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Plankton metabolic balance at two North Atlantic seamounts

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ABSTRACT

We have studied the epipelagic (0–100 m) metabolic balance between gross and net community production (P_g, P_n) and community respiration (R_d) around two seamounts (Seine: 34°N, 14°W; Sedlo: 40°N, 27°W) located in the subtropical northeast Atlantic. We looked for local effects causing seamounts to increase community production and/or community respiration with respect to the surrounding open ocean. Comparatively, Seine presented similar average living plankton biomass—chlorophyll *a* (Chl) and particulate proteins (Pt)—but higher P_g, due to higher R_d, presumably the result of organic matter loading from the NW Africa upwelling system, as supported by field results and satellite imagery. Nevertheless, the large temporal and spatial variability at each seamount make the average differences non-significant. Temporal variability in P, R_d and Chl was evident around the two seamounts. Sedlo showed higher R_d, Chl and Pt during winter, but higher P_n in summer. Seine presented higher Pt, Chl and P_n during spring, but higher R_d in summer. On average, the metabolic balance was heterotrophic ($R_d > P_g$) during all the sampling periods and at most stations of the two seamounts. Both Sedlo and Seine, showed higher R_d with respect to average values reported for the global ocean. A clear seamount effect on phytoplankton was only observed in Seine during spring, when Chl and Pt were enhanced at the summit of the seamount. Our results suggest that, rather than increasing primary production significantly, the two seamounts could act as trapping mechanisms for organic matter, favoured by the development of Taylor Columns on the top of the seamounts. Nevertheless these effects seem to be of a lower magnitude than changes caused by temporal or regional variability, questioning the role of these seamounts as hot-spots of productivity in the oceans.

1. Introduction

The balance between gross production (P_g) and dark-community respiration (R_d) in the upper ocean, the P_g/R_d ratio, sets the potential of surface-water ecosystems to pump organic carbon below the euphotic zone, hence contributing to carbon storage in the deep ocean. Both, P_g and R_d exhibit significant space and time variability (Robinson and Williams, 2005), which arises from the characteristics of different environmental regimes, and from the superposition of many mesoscale processes with a wide range of space and time-scales. Among these, the perturbation of the main flow induced by topographic features, like islands or seamounts, may represent a major source of mesoscale variability in the oceans, with important biological consequences (e.g. Rogers, 1994; Arístegui and Montero, 2005).

Seamounts are widespread along all ocean basins. They are known to interact with ocean currents, generating large spatial and temporal variability in the physical and biological fields (Royer, 1978; Boehlert and Genin, 1987). Most of the studies published in the last two decades regarding seamounts have dealt with the physical environment. Local effects include isopycnal doming above the seamount (Owens and Hogg, 1980), enhancement of vertical mixing (Navatov and Ozmidov, 1988; Lueck and Mudge, 1997; Eriksen, 1998), tidal amplification and rectification (Genin et al., 1989; Eriksen, 1991; Brink, 1990; Kunze and Toole, 1997; Noble and Mullineaux, 1989), or generation of local secondary circulation cells, like bottom-intensified Taylor columns (Roden, 1987; Freeland, 1994). All these hydrographic features can potentially enhance surface productivity by increasing nutrient pumping into the euphotic zone. Seamounts are therefore potentially important in oligotrophic oceans, where they could constitute isles of productivity, benefiting the development of highly diverse and productive pelagic and benthic communities (Rogers, 1994). Indeed, several studies have reported increases in phytoplankton biomass and productivity over seamounts, resulting from the combined effect of nutrient inputs into the euphotic zone and surface-water stratification, associated with isopycnal shallowing (Genin and Boehlert, 1985; Dower et al., 1992; Comeau et al., 1995; Odate and Furuya, 1998; Mouriño et al., 2001). Moreover, some studies have related the presence of highly

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diverse and abundant benthic communities with phytoplankton enrichments around seamounts (Rogers, 1994). For instance, Uchida and Tagami (1984) postulated that the cause of high abundances of groundfish populations in the North Pacific Ocean was related with the presence of numerous seamounts in the region. Other authors have argued, however, that increases in biomass and production over seamounts may be due to the retention and accumulation of living organisms and organic matter, favoured by local anticyclonic circulation cells generated around the topographic features (Dower et al., 1992; Mullineaux and Mills, 1997; Beckmann and Mohn, 2002; Genin, 2004). Overall, however, there is a high degree of uncertainty in the biological responses to flow perturbation by seamounts. Many directed studies looking for cause–effect relationships yielded inconclusive evidence for an enhancement in productivity or biomass accumulation due to physical forcing (Genin and Boehlert, 1985; Dower et al., 1992; Comeau et al., 1995; Odate and Furuya, 1998; Mouriño et al., 2001). Weak or no biological enhancements in plankton communities have been reported from many seamounts studies, in spite of perturbation of the local physical environment (e.g., Dower et al., 1992; Mouriño et al., 2001). Whether these inconsistencies in the biological response to variability in the impinging flow are the rule or the consequence of an inadequate temporal and spatial sampling resolution is still uncertain.

Within the framework of the European project OASIS (OceAnic Seamounts, an Integrated Study), we carried out an interdisciplinary study around two North Atlantic seamounts: Sedlo and Seine. The main goal of our research was to look for biological responses in microplankton ($<200\,\mu$m) biomass and metabolism to seamounts effects, and compare them in the context of temporal and regional variability. Up to 6 stations were sampled around Seine during March 2004 (R.V. *Poseidon 309*) and July 2004 (R.R.S. *Discovery 282*), while up to nine stations were sampled at Sedlo during November 2003 (R.V. *Meteor M60/1*) and July 2004 (R.R.S. *Discovery 282*). We first analysed the differences in the average chlorophyll *a*, microplankton proteins, and community production and community respiration, between the two seamounts. Then, we evaluated the temporal variability at each station, and finally we looked at the spatial variability within each seamount, compared with the far field.

2. Material and methods

2.1. Gross and net community production and respiration by oxygen changes

Discrete samples for metabolic experiments were collected at each station with Niskin-type bottles from six depths ranging from surface to 150 m. Gross (P_g) and net (P_n) community production, and community respiration (R_d) were determined by the oxygen method after incubations inside borosilicate bottles. Samples were incubated in "on-deck" incubators, reproducing the *in situ* light conditions. The attenuation of photosynthetic active radiation (PAR) in the water column was measured with a profiling natural fluorescence PNF300 instrument (Biospherical Co.). PAR irradiances were reproduced in the incubator by screening with neutral-density meshes. The PAR inside each bottle was measured with a quantum scalar irradiance meter QSL-100 (Biospherical Co.). The temperature control of the incubator was achieved by continuous seawater flow inside the incubation chambers. Differences in temperatures between *in situ* depths and the on-deck incubator ranged from 0 to 6 °C at 100 m. Water samples were allowed to reach the incubator temperature, before carefully siphoned using a silicone tube into 4–5 replicate "time-zero", dark and light 125-ml-BOD bottles, and incubated for 24 h. Dissolved oxygen was measured by the micro-Winkler technique, following the recommendations of Carrit and Carpenter (1966), Bryan et al. (1976) and Grasshoff et al. (1983). The entire contents of the bottles were titrated during <3 min by means of an automated, precise titration system, with colorimetric end-point detection (Williams and Jenkinson 1982). The precision achieved in replicates was %CV <0.05. R_d was estimated from the difference in oxygen concentration between the time-zero and dark bottles. P_n in a daily basis was estimated as the difference between the light and time-zero bottles, by assuming that respiration in dark and light were equal. P_g was calculated as the sum of P_n and R_d. A Q_{10} of 2 for *P* and *R* was used to correct for temperature differences with *in situ* values (Robinson and Williams, 1993). The depth of the 1% surface-light ranged from 85 to 120 m; hence, we integrated our metabolic rates down to 100 m, in order to look for the metabolic balance in the euphotic zone.

2.2. Phytoplankton pigments

Chlorophyll *a* (Chl) and phaeo-pigments (Pha) were estimated fluorometrically according to Parsons et al. (1984). Seawater samples (1 L) were filtered through Whatman GF/F fiber-glass filters. The filters were stored in liquid nitrogen until assayed. Pigments were extracted in cold acetone (90% v/v) for 24 h. Fluorescence before and after acidification was measured by means of a Turner Designs bench fluorometer, previously calibrated with pure chlorophyll *a* (Sigma Co.).

2.3. Microplankton proteins

Microplankton proteins (Pt) were determined according to the Peterson′s modification (Peterson, 1983) of the Lowry et al. (1951) method; using a protein assay kit provided by Sigma Co. Water samples (4 L) were concentrated on GF/F filters. Pt were extracted by grinding the filters with Lowry reagent directly and diluting with water afterwards. Sodium dodecylsulfate, included in the Lowry reagent, facilitates the dissolution of relatively insoluble lipoproteins. Replicate assays were run for each sample. Bovine serum albumin (BSA) standards with Pt concentrations between 4 and 400 mg m^{-3} were run at the same time to obtain a calibration curve. The average precision obtained in replicate samples was %CV <3.0.

3. Results

3.1. Hydrographic context

Seine and Sedlo seamounts are located in the same biogeographical region—the North Atlantic Subtropical Gyral (Longhurst, 1998), under the influence of the North Atlantic Central Waters (NACW) in the upper 700 m (Bashmachnikov et al., 2009). The two seamounts are isolated features, but differ in their topography and summit depths (Fig. 1). Seine is a cone-shaped seamount with a single shallow summit (175 m), placed between Madeira and the NW African coast, whilst Sedlo is a chain seamount composed of three deep peaks (being the shallowest at 780 m depth), situated north of Azores. The upper 200-m layer at Sedlo is characterized by a weak and unstable meandering eastward flow, branching from the North Atlantic Current. Seine, however, is situated in the area of direct influence of the more constant eastward flow of the Azores current (AC). Mohn et al. (2009) and Bashmachnikov et al. (2009) described complex hydrographical patterns around both seamounts, but concluded