in April–June and September–November 2003–2005. The route and timing of the cruises enabled the assessment of the seasonal variability of *P*, *R* and *P*/*R* in the N and S gyres, and the comparison of the previously unsampled N gyre centre with the more frequently sampled eastern edge of the gyre. Mean euphotic zone integrated rates (±SE) were $P = 63 \pm 23$ ($n = 31$), $R = 69 \pm 22$ ($n = 30$) mmol O_2 m^{-2} d^{-1} in the N gyre; and $P = 58 \pm 26$ ($n = 30$), $R = 62 \pm 24$ ($n = 30$) mmol O_2 m^{-2} d^{-1} in the S gyre. Overall, the N gyre was heterotrophic ($R > P$) and it was more heterotrophic than the S gyre, but the metabolic balance of both gyres changed with season. Both gyres were net heterotrophic in autumn, and balanced in spring. This seasonal contrast was most pronounced for the S gyre, because it was more autotrophic than the N gyre during spring. This may have arisen from differences in nitrate availability, because spring sampling in the S gyre coincided with periods of deep mixing to the nitracline, more frequently than spring sampling within the N gyre. Our results indicate that the N gyre is less heterotrophic than previous estimates suggested, and that there is an apparent decrease in *R* from the eastern edge to the centre of the N gyre, possibly indicative of an allochthonous organic carbon source to the east of the gyre.

1. Introduction

The magnitude of plankton production (*P*) and respiration (*R*) are crucial to our understanding of the biogeochemistry of the oceans, since the balance between them indicates the amount of biologically fixed carbon available for export to the deep ocean, or for return to the atmosphere. The oligotrophic gyres are of prime importance to our understanding of how atmospheric CO_2 is influenced by the ocean carbon cycle (Neuer et al., 2002). They cover more than 60% of the global ocean, make a significant contribution to global productivity (Marañón et al., 2003; McClain et al., 2004), and export up to 50% of global carbon (Emerson et al., 1997). However, the *P*/*R* balance of these vast regions has not been satisfactorily determined. There is a lack of open ocean *P* and *R* data, with respiration measurements being particularly sparse (Robinson and Williams, 2005).

Analysis of the limited *P* and *R* data that do exist, has led to differing conclusions. Serret et al. (2002) attributed observations of a net heterotrophic ($P < R$) N gyre coincident with a more balanced S gyre to biogeochemical differences in gyre functioning. However, although net heterotrophy has been consistently observed in the subtropical N Atlantic (Duarte et al., 2001; Serret et al., 2001, 2002; Moran et al., 2004), one Atlantic Ocean latitudinal study suggested that the S gyre is more heterotrophic than the N gyre (González et al., 2002). The gyres are not homogeneous, static systems (Marañón et al., 2003; McClain et al., 2004), and these different interpretations may simply be due to different temporal and spatial ranges in the data collected by Serret et al. (2002) and González et al. (2002). The determination of how *P* and *R* vary temporally and spatially within the gyres therefore remains an essential prerequisite to accurately assess the level of autotrophy ($P > R$) to heterotrophy, and so the implied biological source or sink of CO_2 from the ocean to the atmosphere.

Using measurements collected east of 32°W in the N Atlantic, Duarte et al. (2001) estimated the carbon source required for the measured net heterotrophy to be as high as 0.5 Pg C yr^{-1} for the North Atlantic subtropical gyre-east (NAST-E; Longhurst, 1998). This dataset could not confirm whether the observed imbalances

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extended throughout the gyre, or if they were only characteristic of the northeastern region. The analysis of spatial variability is also pertinent within the N gyre because net heterotrophy in the region may be supported by allochthonous carbon sources originating, for example, in the northwest African upwelling, or from atmospheric inputs of organic matter (Robinson et al., 2002; Pelegri et al., 2005; Duarte et al., 2006; Serret et al., 2006), which might lead to a gradient in *R* from the eastern edge to the centre of the gyre (Serret et al., 2006). Certainly, previous estimates of net heterotrophy within the N gyre were too high to be supported by local, simultaneously produced carbon (Duarte et al., 2001; Serret et al., 2002). Both *P*/*R* and primary production (PP) exhibit pronounced seasonal variability (González et al., 2002; Marañón et al., 2003; Teira et al., 2005), and the accumulation of carbon produced during the more productive seasons may lead to the decoupling of *P* and *R* over large spatial or temporal scales (Serret et al., 2001). Inter-annual measurements are also important, as they allow the assessment of both natural temporal variability and long-term trends (Karl et al., 2001). This is particularly important in the context of recent evidence which indicates that the gyres are expanding (McClain et al., 2004), as well as the suggestion that future climate warming could lead to increases in stratification and the geographical extent of the gyres within the oceans (Sarmiento et al., 2004).

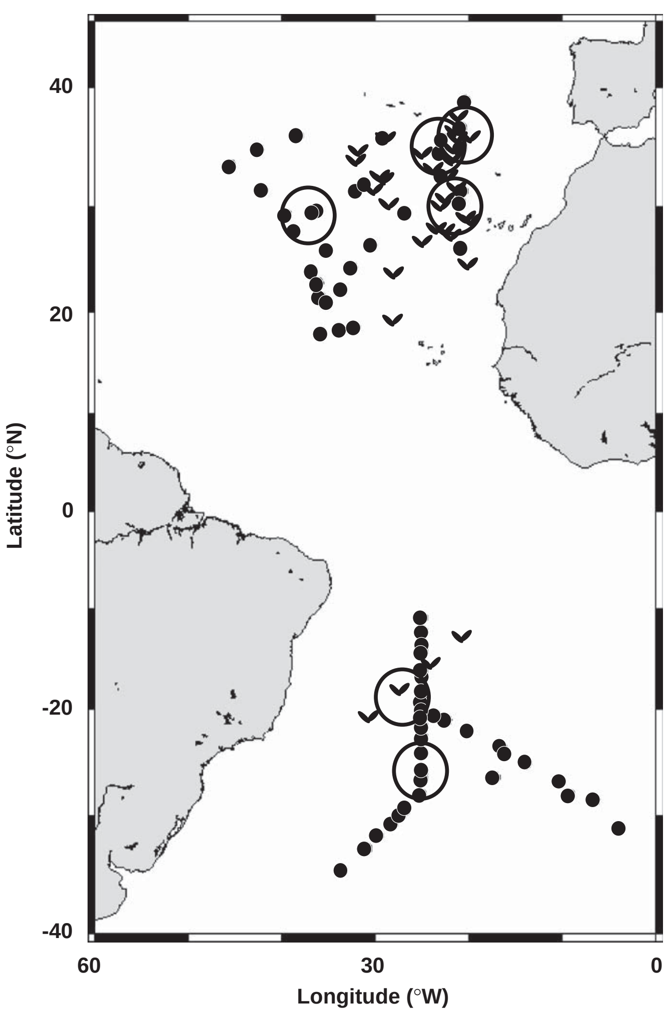

Fig. 1. Locations of the rate measurements considered in our analysis from AMT 12–17 (circles) and from previously published studies (crescents) obtained from www.amt-uk.org/data/respiration.xls. Regions indicated by the large open circles are the approximate positions of the SeaWiFS data given in Fig. 5.

Since 1995, the Atlantic Meridional Transect programme (AMT; www.amt-uk.org) has undertaken biological, chemical and physical oceanographic research during the annual return passage of research vessels between the UK and the South Atlantic. The programme aims to study ocean plankton ecology and biogeochemistry, and their interaction with atmospheric processes. The present study took place during six latitudinal transects, AMT 12–17, in the years 2003–2005. The cruise transects traversed a range of ecosystems, but in the present study we will only consider the N and S Atlantic gyres. Prior to this study, *P*/*R* had not been measured in the N gyre any further west than 32°W, and only two studies had measured *P* and *R* in the S gyre (González et al., 2002; Serret et al., 2002). The bi-annual sampling regime in both gyres enabled the direct comparison of the gyres at the same time of the year (during opposite seasons), and also within the same season (at different times of year). Cruise tracks sampled both the eastern edge of the N gyre and the previously unsampled centre of the N gyre (Fig. 1), allowing the comparison of rates in the two regions.

The aims of this study were (1) to examine the temporal and spatial variability of *P*, *R* and *P*/*R*, and to investigate how this might have affected previous estimates of the metabolic balance of the gyres, (2) to address the idea that contrasting *P*/*R* balances within the N and S gyres arise from characteristic differences in ecosystem functioning and (3) to consider our observations in the context of future global warming.

2. Methods

2.1. Sampling

The six cruises (AMT 12–17) took place between May 2003 and November 2005 on the RRS James Clark Ross (Falkland Island tracks) or the RRS Discovery (South Africa tracks). The northbound cruises (AMT 12, 14 and 16) sampled during boreal spring–summer, embarking from either Port Stanley (Falkland Islands) or Cape Town (South Africa) and disembarking in the UK. The southbound cruises (AMT 13, 15 and 17) started in boreal autumn, departing from the UK and ending in either the Falkland Islands or South Africa. All cruise tracks sampled the centre of the South Atlantic Subtropical Gyre (S gyre, 29 stations) and within the North Atlantic Subtropical Gyre (N gyre, 31 stations). AMT 12, 14, 16 and 17 (June 2003, May 2004, June 2005, October–November 2005) specifically sampled the centre of the N gyre (21°N 35°W, 29°N 37°W, 35°N 43°W, 28°N 39°W) whereas the AMT 13 and 15 cruise tracks (September 2003 and 2004) sampled the east of the N gyre north of the Mauritanian coastal upwelling (Fig. 1).

2.2. Euphotic zone gross production and dark community respiration

Water was collected daily, up to 2 h before dawn, from up to five depths, with a rosette of $24 \times 20\,dm^3$ 'Niskin'-type sampling bottles fitted with a SeaBird 9/11 *plus* CTD system. Gross production (*P*) and dark community respiration (*R*) were determined from *in vitro* changes in dissolved oxygen. Water was collected directly into opaque polypropylene aspirators from depths equivalent to 97% (AMT 14–17 only), 55%, 33%, 14% and 1% of surface irradiance. Irradiance levels were determined from light measurements made the previous day, or by assuming that the deep fluorescence maximum approximated the depth to which 1% of surface irradiance reached (Agusti and Duarte, 1999). The water was siphoned into 125-cm^3 borosilicate glass bottles and 4–5 zero time replicates were fixed within an hour of collection. Two further sets of 4–6 replicates were incubated for