SPATIAL VARIABILITY IN NEAR-SURFACE PLANKTON METABOLIC RATES IN THE SUBTROPICAL AND EQUATORIAL PACIFIC

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By
Donn A. Viviani

Thesis Committee:

Matthew J. Church, Chairperson
David M. Karl
Karin M. Björkman

CHAPTER 1. INTRODUCTION

The past decade has seen considerable controversy over whether the vast regions of oligotrophic open ocean are net autotrophic, and consequently produce more organic matter and oxygen than is locally consumed, or whether these regions are net heterotrophic and thus exhibit rates of respiration exceeding those of photosynthetic oxygen and organic carbon production. Numerous geochemical measurements that integrate over time scales of weeks to months, including *in situ* measurements of net oxygen dynamics, carbon export, and various carbon and oxygen isotopic fractionation patterns, suggest these ocean ecosystems are net autotrophic, and therefore capable of both carbon export to the deep sea and net oxygen efflux to the atmosphere (Jenkins and Goldman 1985, Siegenthaler and Sarmiento 1993, Carlson et al. 1994, Michaels et al. 1994, Emerson et al. 1995, 1997, Luz and Barkan 2000, Riser and Johnson 2008). However, most studies based on direct measurements of daily net oxygen production and consumption find that the oligotrophic regions of the world's oceans are often in a state of net heterotrophy, whereby organic carbon and oxygen are consumed more rapidly than locally produced (del Giorgio et al. 1997, Duarte and Agusti 1998, del Giorgio and Duarte 2002, Serret et al. 2002, Williams et al. 2004). To date, it remains unclear whether these fundamentally different conclusions regarding the net metabolic state of the sea represent methodological problems, or reflect temporal and spatial uncoupling between respiration and production. If the oligotrophic open ocean is in fact net heterotrophic, the difference between the amount of organic carbon fixed locally and local carbon metabolized must be subsidized by organic carbon and oxygen production elsewhere.

The total amount of oxygen produced in marine systems is of clear interest, considering the status of the ocean as a carbon sink (Siegenthaler and Sarmiento 1993, Winn et al. 1994, Takahashi et al. 1997), the slow but steady decrease of atmospheric oxygen as atmospheric carbon dioxide rises (Keeling and Shertz 1992), and the potential for decreased oceanic dissolved oxygen with global warming (Keeling and Garcia 2002). The rate of gross primary production (GPP) constrains the total photosynthetic oxygen production.

$$CO_2 + 2\,H_2O + \text{Energy} \xrightarrow{\text{Photosynthesis}} (CH_2O)_n + H_2O + O_2 \qquad \text{(Equation 1)}$$

In the case of photosynthesis, the energy input is sunlight. Fundamentally, GPP is a measure of the productivity of the phytoplankton community.

Potentially, larger cells tend to exhibit greater rates of primary production (Morán et al. 2004, Marañón et al. 2007); while lower rates of primary production have been found in systems dominated by smaller cyanobacteria (Serret et al. 2001). It has also been suggested that smaller phototrophs appear to contribute less to particulate export to the deep sea than larger cells (Benitez-Nelson et al. 2001); although modeling efforts by Richardson and Jackson (2007) indicate that small phytoplankton can contribute to carbon export in a ratio equivalent to their total net primary production. As the ocean warms, it is likely to become more stratified (Behrenfeld et al. 2006, Polovina et al. 2008), which in turn is likely to select for lower nutrient concentrations and potentially for smaller cells (Bopp et al. 2005). This could decrease GPP, with concomitant decreases in oxygen and organic carbon production. These changes may also decrease the flux of organic carbon to the deep sea. In order to predict the potential future consequences of anthropogenic climate change, it is important to understand the current state of ecosystem metabolism in the ocean, both globally and the specific metabolic balances within different regions of the ocean.

The pool of oxygen and organic matter produced by photosynthesis also has a local rate of biological loss, community respiration (R), which is mediated by both heterotrophic bacteria and respiration by phototrophic organisms.

$$\text{Respiration} \rightarrow$$
$$(CH_2O)_n + O_2 \rightarrow CO_2 + 2\ H_2O + \text{Energy} + \text{Heat} \qquad \text{(Equation 2)}$$

In many oceanic ecosystems, the majority of measured R appears attributed to heterotrophic bacteria (Rivkin and Legendre 2001, Robinson and Williams 2005).

The oxygen loss due to bacterial respiration also reflects remineralization of nutrients and thus their re-supply to the autotrophic population (Azam et al. 1983).

The metabolic theory of ecology (Brown et al. 2004) suggests that bacterial respiration is largely temperature dependent (Rivkin and Legendre 2001, López-Urrutia and Morán 2007). Terrestrial ecosystem respiration rates across much of the Northern Hemisphere, for example, appear linearly related to the temperature (Enquist et al. 2003). However, Robinson et al. (2008) argue that the bacterial fraction of the total community can vary dramatically and in different situations the heterotrophic bacteria make up different percentages of the community; additionally studies have found differences in bacterial production to be driven by primary production increases, not temperature (Kirchman et al. 1995). It remains unclear to what extent microbes in the ocean are metabolically active (Zweifel et al. 1995), with the metabolic state of ocean microorganisms dependent on substrate availability or ambient temperature (Choi et al. 1996, Choi et al. 1999). Regardless of which populations or environmental variables control plankton respiration, the determination of community respiration rates remains an important ecosystem property for understanding elemental cycling and energy flow through a system.