Deep-Sea Research I 92 (2014) 141–151

Contents lists available at ScienceDirect

Deep-Sea Research I

journal homepage: www.elsevier.com/locate/dsri

Plankton metabolism and bacterial growth efficiency in offshore waters along a latitudinal transect between the UK and Svalbard

E.E. García-Martín [a,*], S. McNeill [b], P. Serret [a], R.J.G. Leakey [b]

[a] Dept. Ecología y biología animal, Facultad de Ciencias del Mar, Universidad de Vigo, CP 36210 Vigo (Pontevedra), Spain
[b] Scottish Association for Marine Science, Scottish Marine Institute, Oban, Argyll, PA37 1QA Scotland, UK

ARTICLE INFO

Article history:
Received 6 May 2014
Received in revised form
13 June 2014
Accepted 15 June 2014
Available online 14 July 2014

Keywords:
Gross primary production
Community respiration
Bacterial respiration
Bacterial growth efficiency
Atlantic Sub-Arctic region

ABSTRACT

Euphotic zone gross primary production, community respiration and net community production were determined from *in vitro* changes of dissolved oxygen, and from *in vivo* INT reduction capacity fractionated into two size classes, in offshore waters along a latitudinal transect crossing the North, Norwegian and Greenland Seas between the UK and Svalbard. Rates of gross primary production were higher and more variable than community respiration, so net autotrophy prevailed in the euphotic zone with an average net community production of 164 ± 64 mmol O_2 m^{-2} d^{-1}. Respiration seemed to be mainly attributed to large eukaryotic cells (> 0.8 μm) with smaller cells, mainly bacteria, accounting for a mean of 25% (range 5–48%) of community respiration. Estimates of bacterial growth efficiency were very variable (range 7–69%) due to uncoupling between bacterial respiration and production. Larger cells tended to contribute more towards total respiration in communities with high gross primary production and low community respiration, while bacteria contributed more towards total respiration in communities with lower gross primary production, typical of microbial-dominated systems. This suggests that community respiration is related to the size structure of the plankton community.

1. Introduction

Understanding the biotic mechanisms that mediate the marine carbon cycle is a major research objective in biological oceanography. The main biological processes involved are gross primary production (GPP), community respiration (CR), and the loss of biogenic carbon to sediments (Rivkin and Legendre, 2001). In steady state conditions, the difference between GPP and CR (*i.e.* the net community production, NCP) represents the net contribution of the marine biota to carbon export and hence plays a key role in the regulation of ocean CO_2 concentration, air–sea exchange and climate. However steady-state conditions are seldom, if ever, realised in the ocean and this, along with the complex dynamics of planktonic ecosystems, renders elucidation of the role of marine biota in the marine carbon cycle challenging.

Planktonic primary production is known to be limited by light, temperature and nutrients (Field et al., 1998), while temperature and organic matter availability are the main factors that constrain CR (Sampou and Kemp, 1994). In addition, community structure and dynamics influence trophic connections and the fate of organic matter produced (del Giorgio and Williams, 2005; Pace and Cole, 2000). Knowledge of the processes controlling the magnitude and variability of primary production is sufficient to delineate marine biogeographic provinces (Longhurst, 1998) and to remotely estimate water column primary production from the optical properties of surface waters (Behrenfeld and Falkowski, 1997; Pabi et al., 2008). By contrast, the processes controlling the variability of CR are still poorly understood. The evaluation of the net metabolic balance (*i.e.* NCP) offers an integrative approach to examine the biological contribution to the carbon cycle, encompassing individual autotrophic and heterotrophic processes and the dynamics emerging from their interactions; however, GPP and CR do not respond to environmental factors in a uniform or consistent manner, complicating short-term predictions of NCP. For example, Regaudie-de-Gioux and Duarte (2012) report that the effect of temperature on primary production and respiration depends on the season of the year and region of study across a wide range of ecosystems. Similar observations have been reported by Pomeroy and Wiebe (2001) when studying the effect of temperature and organic material on bacterial activity, while Serret et al. (2009) have found NCP to be dependent on trophic structure and energy flux dynamics.

A positive net metabolic balance implies that a surplus of primary production could be consumed by higher trophic levels of the food web, laterally transported to other communities, or exported vertically to the deep ocean. It is known that the rate of export to deep waters is influenced by the size structure of the

* Corresponding author. Present address: School of Environmental Science, University of East Anglia, Norwich Research Park, Norwich NR4 7TJ, UK. Tel.: +44 1603 593162.
E-mail address: Enma.Garcia-Martin@uea.ac.uk (E.E. García-Martín).

http://dx.doi.org/10.1016/j.dsr.2014.06.004
0967-0637/

planktonic community: a community composed of small cells are expected to have a lower rate of sedimentation compared to a community composed of larger organisms where grazing is less tightly coupled and sinking rates are higher (Kiørboe, 1993; Legendre and Rassoulzadegan, 1995). Moreover, communities dominated by small organisms and complex food webs are expected to respire a larger proportion of autotrophic production within the euphotic zone leaving less organic matter available for export (Michaels and Silver, 1988). Indeed, low rates of primary production are often associated with plankton communities dominated by small-sized cells (Kiørboe, 1993; Legendre and Le Fevre, 1991) with a high contribution of heterotrophic microorganisms to CR and resulting low or negative NCP. During the last two decades considerable attention has been paid to the relationship between primary production and phytoplankton size (Legendre and Le Fevre, 1991), the trophic structure of the food web (Kiørboe, 1993; Serret et al., 2001; Smith and Kemp, 2003) and the export rate (Legendre and Rassoulzadegan, 1995; Tremblay and Legendre, 1994; Wassmann, 1990); however, the contributions of different components of the plankton community to CR and NCP are still poorly understood.

Measurements of CR and, especially, bacterial respiration (BR) are rare compared to the data available on primary production. Bacteria are considered to be major contributors to total CR (del Giorgio et al., 2011; Lemée et al., 2002; Rivkin and Legendre, 2001) remineralising the bulk of organic matter within the water column and thereby exerting a major influence on carbon and nutrient cycles. BR has usually been estimated from changes in the dissolved oxygen concentration in a pre-filtered sample after *in vitro* incubations (Reinthaler and Herndl, 2005; Robinson et al., 2002b), or derived indirectly from CR (Robinson and Williams, 2005) or bacterial production (BP) measurements (del Giorgio and Cole, 2000; del Giorgio and Cole, 1998). The latter approach has the disadvantage of assuming a constant relationship of BR to BP or CR, while the former has been criticised due to filtration and incubation effects. The physical separation of cells of different size by filtration alters both the community structure (Gasol and Morán, 1999) and the activities of each size class (Aranguren-Gassis et al., 2012). Long incubations times, as required for BR measurements (at least 24 h in non-cultured samples), lead to further bias. BR estimates based on short incubation times, or an improved evaluation of the relationship between BR and CR/BP, are therefore required across different regions to improve the characterisation of the carbon flow through bacteria and its impact on food web dynamics, net metabolic balance and the carbon cycle. Furthermore, it is important to attain BR and BP measured concurrently at the same temporal and spatial scale in order to calculate bacterial growth efficiency (BGE = BP/(BP + BR)) which, in turn, determines the relationship between bacterial carbon demand and bacterial biomass produced (del Giorgio and Cole, 1998).

Recently the *in vivo* reduction of the 2-(*ρ*-iodophenyl)-3-(*ρ*-nitrophenyl)-5phenyl tetrazolium salt (INT) has been employed as a proxy for estimating respiration (Martínez-García et al., 2009). This approach enables estimation of BR during short (<5 h) incubations without pre-filtration, thus avoiding problems associated with long incubation times and the community disruption; however, it has received substantial criticism based on the claim that the method is not specific to enzymes associated with the electron transport system and therefore does not derive an accurate measure of respiration (Maldonado et al., 2012). Despite this criticism, comparisons made between *in vivo* INT reduction capacity and the standard approach of measuring *in vitro* changes in dissolved oxygen in incubated samples, based on data from different oceanographic areas and trophic conditions, reveal that the technique has value as a proxy for estimating respiration (García-Martín et al., *in prep*). Further studies are therefore required in order to establish the validity of INT reduction capacity as a proxy of respiration.

Comparative studies along latitudinal transects are well suited to the study of plankton dynamics in open, non-steady state ocean systems where rapid changes in communities indicate that transient non-equilibrium situations are frequent at small temporal and spatial scales. Such studies allow correlation of biogeochemical and ecological variables in planktonic ecosystems, evaluating general trends, functions and relationships as a function of contrasting biotic and abiotic factors (Robinson et al., 2006). However, it is difficult to discern causality from such studies, especially when the focus is on complex community dynamics due to the interactions with, and feedbacks from, community structure and function. Most studies of plankton metabolism conducted using latitudinal transects have been performed across temperate and/or tropical waters (Morán et al., 2004; Robinson et al., 2002a; Serret et al., 2002) with few undertaken across temperate and Arctic waters (Gosselin et al., 1997; Luchetta et al., 2000; Rey et al., 2000).

The aim of the present study was to characterise microbial plankton metabolism and associated physicochemical variables in offshore waters along a latitudinal transect between the UK and Svalbard, crossing three marine biogeochemical provinces. In particular (i) GPP, CR and NCP were determined from *in vitro* changes in dissolved oxygen concentration in the euphotic zone, contributing to the meagre database of CR and NCP values available from high latitude waters; (ii) BR was determined in non-fractionated samples, for the first time in these waters, via the *in vivo* INT reduction capacity of plankton cells during short incubations (2–4 h); and (iii) BGE was determined from estimations of BR and BP conducted concurrently over similar time scales, thereby reducing the potential bias associated with the conventional approach of combining BR and BP measurements undertaken using differential incubation times.

2. Materials and methods

2.1. Study site

The study was undertaken between the 14 and 19 June 2010 as part of the UK ICECHASER II research cruise on the RSS *James Clark Ross* (cruise JR219). Six stations were sampled in offshore waters along a latitudinal transect from the UK to the Svalbard archipelago crossing the North, Norwegian and Greenland Seas (Fig. 1 and Table 1). The transect encompassed three oceanographic provinces, as defined by Longhurst (1998): (i) the Northeast Atlantic Shelves province (NECS) which included the Central North Sea (CNS) and Northern North Sea (NNS) stations; (ii) the Atlantic Subarctic province (SARC) which included the Southern Norwegian Sea (SNWS), Central Norwegian Sea (CNWS) and Northern Norwegian Sea (NNWS) stations; and (iii) the Atlantic Arctic Province (ARCT) which included the Eastern Greenland Sea (EGS) station.

2.2. Physical and chemical variables

Shipboard temperature, salinity and fluorescence measurements were undertaken at each station using Sea-Bird Electronics SBE 911 and SBE 917 series CTD profilers and a Chelsea Aqua 3 fluorometer. The salinity sensors were calibrated during the cruise. Fluorescence values were converted to units of chlorophyll using a depth-dependent conversion factor derived from chlorophyll measurements undertaken on water samples collected during the cruise (T. Jackson personal communication). To determine inorganic nitrate + nitrite, ammonium, silicate and phosphate concentrations, water samples ($\sim$40 ml) were collected using 10 l