PATTERNS IN OCEAN METABOLISM: RATES, BALANCE AND CONTROLS

Academic Ph.D.

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Abstract

The balance between the gross primary production (GPP) and the community respiration (CR) in oceanic ecosystems has been the subject of much discussion and controversy in the scientific community. The expanded observational basis resulting from these debates provided an opportunity to elucidate patterns in the metabolic balance in the Ocean, including examination of the magnitude of the differences in rates derived by different methods and describe the scaling among different metrics of plankton metabolic rates, evaluate regional and global variability in plankton metabolism and determine the threshold gross primary production separating heterotrophic from autotrophic communities. We analyse also here environmental parameters such as irradiance or water temperature that play an important role in controlling the metabolic balance of planktonic communities. We show here that the metabolism of plankton communities varies greatly across different oceanic regions with heterotrophic plankton communities more prevalent in the continental shelf consistent with high allochthonous inputs to the coastal ocean. The existence of a threshold of GPP of, on average 1.1 mmol O_2 m^{-3} d^{-1}, separating less productive from more productive is exposed also here, providing evidence that less productive planktonic communities tend to be net heterotrophic. We report also in this work the evidence that the compensation depth for plankton community metabolism averages 36 ± 9 m. Furthermore, a threshold temperature of 23.5 ºC has been exposed here for a P/R ratio of 1, indicative of metabolic balance.

The results presented in this dissertation reveal, in summary, important patterns of metabolic balance for planktonic communities across the ocean, their rates and controls. Continuing to explore the oceans and evaluating the metabolic balance of their planktonic communities is fundamental considering the major role planktonic community play in the global carbon cycle.

Resum

L'equilibri entre la producció primària bruta (GPP) i la respiració de la comunitat (CR) en els ecosistemes oceànics ha estat objecte de molta discussió i controvèrsia en la comunitat científica. L'àmplia base d'observació resultant d'aquests debats ens proporciona l'oportunitat d'aclarir els patrons en l'equilibri metabòlic a l'oceà, inclòs l'estudi de la magnitud de les diferències en les taxes obtingudes per diferents mètodes i descriure l'escala entre els diferents mesures de taxes metabòliques de plàncton, avaluar la variabilitat regional i global en el metabolisme del plàncton i determinar el llindar que separa la producció primària bruta de les comunitats heterotròfiques i autotròfiques i la irradiància llindar necessària per equilibrar la producció primària i la respiració. S'analitzen també els paràmetres ambientals com ara la llum o la temperatura de l'aigua que juguen un paper important en el control de l'equilibri metabòlic de les comunitats planctòniques. Hem demostrat que el metabolisme de les comunitats planctòniques varia enormement entre diferents regions oceàniques. Les comunitats de plàncton heteròtrofes són freqüents a la plataforma continental de conformitat amb elevada aportació alòctona a l'oceà costaner. L'existència d'un llindar de GPP de mitjana 1.1 mmol O_2 m^{-3} d^{-1}, que separa els menys productius dels més productius s'exposa també aquí, proporcionant evidència que les comunitats planctòniques menys productivess tendeixen a ser netament hetertròfiques. Es presenta també en aquest treball l'evidència que la profunditat de compensació pel metabolisme de la comunitat de plàncton és de 36 ± 9 m. D'altra banda, un llindar de temperatura de 23.5 º C s'ha exposat aquí per obtenir una relació P / R de 1, indicatiu de balanç metabòlic.

Els resultats presentats en aquesta tesi revelen, en resum, importsants patrons d'equilibri metabòlic important per a les comunitats planctòniques a través de l'oceà, els seus tipus i controls. Continuar estudiant els oceans i l'avaluació del balanç metabòlic de les seves comunitats planctòniques és fonamental considerant l'important paper que juga la comunitat planctònica en el cicle global del carboni.

Résumé

L'équilibre entre la production primaire brute (GPP) et la respiration (CR) de la communauté planctonique dans les écosystèmes océaniques a fait l'objet de multiples discussions et de controverses au sein de la communauté scientifique. La large base de données provenant de ces débats a permis d'élucider les tendances de l'équilibre métabolique dans l'océan qui inclut l'examen de l'ampleur des différences au sein des taux métaboliques dûes à différentes méthodes, la description de l'échelle de différence des taux du métabolisme planctonique, l'évaluation de la variation régionale et globale du métabolisme, la détermination de la limite de GPP séparant les communautés hétérotrophes d'autotrophes. On a analysé également dans ce travail les paramètres environnementaux telle que la lumière et la température de l'eau qui jouent un rôle important dans le contrôle de l'équilibre métabolique de la communauté planctonique. On a montré que le métabolisme de la communauté planctonique varie de manière importante le long des différentes régions océaniques où les communautés planctoniques hétérotrophes sont plus répandues sur le plateau continental en accord avec les forts apports allochtones de l'océan côtier. L'existence d'une limite de GPP, en moyenne de 1.1 mmol O_2 m^{-3} d^{-1}, séparant les communautés moins productives des plus productives a été exposée ici, apportant l'évidence que les communautés planctonique les moins productives tendent à être hétérotrophes. On a rapporté également dans ce travail l'évidence que la profondeur de compensation pour la communauté planctonique environnée 36 ± 9 m. De plus, une limite de température de 23.5 ºC a été montrée ici pour un rapport P/R de 1, indiquant un équilibre métabolique.

Les résultats présentés dans ce manuscrit révèlent, en résumé, d'importantes tendances de l'équilibre métabolique de la communauté planctonique au travers les océans, leurs taux et leurs contrôles. L'exploration des océans et l'évaluation de l'équilibre métabolique des communautés planctoniques sont fondamentales si on considère le rôle majeur de la communauté planctonique dans le cycle global du carbone.

General Introduction

Covering 71 % of the Earth's surface, the Oceans represent the largest component of our biosphere, playing a dominant role in the functioning of the biosphere. The regulation of the gaseous composition of the atmosphere is a major role of the ocean, exerted through gas exchange across the sea-air interface. Whereas the ocean is believed to have acted as a weak source of CO_2 to the atmosphere throughout the Holocene (Raynaud *et al*., 2004; Lourey *et al*., 2004), it acts as an important sink of CO_2 at present, sequestering about 2 Gt C yr^{-1}. Whereas some models implicitly assume this to be due to the role of biota in capturing CO_2 (e.g. IPCC 2001), this shifting role is most easily explained as a consequence of the increased solubility of CO_2 in seawater to reach equilibrium as atmospheric of CO_2 increases due to anthropogenic emissions. However, ocean biota does play, through their metabolic processes, a major role in controlling the CO_2 partial pressure in seawater and, hence, air-sea exchange (Fig. 1).

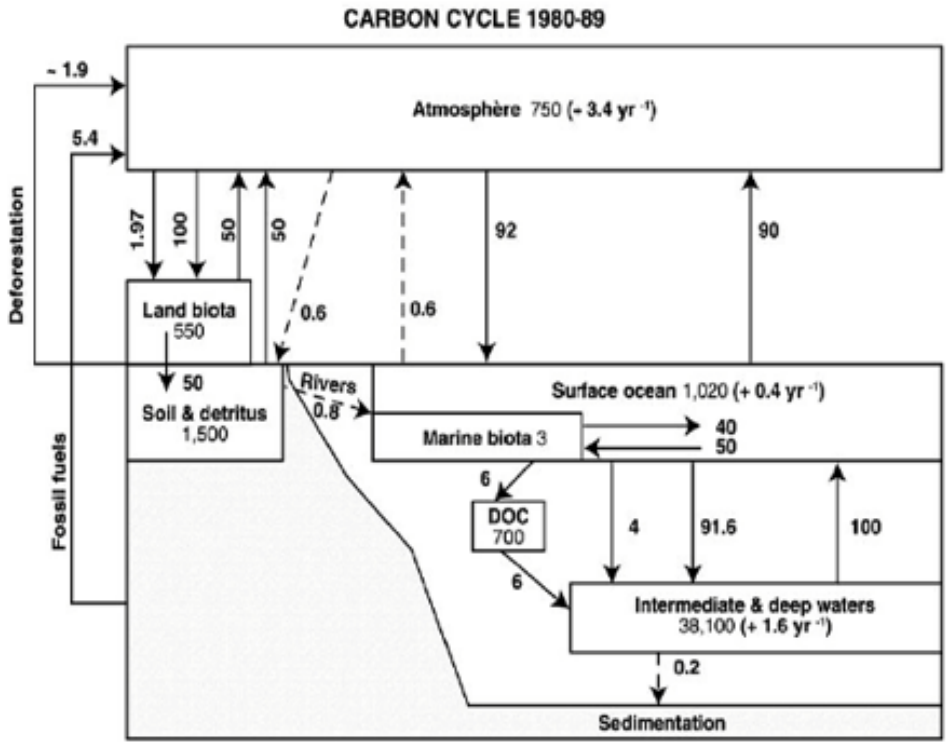

Figure 1 Diagram of carbon cycle after pre-industrial era (*Siegenthaler and Sarmiento (1993) Nature, 365: 119-125*).

The global carbon budget is the balance of the exchanges (inputs and outputs) of carbon between the carbon reservoirs. An examination of the carbon budget of a reservoir allows to determine if this acts as a source or sink for CO_2. The oceans represent the greatest reservoir of carbon, which is present mostly in the form of bicarbonate ion, with dissolved organic carbon being the second largest pool, much larger than that of particular organic carbon (POC).

The biota of the ocean have an important impact on the quantity and the form of carbon through their metabolism. The ecosystem metabolism refers to the biochemical modifications of chemical components in living organisms and cells through the biosynthesis of complex organic molecules (anabolism) and their breakdown (catabolism). Two principal processes capture these two components of marine ecosystem metabolism: Production and Respiration of organic matter. At the most fundamental level, production of organic matter is represented by the primary production: the capture of energy in the form of electromagnetic radiation through photosynthesis resumed by the simplified equation:

$$CO_2 + H_2O + \text{light} \rightarrow CH_2O + O_2 \qquad \text{(Eq. 1)}$$

Primary production can also be achieved using strong chemical gradients (chemiosynthesis) and its conversion to, and storage as, chemical energy in organic matter by living organisms. This energy is used to synthesise complex organic molecules (such as glucose or other sugars that are used to synthesise molecules like proteins, lipids, nucleic acids, among others) from simpler inorganic compounds such as carbon dioxide (CO_2), water (H_2O) and inorganic nutrients (Field *et al.*, 1998; Behrenfeld *et al.*, 2001).

Respiration of organic matter represents the oxidative breakdown of organic molecules into its inorganic constituents (CO_2 and inorganic nutrients) to free energy to support various processes (Fig. 2) and can be resumed by the simplified equation:

$$CH_2O + O_2 \rightarrow CO_2 + H_2O + \text{energy} \qquad \text{(Eq. 2)}$$

Respiration consumes O_2 although there are respiratory pathways, confined to hypoxic and anoxic environments that use oxidized molecules other than oxygen as the electron donor.

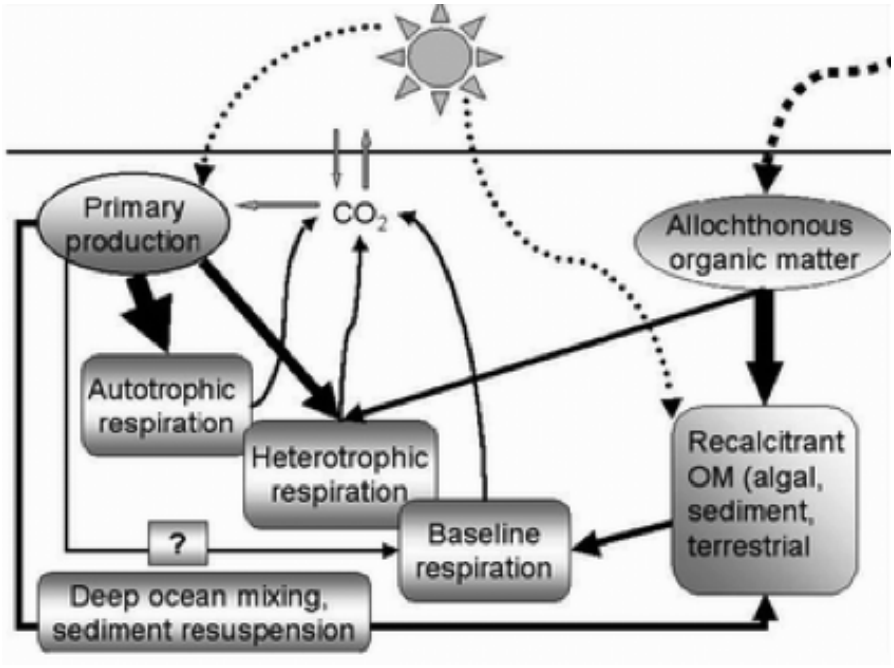

Figure 2 Schematic diagram of the main components of aquatic respiration, and its links to other aspects of ecosystem function (*del Giorgio and Williams (2005): Respiration in Aquatic Ecosystems* book*, Chp. 14: 268-304*).

The metabolic balance of a community or ecosystem refers to the balance between primary production (i.e. organic matter production) and respiration (i.e. organic matter oxidation) (Fig. 2). The metabolic balance of ecosystems is defined by the balance between the gross primary production (GPP) and the community respiration (R) (Duarte *et al*., 2004), also referred to as net community production (NCP = GPP – R). Depending on the dominance of each of these processes, ecosystems or communities can be classified as autotrophic, indicating that the community produces organic matter in excess of its respiratory requirements; heterotrophic, which consume more organic matter through respiratory processes that they produce; and metabolically balanced, where production and respiration are of equal magnitude (Duarte *et al.*, 2005). It is important to note that heterotrophic ecosystems require external, allochthonous inputs of organic matter to meet their requirements, thereby creating links between autotrophic

ecosystems, i.e. those that produce organic matter in excess relative to local requirements, and heterotrophic ones, that use the excess produced by autotrophic ones. Recent assessments have provided evidence that unproductive ecosystems tend to be heterotrophic (Duarte *et al*., 1998; Duarte and Prairie, 2005), whereas highly productive ones, such as vegetated coastal habitats, tend to be autotrophic (Duarte *et al*., 2005).

Considering the important consequences of the metabolic balance of ecosystems, both production and respiration must be studied in concert. However, traditionally, productive processes have received far more attention than respiratory processes (del Giorgio and Williams, 2005; del Giorgio and Duarte, 2002). Scientists traditionally believed that most marine ecosystems were net autotrophic and that heterotrophic ecosystem only occurred under pollution or disturbance (Odum, 1956). However, the recent increase of estimates of respiration and net community production has provided evidence that autotrophy is not prevalent in the ocean, and that many ocean regions are heterotrophic. All organisms respire and respiration is an ubiquitous process in the ocean, from the ocean surface to the sea floor, whereas autotrophic processes are restricted to, mostly, photosynthetic organisms, and occur mostly in the euphotic layer (< 200 m) (del Giorgio and Williams, 2005; Duarte and Prairie, 2005; del Giorgio and Duarte, 2002; Agustí *et al*., 2005).

As it has been explained previously, the organisms present in the ecosystem control ocean metabolism. Hence, the community structure of the biota must greatly constraint planktonic metabolism. In addition, the growth efficiency of the heterotrophic organisms, defined as also affects the CO_2 yield for a given carbon flux in the food web and is, therefore, an important determinant of the metabolic balance of the ecosystems.

Objectives

The main objectives of the present Ph.D. project is 1) elucidate, through a meta-analysis of existing information as well as direct experimental research, patterns in the metabolic balance of the ocean, and 2) to resolve the main factors controlling the metabolic balance of the ocean. This objective will help 1) improve our understanding on the role of the ocean in planetary metabolism, 2) develop a basis to predict past and

future changes in ocean metabolism, and 3) better understand the broad range of metabolic rates and processes present across the ocean.

In order to achieve this goal, we will address a number of specific questions, corresponding of the different chapters composing the thesis presented here:

Chapter 1 - Scaling metrics of plankton primary production

Different approaches to measure primary production have been compared in a series of papers examining the rates delivered by different methods for specific locations, cruises or sampling time. However, these comparisons have remained local and cannot be used to scale different methods.

The main goal of this study is to provide new critical view on GPP measurements using a broad database of planktonic metabolism in the ocean. Here we examine the magnitude of the differences in rates derived by different methods and describe the scaling among different metrics of planktonic primary production, providing equations that allow comparisons of estimates among different methods. When the GPP has been measured during the same study with different techniques, we evaluate so through the database, the metabolic rates differences between each method across the ocean and understand what is the basis for differences among the different approaches to resolve metabolic rates and balances in the ocean.

Chapter 2 - Threshold of gross primary production for marine planktonic metabolism

The threshold of GPP for the planktonic communities allows to evaluate the value of GPP where the planktonic communities metabolism is balanced (GPP = CR). The estimate of the GPP threshold allow the discussion of the consistency of the estimates derived using different approaches and identifying patterns in the variability of these thresholds across regions. Using recent estimates of the magnitude of allochthonous organic carbon inputs, we then focus on the processes supporting plankton community respiration in the absence of, or under low primary production and test the proposed role of allochthonous organic carbon inputs in supporting net heterotrophy.

Chapter 3 - Regional and global variability in the pelagic metabolism in the ocean

In order to better understand the metabolic balances of the planktonic communities along the different oceanic regions and latitudinal bands, we examine here global patterns in planktonic metabolic balance in the ocean. We do so on the basis of an expanded data set of planktonic metabolism in the euphotic layer of the ocean, more than twice larger than the data set compiled by Robinson and Williams (2005). We examine the distribution of volumetric and depth-integrated planktonic gross primary production (GPP), community respiration (CR), net community production (NCP = GPP – CR) and the ratio of GPP to CR (P/R ratio) and the relationships between CR and GPP CR for the global data set, and tested for possible differences between coastal and open ocean communities, differences between communities in different hemispheres and latitudes, and between communities in different ocean basins.
We exposed also in this chapter the patterns of the planktonic metabolism in three specific oceanic regions: the Mediterranean Sea, the Eastern Arctic Ocean and the Antarctic Peninsula.

Chapter 4 - The compensation irradiance for planktonic community in the ocean

The compensation irradiance is defined as the irradiance where photosynthesis equals respiration. It can be considered as the irradiance threshold for community metabolism. At lower irradiance the community would be heterotrophic. Where autotrophic processes are dominated by photosynthesis, it is possible to define the compensation irradiance for metabolic balance as the irradiance at which photosynthesis equals respiration. The compensation irradiance is likely to increase as respiration rate approaches gross production, to reach 100% of irradiance, by definition, in net heterotrophic communities. We determine here the compensation irradiance of planktonic communities in different oceanic regions. Knowledge of the compensation irradiance and its control of the oceanic communities may help understand and integrate the metabolic balance of the ocean.

Chapter 5 - Temperature dependence of planktonic metabolism in the ocean.

Standard metabolic theory predicts that both respiration and photosynthesis should increase with increasing temperature, albeit at different rates. However, test of this prediction for ocean planktonic communities is limited, despite the broad consequences of this prediction in the present context of global ocean warming. We compiled a large data set on planktonic metabolism and tested the relationship between standardised metabolic rates and water temperature. These relationships can be used to predict the effect of warming on ocean metabolism and, thus, the role of planktonic communities in the flow of carbon in the global ocean.

References

Agustí S, Duarte CM (2005) Threshold of gross primary production for planktonic metabolic balance in the Southern Ocean: An experiment test. Limnol Oceanogr 50(4): 1334-1339.

Behrenfeld MJ, Randerson JT, McClain CR, Feldman GC, Los SO, Tucker CJ, Falkowski PG, Field CB, Frouin R, Esaias WE, Kolber DD, Pollack NH (2001) Biospheric Primary Production During an ENSO Transition. Science 291: 2594-2597

del Giorgio PA, Duarte CM (2002) Respiration in the open ocean. Nature 420: 379-384

del Giorgio PA, Williams PJLeB (2005) The global significance of respiration in aquatic ecosystems: from single cells to the biosphere. In: del Giorgio P.A. and Williams, P.J.leB. (Ed.), Respiration in aquatic ecosystems. Oxford University Press, p. 328.

Duarte CM, Agustí S (1998) The CO_2 balance of unproductive aquatic ecosystems. Science 281

Duarte CM, Agustí S, Vaqué D (2004) Controls on planktonic metabolism in the Bay of Blanes, northwestern Mediterranean littoral. Limnol Oceanogr 49(6): 2162-2170

Duarte CM, Prairie YM (2005) Prevalence of heterotrophy and atmospheric CO_2 emissions from aquatic ecosystems. Ecosystems 8: 862-870

Field CB, Behrenfeld MJ, Randerson JT, Falkowski P (1998) Primary production of the Biosphere: Integrating Terrestrial and Oceanic Components. Science 281: 237-240

Lourey MJ, Trull TW, Tilbrook B (2004) Sensitivity of $\delta^{13}C$ of the Southern Ocean suspended and sinking organic matter to temperature, nutrient utilization, and atmospheric CO_2. Deep-sea Res Pt I 51: 281-305

Odum HT (1956) Primary production in flowing waters. Limnol Oceanogr 1(2) : 102-117

Raynaud D, Lorius C (2004) Climat et atmosphere: la mémoire des glaces. Comptes Rendus Geosc 336 : 647-656

Robinson C, Williams PJLeB (2005) Respiration and its measurementin surface marine waters. In: del Giorgio PA, Williams PJLeB (Ed.), Respiration in aquatic ecosystems. Oxford University Press, p. 328

Siegenthaler U, Sarmiento JL (1993) Atmospheric carbon dioxide and the ocean. Nature 365: 119-125

Chapter 1

Scaling metrics of plankton primary production

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Abstract

Different approaches to measure primary production have been compared in a series of papers examining the rates delivered for specific locations, cruises or sampling time. However, these comparisons have remained local and cannot be used to scale different methods. Here we examine the magnitude of the differences in rates derived by different methods and describe the scaling among different metrics of planktonic primary production, providing equations that allow comparisons of estimates among different methods. We do so on the basis of a compilation of data on volumetric estimates of primary production rates concurrently estimated with at least two different methods, thereby allowing the comparison among the rates derived. No significant differences were observed between the GPP measured by the ^{14}C method (when total production TPP was considered) and the Winkler method whatever the productivity rate of the planktonic community. In high productive ecosystems, the Winkler method seems to underestimate the GPP rates may be due to the lack of consideration of light respiration, probably higher in productive planktonic communities. The differences observed between the different methods to determine the GPP rates can be explained by the C losses incompleting the POC collection by the ^{14}C method. The caution to determine the GPP rates with better accuracy should be to use the ^{18}O method to determine the GPP and use the Winkler method to evaluate the NCP in the light and CR in the dark. The comparison between those two methods has to be reinforced in order to understand what factors should allow a light respiration higher than dark respiration.

Introduction

Oceanic photosynthesis is responsible for about half of the primary production in the Biosphere (Field *et al*., 1998) and plankton primary production is, therefore, a fundamental process at the global and the ecosystem scale. At the global scale, plankton primary production affects oxygen and CO_2 fluxes, constraining gas exchange with the atmosphere and, thus, the gaseous composition of the atmosphere (Duarte *et al*., 1999). Phytoplankton photosynthesis has controlled the atmospheric carbon dioxide-oxygen balance since the early Precambrian, when algal abundance became sufficient to convert the reducing atmosphere to an oxidizing one (Tappan, 1968). At the ecosystem level, primary production sets an ultimate limit to the carbon flow in marine food webs, constraining fisheries production (Ryther, 1969), bacterial production (Cole *et al*., 1988) and the subsidies biota deeper in the water column receive from the photic layer (Suess,

1980). The measurement of plankton primary production is, thus, a fundamental property of the ocean ecosystem, receiving considerable effort that has resulted in several million estimates available to-date (del Giorgio and Williams, 2005).

Photosynthetic rates of marine phytoplankton were first measured using the oxygen evolution method in phytoplankton communities in the Oslo Fjord by Gaarder and Gran (1927). This method originally suffered from poor resolution, being unable to resolve the low primary production rates in the less productive regions of the ocean (Truesdale *et al*., 1955; Mortimer, 1956; Richards and Corwin, 1956). These limitations were resolved with the advent of high-precision Winkler analyses using automatic titrators and end-point detection of the Winkler reaction (Carpenter, 1965; Carrit and Carpenter, 1966), which allow low primary production rates to be resolved. However, the ^{14}C method was developed before improved oxygen-based techniques were developed (Steeman-Nielsen, 1952) and rapidly became the standard for the oceanographic community, used to calibrate remote sensing algorithms, despite recurrent caveats as to what exactly does the ^{14}C incorporation method measures (Dring and Jewson, 1982; Behrenfeld and Falkowski, 1997). Since, other approaches have been derived, such as the use of tracer methods based on stable isotope additions, such as ^{13}C (Slawyk *et al*., 1977) and ^{18}O (Grande *et al*., 1982; Bender *et al*., 1987), and more recently approaches based on triple O_2-isotope fields (Luz *et al*., 2000). These methods, differ however in assumptions or the particular process through which primary production is represented and, thus, may yield somewhat different results when applied to any one community.

Different approaches to measure primary production have been compared in a series of papers examining the rates delivered by different methods for specific locations, cruises or sampling events (Williams *et al*., 1983; Bender *et al.,* 1987; Grande *et al*., 1989; Juranek *et al*., 2005; Gazeau *et al*., 2007; González *et al*., 2008). Most of these comparisons revealed differences among methods, varying in magnitude, attributable to differences in the specific components of primary production addressed by each method as well as by their inherent assumptions. However, these comparisons have remained local and cannot be used to scale different methods to allow comparisons among data produced with different methods and estimation of, for instance, gross primary production from satellite-based primary production estimates, which are calibrated against the particulate ^{14}C primary production method.

Here we examine the magnitude of the differences in rates derived by different methods and describe the scaling among different metrics of planktonic primary production, providing equations that allow conversion of estimates among different methods. We do so on the basis of a compilation of data on volumetric estimates of primary production rates concurrently estimated with at least two different methods, thereby allowing the comparison among the rates derived.

Methods

We searched the published literature for estimates of primary production of natural marine plankton communities produced using at least two different methods analysed concurrently. The methods compared include primary production derived using the Winkler method, the ^{18}O-labeled H_2O method and the ^{14}C method. Whereas the addition of ^{13}C-labelled bicarbonate has also been proposed (Slawyk *et al*., 1977), data comparing results derived from this method with those derived with other methods for the same natural marine phytoplankton communities are too sparse to allow adequate comparisons. The triple isotope method (Luz *et al*., 2000) estimates time-integrated rates of photosynthesis and respiration from the difference between the triple oxygen isotopes (^{18}O, ^{17}O and ^{16}O). Considering solely biological production and consumption, there is an excess of ^{17}O in comparison to air O_2. One of the advantages of this method is the lack of bottle incubation. This method allows to evaluate photosynthesis and respiration rates *in situ* integrated over week to month periods, which is impossible to measure directly with bottle incubations. This method involves, however, considerable error associated with the multiple assumptions on water column mixing and air-sea O_2 exchange rates (Robinson and Williams, 2005), although a complete error propagation analysis, required to estimate the error involved in this method, is still pending. Indeed, the uncertainty on gross primary production with the triple isotope method is of the order of 40 %, affecting the interpretation of the estimates and their use to derive carbon budgets (Juranek *et al*., 2005; Robinson and Williams, 2005). Moreover, because the method integrates over week to month time scales, it cannot be compared directly with other primary production methods, which resolve primary production over hourly to daily scales.

The bulk oxygen evolution method consists in the evaluation of changes in oxygen concentration using high-precision Winkler method, allowing 0.1 % precision in oxygen determinations (Carpenter, 1965; Carrit and Carpenter, 1966), following the

incubation, typically for 24 h, of natural plankton communities enclosed in clear and dark bottles. Primary production is calculated as the sum of the rate of change in oxygen concentration in clear bottles, the net community production, and that in dark bottles, dark respiration. This estimate, which is calculated rather than derived directly, corresponds to the gross primary production (GPP), defined as the total photosynthetic oxygen production prior to any losses, but relies on the assumption that respiration in the light does not differ from that in the light (Table 1.1). Moreover, the method requires the confinement of the communities and is, thereby, potentially affected by artefacts derived from bottle effects, such as modifications of the light field (Kirk, 1994), as all incubations have been conducted with borosilicate bottles, a material that excludes UV radiation.

The ^{18}O-labeled H_2O method (Grande *et al*., 1982; Bender *et al*., 1987) measures the GPP using the stable isotope ^{18}O as a tracer of molecular oxygen production through photosynthesis. The sample water is artificially enriched in ^{18}O derived by the photosynthetic release of ^{18}O from $H_2{}^{18}O$ during daytime (Table 1.1), and provides, therefore, an estimate free of assumptions on the effect of light on respiration, but still subject to the potential bottle effects indicated above (Table 1.1).

The ^{14}C method (Steeman Nielsen, 1952) consists in measuring the photosynthetic incorporation of ^{14}C labelled inorganic C, added as a $NaH^{14}CO_3$ solution, into particulate and dissolved organic carbon. Whereas most measurements focussed on the ^{14}C incorporated into particles retained in filters, as originally proposed Steeman-Nielsen (1952), the technique also allows the measurement of total organic carbon (TOC) production (i.e. ^{14}C incorporated into DOC and POC), from measurements of the ^{14}C activity in the water sample. This requires use of high $NaH^{14}CO_3$ activity to the sample. This method has the advantage that allows to differentiate photosynthetic carbon retained into dissolved and particulate fractions, although most (> 90%) of estimates refer to particular production alone, and allows precise estimates to be derived over short time intervals (Table 1.1). However, it is also subject to bottle effects and can also underestimate primary production as it does not include any organic carbon produced along the experiment that has been respired by the algae or by the heterotrophic community after being released to the dissolved phase (Table 1.1).

Table 1.1. Summary of the main characteristics, advantages and limitations of different approaches to measure planktonic primary production.

References	Method	Definition	Measurement	Advantages	Disadvantages
Carpenter (1965)	Winkler method	Analysis for dissolved oxygen changes over 24 h	Net Community Production (NCP) Community Respiration (CR)	Accuracy (0.1% precision) Calculate Gross Primary Production (GPP = NCP + CR)	Bottle effect Assumes that dark respiration equals light respiration
Steeman (1952)	^{14}C method	Photosynthetic incorporation of organic carbon into particulate and dissolved fraction	Dissolved Organic Carbon (DOC) Particulate Organic Caron (POC) Total Organic Carbon (TOC)	Differentiate particulate and dissolved fractions	Bottle effect Misses remineralised production
Slawyk et al. (1977)	^{13}C method	Photosynthetic incorporation of organic carbon into particulate and dissolved fraction	Dissolved Organic Carbon (DOC) Particulate Organic Caron (POC) Total Organic Carbon (TOC)	Differentiate particulate and dissolved fractions Avoid to use radioisotope	Bottle effect Misses remineralised production
Grande et al. (1982)	^{18}O method	Photosynthetic release of ^{18}O from $H_2{}^{18}O$ during daytime	Gross Primary Production (GPP)	Direct measurement of GPP Allows calculation of respiration in the light	Bottle effect
Luz et al. (2000)	Triple isotope method	Estimate time-integrated rates of Community Respiration and Gross Primary Production	Gross Primary Production (GPP) Community Respiration (CR)	Measurement in situ Integrate measurement over weeks, month…	Prone to errors derived from gas exchange (30 % error) and of fractionation of photosynthetis and community respiration

Table 1.2. References, description of the location, number of stations and of estimates of the different studies analysed here measuring GPP rate by two different methods.

GPP Methods used	References	Location	Studied Location	Number of stations	Number of estimates
^{14}C and Winkler methods					
	Williams *et al*., 1983	Pacific Ocean	North Subtropical Pacific	5	5
	Moran *et al*., 2007	Atlantic Ocean	North Subtropical Atlantic	6	24
	Gonzalez *et al*., 2008	Mediterranean Sea	Western Mediterranean	8	32
	Regaudie-de-Gioux and Duarte, 2010; Lasternas *et al*., unpublished data	Arctic Ocean	Eastern Arctic	13	29
	Navarro *et al*., unpublished data	Southern Ocean	Antarctic Peninsula	6	21
	Regaudie-de-Gioux *et al*., unpublished data; Lasternas *et al*., unpublished data	Atlantic Ocean	North Subtropical Atlantic	8	8
	Regaudie-de-Gioux *et al*., unpublished data; Lasternas *et al*., unpublished data	Southern Ocean	Antarctic Peninsula	24	64
	Total			***70***	***183***
^{14}C and ^{18}O methods					
	Juranek and Quay, 2005	Pacific Ocean	North Subtropical Pacific	4	20
	Gonzalez *et al*., 2008	Mediterranean Sea	Western Mediterranean	8	32
	Total			***12***	***52***
Winkler and ^{18}O methods					
	Bender *et al*., 2000	Southern Ocean	Ross Sea	9	52
	Dickson *et al*., 2001	Southern Ocean	Antarctic Polar Front	14	78
	Gonzalez *et al*., 2008	Mediterranean Sea	Western Mediterranean	8	31
	Total			***31***	***161***

Three published studies have been found measuring primary production concurrently using ^{14}C and Winkler methods (Williams *et al*., 1983; Moran *et al*., 2007; González *et al*., 2008), which we complemented with our own unpublished data pertaining to four different cruises (Table 2.1). Three published studies measured primary production concurrently using ^{18}O and Winkler methods (Bender *et al*., 2000; Dickson *et al*., 2001; González *et al*., 2008), and two studies measured primary production concurrently using ^{14}C and ^{18}O methods (Juranek and Quay, 2005; González *et al*., 2008).

The relationship between paired primary production estimates derived using different methods was described using Model II (orthogonal regression), principal components regression analysis on log-transformed data, which was found necessary to address the problem of heteroscadicity affecting the untransformed relationships between variables.

Results

^{14}C-POC yielded the lowest estimate of primary production and was always much smaller than ^{14}C TOC production and than GPP-O_2 (Wilcoxon ranked sign test, $p < 0.0001$). The ratio of ^{14}C-TOC to ^{14}C-POC averaged 2.30 ± 0.12 (median, 1.99) and that of GPP-O_2 to ^{14}C-POC averaged 3.27 ± 0.37 (median, 2.15) (Table 3.1). ^{14}C-TOC was lower than GPP-$^{18}O_2$ estimates (Wilcoxon ranked sign test, $p < 0.0001$) and was higher than ^{14}C-DOC and ^{14}C-POC estimates (Wilcoxon ranked test, $p < 0.0001$). No consistent difference was observed between ^{14}C-TOC and GPP-O_2 estimates (Wilcoxon ranked test, $p = 0.388$). The ratio of GPP-O_2 to ^{14}C-TOC averaged 1.99 ± 0.24 (median, 1.18) and that of GPP-$^{18}O_2$ to ^{14}C-TOC averaged 2.68 ± 0.38 (median, 1.94) (Table 1.3). GPP-$^{18}O_2$ was higher than GPP-O_2 (Wilcoxon ranked test, $p = 0.0008$). The ratio of GPP-$^{18}O_2$ to GPP-O_2 averaged 1.40 ± 0.16 (median, 1.15, Table 1.3).

Table 1.3. Mean (± SE), median, minimum, maximum and number of observations (n) of the ratio between the production of total organic carbon (^{14}C-TOC) and particulate organic carbon (^{14}C-POC) and dissolved organic carbon (^{14}C-DOC), the production of oxygen measured by the Winkler method (GPP-O_2) or the ^{18}O method (GPP-^{18}O) and the consumption of carbon measured by the ^{14}C method (^{14}C-TOC or ^{14}C-POC), and finally of the ratio between the production of oxygen measured by the ^{18}O method (GPP-^{18}O) and measured by the Winkler method (GPP-O_2) of the planktonic community in the ocean.

	^{14}C-TOC/^{14}C-POC	**^{14}C-TOC/^{14}C-DOC**
Mean (± SE)	2.30 (± 0.12)	7.89 (± 3.28)
Median	1.99	2.01
Min.	1	1
Max.	8.34	376.43
n	117	117

	GPP-O_2 / ^{14}C-TOC	**GPP-^{18}O / ^{14}C-TOC**
Mean (± SE)	1.99 (± 0.24)	2.68 (± 0.38)
Median	1.18	1.94
Min.	0.02	0.36
Max.	28.2	15.57
n	157	52

	GPP-O_2 / ^{14}C-POC	**GPP-^{18}O / ^{14}C-POC**
Mean (± SE)	3.27 (± 0.37)	n.d.
Median	2.15	n.d.
Min.	0.16	n.d.
Max.	39.45	n.d.
n	141	

	GPP-^{18}O / GPP-O_2
Mean (± SE)	1.40 (± 0.16)
Median	1.15
Min.	0.05
Max.	25
n	161

All pairwise comparisons between methods resulted in significant correlations among methods, but these were much weaker than expected (Table 1.4). The differences observed for the primary production of method pairs were not consistent with sampling depth (t-test, $p > 0.05$). The slope describing the log-log relationship between ^{14}C-TOC and GPP-O_2 (Table 1.4, $R^2 = 0.50$, Fig. 1.1) differed significantly from 1 (t-test, $p < 0.05$), with measurements that showed considerable differences among them, particularly at low primary production.

Table 1.4. Principal component regression equations of the form log Y = a + b log X showing the relationship between estimates of primary production derived in parallel using different methods, along with the corresponding coefficient of determination (R^2) and the associated probability (p). On the table, the regression slope corresponds to b in the equation, and the intercept corresponds to 10^a.

	Slope (± SE)	Intercept (± SE)	R^2	p	n
^{14}C-TOC vs. GPP-O_2	1.11 (± 0.04)	0.75 (± 0.09)	0.5	< 0.0001	158
^{14}C-DOC vs. GPP-O_2	1.31 (± 0.10)	0.26 (± 0.05)	0.34	< 0.0001	118
^{14}C-POC vs. GPP-O_2	1.11 (± 0.06)	0.43 (± 0.05)	0.65	< 0.0001	141
^{14}C-TOC vs. GPP-^{18}O	0.87 (± 0.08)	0.50 (± 0.04)	0.55	< 0.0001	48
GPP-O_2 vs. GPP-^{18}O	0.86 (± 0.04)	1.07 (± 0.06)	0.66	< 0.0001	161

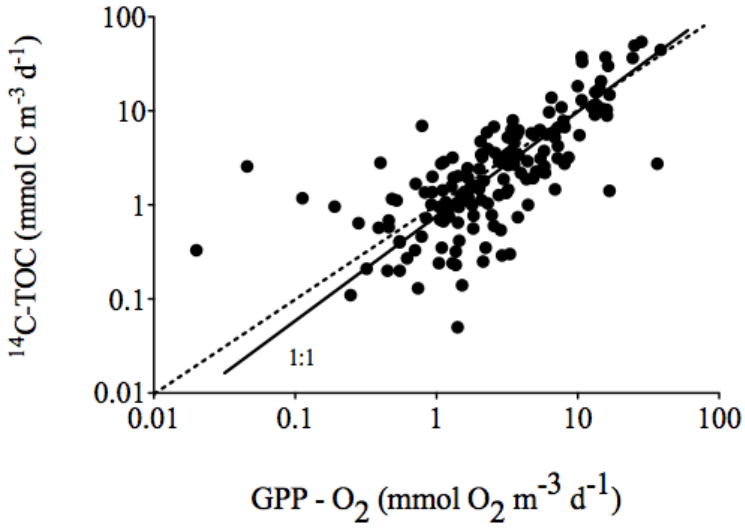

Figure 1.1. Relationship between the daily ^{14}C- TOC (mmol C m^{-3} d^{-1}) and the GPP-O_2 measured by the Winkler method (mmol O_2 m^{-3} d^{-1}). The dashed line represents the 1:1 line. The solid line represents the log-log regression (see details of equations parameters in table 1.4).

^{14}C-POC and ^{14}C-DOC were correlated with GPP-O_2 although the relationship with ^{14}C-POC (Table 1.4, Fig. 1.2, R^2 = 0.65) was stronger than that with ^{14}C-DOC (Table 1.4, Fig. 1.2, R^2 = 0.34). The slope describing the log-log relationship between ^{14}C-DOC vs. GPP-O_2 was significantly greater than 1 (t-test, $p < 0.05$), contrary to the slope

log-log ^{14}C-POC vs. GPP-O_2 (t-test, $p > 0.05$). ^{14}C-TOC and GPP-^{18}O-based primary production rates were significantly correlated ($R^2 = 0.55$, Fig. 1.3) with a slope not significantly different from 1 (t-test, $p > 0.05$, Table 1.4) and GPP-O_2 and GPP-^{18}O-based primary production showed a log-log relationship (Table 1.4, Fig. 1.4, $R^2 = 0.66$) with a slope significantly different less than 1 (t-test, $p < 0.05$).

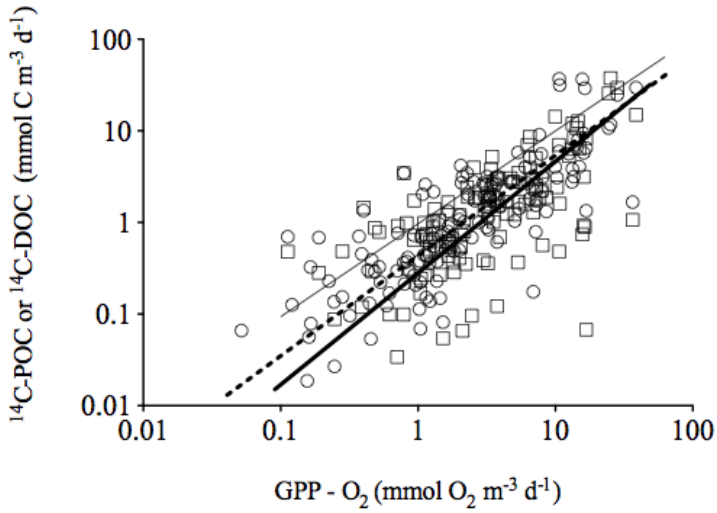

Figure 1.2. Relationships between the daily ^{14}C-POC (open circles) and ^{14}C-DOC (open squares) (mmol C m^{-3} d^{-1}) and the GPP-O_2 measured by the Winkler method (mmol O_2 m^{-3} d^{-1}). The solid and the dashed line represents the log-log regressions (see details of equations parameters in table 4). The thin line represents the 1:1 line.

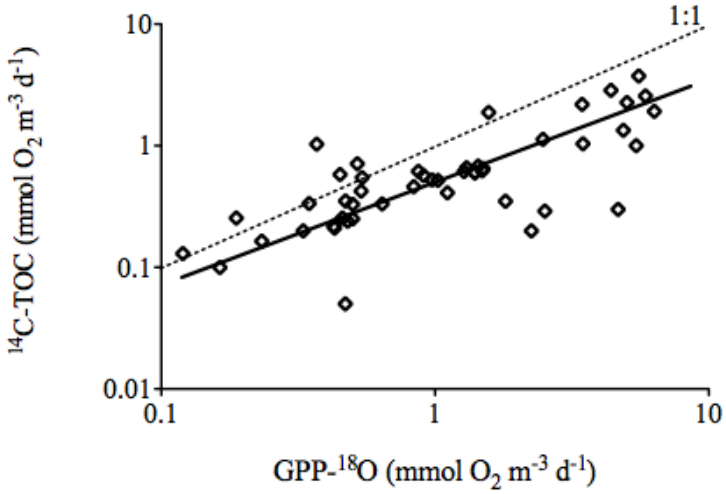

Figure 1.3. Relationships between the daily ^{14}C- TOC (mmol C m^{-3} d^{-1}) and the GPP-^{18}O (mmol O_2 m^{-3} d^{-1}). Solid line represents the log-log regression (see details of equations parameters in table 1.4).

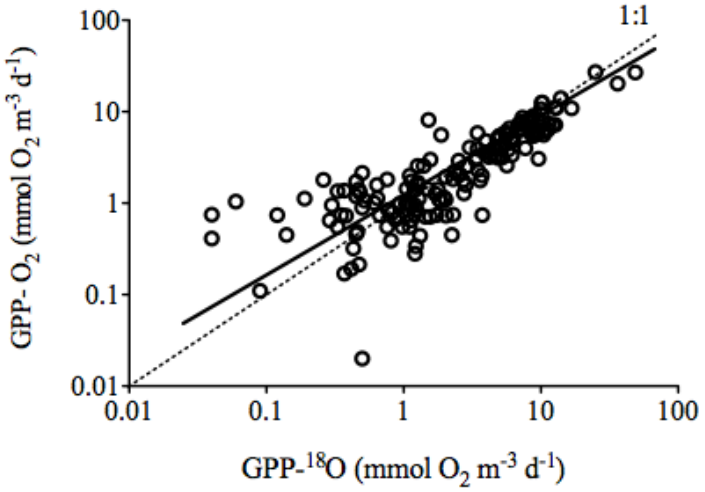

Figure 1.4. Relationships between the GPP-O_2 by the Winkler method (mmol O_2 m^{-3} d^{-1}), and the GPP-^{18}O (mmol O_2 m^{-3} d^{-1}). Solid line represents the log-log regression (see details of equations parameters in table 1.4). Dashed line represents the 1:1 line.

Discussion

For most of published reports, the primary production measured by the ^{14}C method was lower than the gross production measured by oxygen-based methods (e.g. Winkler and ^{18}O method). ^{14}C incorporation into particulate matter, the method most widely used to measure primary production yields the lowest estimates, more than 3 times lower than those derived by the bulk O_2 method. This large difference is due to the fact that the ^{14}C incorporation into particulate matter does not account for DOC release nor respiratory losses by the autotrophs themselves (Bender *et al*., 1987). Thus, ^{14}C incorporation into particulate matter has been argued to measure net primary production (i.e. NCP = GPP – DOC release – Autotroph respiration). This is, however, not entirely correct, as some of the DOC released may have been incorporated into particulate material, which will then be included in the estimate. The measurement of ^{14}C incorporation into total organic matter partially overcomes this problem by accounting for the ^{14}C recovered in the DOC pool, which can be substantial (González *et al*., 2008). Yet, this estimate of primary production fails sort of accounting for respiratory losses, both by autotrophs and respiratory use of primary production released as DOC (Bender *et al*., 1987). Oxygen-based estimates are believe to derive estimates closely approaching gross primary production (González *et al*., 2008), and Peterson *et al*. (1980) reported that ^{14}C method underestimated GPP rates about a factor

of 2 to 100. Indeed, the results obtained here indicate that, on average, ^{14}C-TOC significantly underestimate GPP by 2 (bulk oxygen) to 2.60 (^{18}O) fold, in contrast to the conclusion by Williams *et al*. (1983), Bender *et al*. (1987) and González *et al*. (2008), derived from much smaller data sets than that compiled here, that the estimates of primary production derived by ^{14}C-TOC were not significantly different from those derived using the O_2 method.

Our results confirm that the highest primary production estimates are derived using the ^{18}O method, which best approaches gross primary production. These results are consistent with those of Grande *et al*. (1989), who showed that the ^{18}O content of the dissolved oxygen pool increased with photosynthesis and is 2 to 3 times larger than the pool of POC labelled by the ^{14}C. Juranek *et al*. (2005) observed that the GPP-^{18}O rates were 1.5 to 2 times higher than ^{14}C-TOC rates. Grande *et al*. (1989) indicated that the difference between ^{14}C-TOC and GPP-^{18}O rates was due to respiratory ^{14}C losses by both autotrophs and heterotrophs. Accordingly, GPP-^{18}O rates were significantly higher than ^{14}C-TOC rates, as well as GPP-O_2 rates. Bender *et al*. (1987) and Grande *et al*. (1989) argued that the GPP-O_2 measured by the Winkler method underestimates gross production because respiration in the light tends to exceed that in the dark, whereas the GPP-O_2 method assumed dark and light respiration to be equal. The observation here that GPP-^{18}O rates tend to exceed GPP-O_2 rates measured with the dark and light bottle method by 40 ± 16 % provides an estimate of the excess community respiration in the light relative to that in the dark. Respiration in the light was calculated, following Grande *et al*. (1989), at a mean value of 2.65 ± 0.25 mmol O_2 m^{-3} d^{-1} (median 1.74 ± 0.31 mmol O_2 m^{-3} d^{-1}) in the estimates in the data base compiled here, significantly higher than respiration in the dark for the same communities, estimated to average 1.81 ± 0.13 mmol O_2 m^{-3} d^{-1}. These results are in agreement with findings by Dickson and Orchado (2001) and Bender *et al*. (2000), but differ from those Marra and Barber (2004) and González *et al*. (2008), which did not find significant differences in their, more limited, data sets.

The ratios between different metrics of primary production derived here can be used to derive rules of thumb to convert estimates derived with different methods, thereby providing a basis for comparison. The conversion factors, scaled to as the most commonly used metric of primary production, are 6.1 GPP-^{18}O : 3.27 GPP-O_2 : 2.3 ^{14}C-TOC : 1 ^{14}C-POC. Hence, there is a 6.1-fold difference between primary production estimates derived from ^{14}C incorporation into POC, which derive the lowest

estimates, and those provided by the ^{18}O method, which yields the best approximation to gross primary production. However, the fact that different methods are scaled to each other with powers different than 1, indicates that the conversion factors are dependent on the level of primary production and that the log-log regression equations provided here should yield more robust conversions among different metrics of primary production. For instance, GPP-O_2 production is scaled as the 1.30 power of estimates derived using ^{14}C-POC. This indicates, that the difference between ^{14}C-POC and GPP-O_2 estimates is greatest in communities with low production rates. This is consistent with evidence that the proportion of TOC production released as DOC is highest in communities supporting low production rates (Morán *et al*., 2002; Teira *et al*., 2001). Likewise GPP-O_2 is scaled as the 0.86 power of GPP-^{18}O rates, suggesting that the difference between production estimates derived using GPP-O_2 and GPP-^{18}O increases with increasing primary production. Indeed, Steeman-Nielsen (1975) argued that photorespiration is correlated with the internal O_2 concentration, which is highest at high protosynthetic rates, thereby accounting for the increased difference between GPP-O_2 and GPP-^{18}O estimates with increasing primary production.

The results presented here shows broad, six-fold differences between estimate of primary production derived using different methods, and provide conversion factors and regression equations to interconvert and compare results derived using different methods. These results also confirm that the ^{18}O method should be the method of choice when estimates of total carbon flux by primary production (i.e. gross primary production) or community respiration are sought. However, net community production can only be estimated using the bulk O_2 approach with clear-bottle incubations. Whereas estimates of ^{14}C incorporation into POC yield the lowest estimates, these estimates can still be informative when the interest resides in evaluating biomass production. Those estimates can be of interest to evaluate, for instance, ceilings to fisheries production, but use of these estimates to resolve ecosystem carbon budgets, which require accounting for total carbon flux, can lead to major errors.

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References

Behrenfeld MJ, Falkowski PG (1997) A consumer's guide to phytoplankton primary productivity models. Limnol Oceanogr 42(7): 1479-1491

Bender ML, Dickson ML, Orchardo J (2000) Net and gross production in the Ross sea as determined by incubation experiments and dissolved O_2 studies. Deep Sea Res Pt II 47: 3141-3158

Bender ML, Grande K, Johnson K, Marra J, Williams PJLeB, Sieburth J, Pilson M, Langdon C, Hitchcock G, Orchardo J, Hunt C, Donaghay P, Heinemann K (1987) A comparison of four methods for determining planktonic community production. Limnol Oceanogr 32(5): 1085-1098

Carpenter JH (1965) The accuracy of the Winkler method for dissolved oxygen analysis. Limnol Oceanogr 10: 135-140

Carrit DE, Carpenter JH (1966) Comparison and evaluation of currently employed modifications of the Winkler method for determining dissolved oxygen in sea-water. J Mar Res 24: 286-318

Cole JJ, Findlay S, Pace ML (1988) Bacterial production in fresh and saltwater ecosystems: a cross-system overview. Mar Ecol Prog Ser 43: 1-10

del Giorgio PA, Williams PJLeB. (Ed.) Respiration in aquatic ecosystems. Oxford University Press, p. 328

Dickson MJ, Orchado J, Barber RT, Marra J, McCarthy JJ, Sambrotto RN (2001) Production and respiration rates in the Arabian Sea during the 1995 Northeast and Southwest Monsoons. Deep Sea Res Pt II 48: 1199-1230

Dring MJ, Jewson DH (1982) What does ^{14}C uptake by phytoplankton really measure? A theoretical modelling approach. Roy S Publish 214(1196): 351-368

Duarte CM, Agustí S, Kennedy H, Vaqué D (1999) The Mediterranean climate as a template for Mediterranean marine ecosystems: the example of the northeast Spanish littoral *Prog Oceanogr 44:* 245-270

Falkowski PG, Barber RT, Smetacek V (1998) Biogeochemical controls and feedbacks on ocean primary production. Science 281, doi:10.1116/science.281.5374.200

Field CB, Behrenfeld MJ, Randerson JT, Falwoski P (1998) Primary production of the biosphere: Integrating terrestrial and oceanic components. Science 281: 237 doi: 10.1126/science.281.5374.237

Gaarder T, Gran HH (1927) Production of plankton in Oslo Fjord. Rapp Cons Explor Mer Vol. XLII

Gazeau F, Middelburg JJ, Loijens M, Vanderbroght J-P, Pizay M-D, Gattuso J-P (2007) Planktonic primary production in estuaries: comparison of ^{14}C, O_2 and ^{18}O methods. Aquat Microb Ecol 46: 95-106

González N, Gattuso J-P, Middelburg JJ (2008) Oxygen production and carbon fixation in oligotrophic coastal bays and the relationship with gross and net primary production. Aquat Microb Ecol 52: 119-130

Grande KD, Wiliiams PJleB, Marra J, Purdie DA, Heinemann K, Eppley RW, Bender ML (1989) Primary production in the North Pacific gyre: a comparison of rates determined by the ^{14}C, O_2 concentration and ^{18}O methods. Deep Sea Res 36(11): 1621-1634

Grande KD, Kroopnick P, Burns D, Bender ML (1982) ^{18}O as a tracer for measuring gross primary production in bottle experiments. Eos.

Juranek LW, Quay PD (2005) In vitro and in situ gross primary and net community production in the North Pacific Subtropical Gyre using labelled and natural abundance isotopes of dissolved. Global Biogeoch Cy 19: 1-15

Kirk JTO (1994) Light and photosynthesis in aquatic ecosystems, 2nd ed., 528 pp., Cambridge Univ. Press

Luz B, Barkan E (2000) Assessment of oceanic productivity with the triple-isotope composition of dissolved oxygen. Science 288: 2028-2031

Marra J, Barber RT (2004) Phytoplankton and heterotrophic respiration in the surface layer of the ocean. Geophys Res Letter 31: L09314

Morán XAG, Pérez V, Fernández E (2007) Mismatch between community respiration and the contribution of heterotrophic bacteria in the NE Atlantic open ocean: What causes high respiration in oligotrophic waters? J Mar Res 65: 545-560

Morán XAG, Estrada M, Gasol JM, Pedrós-Alió C (2002) Disolved primary production and the strength of phytoplankton-bacterioplankton coupling in contrasting marine regions. Microb Ecol 44: 217-223

Mortimer CH (1956) The oxygen contento f air-saturated fresh waters, and aids in calculating percentage saturation. Intern Assoc Theoret Appl Limnol Común 6

Peterson BJ (1980) Aquatic primary production and the ^{14}C-CO_2 method: a history of the productivity problem. Annu Rev Ecol Syst 11: 359-385

Richards FA, Corwin N (1956) Some oceanographic applications of recent determinations of the solubility of oxygen in sea water. Limnol Oceanog 1: 263-267

Robinson C, Williams PJLeB (2005) Respiration and its measurement in surface marine waters. In: del Giorgio PA, Williams PJLeB (Ed.), Respiration in aquatic ecosystems. Oxford University Press, p. 328

Ryther JH (1969) Photosynthesis and fish production in the sea. Science 166(3901): 72-76

Slawyk G, Collos Y, Auclair J-C (1977) The use of the ^{13}C and ^{15}N isotopes for the simultaneous measurement of carbon and nitrogen turnover rates in marine phytoplankton. Limnol Oceanogr 22(5): 925-932

Steeman Nielsen E (1952) The use of radioactive carbon (^{14}C) for measuring production in the sea. J Cons Perm int Explor Mer 18: 117-140

Steeman Nielsen E (1975) Marine photosynthesis. Elsev Oceanogr Series, 141 pp

Tappan H (1968) Primary production, isotopes, extinctions and the atmosphere. Palaeogeogr Palaeoecl 4(3), 187-210

Teira E, Pazó MJ, Serret P, Fernández E (2001) Disolved organic carbon production by microbial populations in the Atlantic Ocean. Limnol Oceanog 46(6): 1370-1377

Truesdale GA, Downing AL, Lowden GF (1955) The solubility of oxygen in pure water and sea-water. J Appl Chem London 5: 53-62

Williams PJleB, Heinemann KR, Marra J, Purdie DA (1983) Comparison of ^{14}C and O_2 measurements of phytoplankton production in oligotorphic waters. Nature 305: 49-50

Chapter 2

Thresholds of gross primary production for the metabolic balance of marine planktonic communities

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Abstract

The notion that less productive marine planktonic communities tend to be heterotrophic was tested by synthesizing reported estimates of the relationships between the net community production or community respiration and gross primary production (GPP), allowing calculation of the threshold GPP separating less productive, heterotrophic communities from more productive, autotrophic ones. A total of 35 estimates of the threshold GPP were assembled, derived from reports of comparative analyses of individual regions (Mediterranean Sea, Atlantic Ocean, Southern Ocean, Pacific Ocean, and Indian Ocean) and global comparative analyses for open-ocean and coastal environments, time-series analyses of changes in planktonic metabolism at individual locations, experimental manipulations in mesocosms, and a semi-empirical modelling exercise.

Planktonic communities of the open ocean and continental shelf showed threshold GPP values ranging 30-fold, from 0.34 mmol O_2 m^{-3} d^{-1} to 9.45 mmol O_2 m^{-3} d^{-1}, with those for estuarine and coastal locations reaching 50.60 mmol O_2 m^{-3} d^{-1}. Antarctic and ultra-oligotrophic ecosystems showed the lowest threshold GPP values (< 2.2 mmol O_2 m^{-3} d^{-1}), with a general consistency across approaches for a given ecosystem. Plankton community respiration in the absence of or under low primary production is not negligible and is supported by semi-labile dissolved organic carbon. The analysis of GPP thresholds suggests that allochthonous organic inputs to the less productive regions of the ocean must be in the order of 5–6 mmol O_2 m^{-3} d^{-1}, consistent with recent estimates of allochthonous inputs of organic carbon to the ocean.

Introduction

The metabolic balance of marine communities, the balance between their rates of autotrophic production of organic matter (gross primary production, GPP) and their respiratory remineralization (community respiration, R), is a key property determining net community production (NCP = GPP - R) of the communities. NCP affects the function and role of marine communities in material fluxes (Odum, 1956). Autotrophic communities (GPP > R, NCP < 0) act as sinks of CO_2 and inorganic nutrients and sources of organic matter and O_2. Conversely, heterotrophic communities (GPP < R, NCP < 0) act as sources of CO_2 and inorganic nutrients and sinks of organic matter and O_2.

Early depictions of the metabolic balance of aquatic ecosystems assumed the ocean to be in close metabolic balance, being marginally autotrophic (Odum, 1956) to support carbon burial and fisheries yield. This perception has dominated views of oceanographers for decades (Williams, 1998), to become implicit in consensus depictions of the ocean carbon (Prentice *et al*., 2001). However, recent reports of net heterotrophic community metabolism (i.e., NCP < 0) of planktonic communities studied in various regions of the ocean, including the subtropical Atlantic (Duarte *et al*., 2001; González *et al*., 2001; Harrison *et al*. 2001), the subtropical N. Pacific (Williams *et al*., 2004), and the Southern Ocean (Agustí *et al*., 2004), have revealed a wider prevalence of heterotrophic communities in the ocean than previously considered, particularly in the least productive oceanic regions (Duarte and Prairie, 2005). A comparative analysis of aquatic community metabolism conducted a decade ago (Duarte and Agustí, 1998) concluded volumetric oceanic respiration rates to be scaled as the half-power of GPP (i.e., $R \sim GPP^{0.5}$), implying that highly productive communities tend to be autotrophic whereas the least productive ones tend to be heterotrophic. Duarte and Agustí (1998) inferred a threshold GPP of 1.09 mmol O_2 m^{-3} d^{-1} separating less productive, heterotrophic oceanic planktonic communities from more productive, autotrophic planktonic communities. However, these inferences, apparently in conflict with parallel claims of a widespread close metabolic balance in marine communities and proportionate scaling of R to GPP (i.e., $R \sim GPP^{1}$; Williams, 1998), were argued to be the result of artifacts resulting from the use of Model I regression analysis and volumetric, instead of areally integrated, rates (Williams and Bower, 1999). The ensuing debate has not yet delivered a clear consensus on this issue (cf., del Giorgio and Duarte, 2002; Karl *et al*., 2003; Duarte and Prairie, 2005). However, it has stimulated much-needed research to expand the meagre (Williams and del Giorgio, 2005) empirical basis upon which these debates were originally based (Duarte *et al*., 1999; Williams and Bower, 1999; del Giorgio and Duarte, 2002). The number of analyses of the relationship between R and GPP in marine ecosystems, including regional surveys (Duarte *et al*., 2001; Serret *et al*., 2002; Agustí *et al*., 2004), time-series analyses (Duarte *et al*., 2004; Navarro *et al*., 2004; Williams and Duarte, 2004), experimental tests (Duarte *et al*., 2004; Agustí and Duarte 2005; Olsen *et al*., 2006), and modelling analyses (López-Urrutia *et al*., 2006), and a global data base of published marine planktonic GPP and R estimates (Robinson and Williams, 2005), has increased greatly in response to this debate. This enhanced empirical basis provides a new test of the

existence, magnitude and generality of the threshold GPP separating less productive, heterotrophic marine planktonic communities from more productive, autotrophic planktonic communities.

Here we conduct such reassessment, on the basis of a review of existing literature and the analysis of unpublished data sets on marine planktonic GPP and R, and provide a discussion of possible explanations for the existence of such threshold GPP for planktonic metabolic balance. Following Duarte and Agustí (1998), when referring to planktonic communities, we use the term 'less productive' as equivalent to 'heterotrophic' and 'more productive' as equivalent to 'autotrophic' throughout the manuscript. This analysis provides a first thorough compilation of estimates of the threshold GPP for planktonic metabolic balance in the ocean, allowing the discussion of the consistency of the estimates derived using different approaches and identifying patterns in the variability of these thresholds across regions. Using recent estimates of the magnitude of allochthonous organic carbon inputs, we then focus on the processes supporting plankton community respiration in the absence of or under low primary production and test the proposed role of allochthonous organic carbon inputs in supporting net heterotrophy.

Methods

We reviewed the published literature along with unpublished data sources for estimates of the threshold GPP separating heterotrophic from autotrophic marine planktonic communities, or estimates of volumetric GPP and R of marine planktonic communities allowing the calculation of this threshold. The majority of the reports used the clear–dark bottle method, along with O_2 determinations using high-precision automatic titration to estimate planktonic GPP and R. One of the reports (Hendricks *et al*., 2004) used the triple-oxygen technique, which examines the relative abundance of O^{18}, O^{16}, and O^{17} in the mixed layer, relative to the isotopic partitioning expected under a photosynthetic vs. atmospheric oxygen source, to infer GPP and NCP across the water column without the need for incubations (Luz and Barkan, 2000). Carbon units were converted to oxygen units using respiratory and photosynthetic quotients of 1, because the small deviations these ratios may exhibit are negligible relative to the range of variability of the threshold values.

The threshold GPP for metabolic balance was only directly reported for nine of the 35 studies in Table 2.1. We calculated the threshold GPP for those studies that did

not report it and recalculated them for those studies that reported it using Type I regression model. The threshold GPP for metabolic balance (GPP = R) was calculated by solving for NCP = 0 in the regression equation describing net community production (NCP) as a function of GPP (27 regression equations), solving for P/R = 1 in the linear relationship between P/R and GPP (3 regression equations), or solving for GPP = R in relationships between R and GPP (5 regression equations), depending on the data reported (Table 2.1). All regression equations were fitted using Type II, principal components, regression analysis as recommended by Williams and Bower (1999). X and Y variables were log-transformed when necessary to comply with the assumptions of linear regression analysis (three out of 35 regression equations). The intercepts and slopes of the fitted regression equations, along with their standard errors, from which the threshold GPP values are calculated, and the corresponding R^2, are reported in Table 2.1.

Results

A total of 35 estimates of the threshold GPP separating heterotrophic from autotrophic marine planktonic communities were assembled, deriving from comparative analyses of individual regions (Mediterranean Sea, Atlantic Ocean, Southern Ocean, Pacific Ocean, Arctic Ocean, and Indian Ocean) and global synthesis for the open ocean (Duarte and Agustí, 1998; Robinson and Williams, 2005) and coastal and estuarine environments (Duarte and Agustí, 1998); time-series analyses of changes in planktonic metabolism across time scales longer than annual at individual locations; experimental manipulations, using large-volume (> 10,000 m^3) mesocosm units aimed at generating a range of GPP (Duarte *et al*., 2004; Agustí and Duarte, 2005; Olsen *et al*., 2006), and testing the effects of deep-water entrainment on surface-water metabolism (McAndrew *et al*., 2007); and a semi-empirical model (López-Urrutia *et al*., 2006), based on the combination of size-structure and metabolic theory to derive Atlantic planktonic metabolism (Table 2.1).

Table 2.1. Estimates of the threshold gross primary production separating heterotrophic from autotrophic planktonic communities derived from cross-comparative synthesis studies, time-series, experimental and modelling studies. GPP = gross primary production; NCP = net community production; R = community respiration; ns = not statistically significant (see text). Threshold GPP and intercept are expressed in mmol O_2 m^{-3} d^{-1}. (this table corresponds to the erratum submitted)

Approach and Region	Y vs. X	Intercept	SE	Slope	SE	R^2 adj	Threshold GPP (mmol O_2 m^{-3} d^{-1})	Reference
Comparative analyses								
NW Indian Ocean	NCP vs. GPP	-3.18	0.33	0.76	0.06	0.83	4.20	Robinson and Williams (1999)
Subtropical Atlantic Gyre	log GPP/R vs. Log GPP	0.99	1.22	1.14	0.16	0.65	1.01	González et al. (2001)
Subtropical NE Atlantic	logGPP/R vs. logGPP	0.67	0.06	1.22	0.97	0.53	1.39	Duarte et al. (2001)
N. Atlantic	NCP vs. GPP	-2.56	0.27	1.24	0.10	0.24	2.06	González et al. (2002)
North Sea	NCP vs. GPP	-4.06	0.49	1.22	0.15	0.52	3.32	Robinson et al. (2002a)
Subtropical E Atlantic	NCP vs. GPP	-3.34	0.45	0.94	0.04	0.94	3.56	Robinson et al. (2002b)
Eastern N. Atlantic	NCP vs. GPP	-1.83	0.19	0.87	0.04	0.79	2.10	Serret et al. (2002)
N. Atlantic	NCP vs. GPP	-1.91	0.15	0.98	0.02	0.98	1.94	Arístegui and Harrison (2002)
Subtropical NE Atlantic	NCP vs. GPP	-1.16	0.26	0.80	0.06	0.63	1.45	Navarro et al. (unpubl. data)
Subtropical Atlantic	NCP vs. GPP	-3.32	0.32	2.02	0.22	0.21	1.65	Agustí (unpubl. data)
Subtropical NE Atlantic	NCP vs. GPP	-0.63	0.04	0.99	0.01	0.99	0.63	Regaudie-de-Gioux (unpubl. Data)
N. Atlantic	NCP vs. GPP	-2.06	0.38	0.73	0.05	0.76	2.83	Kiddon et al. (1995)
SW Atlantic coast	NCP vs. GPP	-1.50	0.80	0.83	0.04	0.89	1.81	Schloss et al. (2007)
Southern Ocean	NCP vs. GPP	-1.94	0.25	0.88	0.02	0.92	2.20	Agustí et al. (2004)
Southern Ocean	NCP vs. GPP	-0.45	0.13	0.46	0.05	0.82	0.97	Odate et al. (2002)
Southern Ocean	NCP vs. GPP	-0.74	0.21	0.94	0.03	0.96	0.78	Navarro et al. (unpubl. data)
Southern Ocean*	NCP vs. GPP	-0.13	0.06	0.15	0.02	0.31	0.89	Hendricks et al. (2004)
Southern Ocean[ns,†]	NCP vs. GPP	-0.27	1.09	0.59	0.07	0.67	0.46	Arístegui et al. (1996)
Arctic Ocean	NCP vs. GPP	-7.11	1.06	1.30	0.13	0.38	5.45	Regaudie-de-Gioux and Duarte -2010
Subtropical N. Pacific	NCP vs. GPP	-1.14	0.33	1.37	0.35	0.16	0.83	Williams and Purdie (1991)
NW Mediterranean Sea	NCP vs. GPP	-1.29	0.18	0.67	0.04	0.73	1.93	Lefevre et al. (1997) DSRII
Mediterranean Sea	NCP vs. GPP	-9.67	1.61	1.65	0.30	0.43	5.86	Vaquer-Sunyer et al. (see Regaudie-de-Gioux et al. 2009))
Mediterranean Sea	NCP vs. GPP	-3.16	0.41	1.59	0.23	0.29	1.99	Regaudie-de-Gioux et al. (2009)
European coast	NCP vs. GPP	-6.24	0.58	1.08	0.04	0.83	5.76	Gattuso (unpub. data)
Global Coastal	log R vs log GPP	0.46		0.72	0.04	0.60	50.60	Duarte and Agustí (1998)
Global	log R vs log GPP	0.05	0.04	0.50		0.42	1.09	Duarte and Agustí (1998)
Global‡	log R vs log GPP	0.04		0.62		0.46	1.27	Robinson and Williams (2005)
Time series								
Subtropical N. Pacific	NCP vs. GPP	-0.56	0.05	0.66	0.08	0.23	0.84	Williams et al. (2004)
Blanes Bay (Mediterranean)	NCP vs. GPP	-7.43	0.40	2.12	0.11	0.00	3.51	Duarte et al. (2004)
Palma Bay (Mediterranean)	NCP vs. GPP	-3.80	0.91	0.96	0.20	0.41	3.97	Navarro et al. (2004)
Experiments								
Mediterranean coast	NCP vs. GPP	-3.81		0.92	0.00	0.99	4.14	Duarte et al. (2004)
European coast§	R vs. GPP	2.62	0.00	0.39	0.04	0.82	4.25	Olsen et al. (2006)
Southern Ocean	R vs GPP	1.26		0.59	0.07	0.90	3.07	Agustí and Duarte (2005)
North Pacific	NCP vs. GPP	-1.98	0.84	0.84	0.05	0.97	2.34	MacAndrew et al. (2007)
Modelling								
Atlantic Ocean||	lnR vs. Ln GPP	0.79		0.74		0.67	0.41	López-Urrutia et al. (2006)

*Based on the triple oxygen isotope technique. Areal rates were converted to volumetric using a 50 m mixed layer depth.

† Primary production from 14C.

‡ Includes records 1-3,5-9,16-19.

§ Based on inverse modelling.

|| Based on Size spectra combined with allometric and metabolic theory to estimate GPP and R.

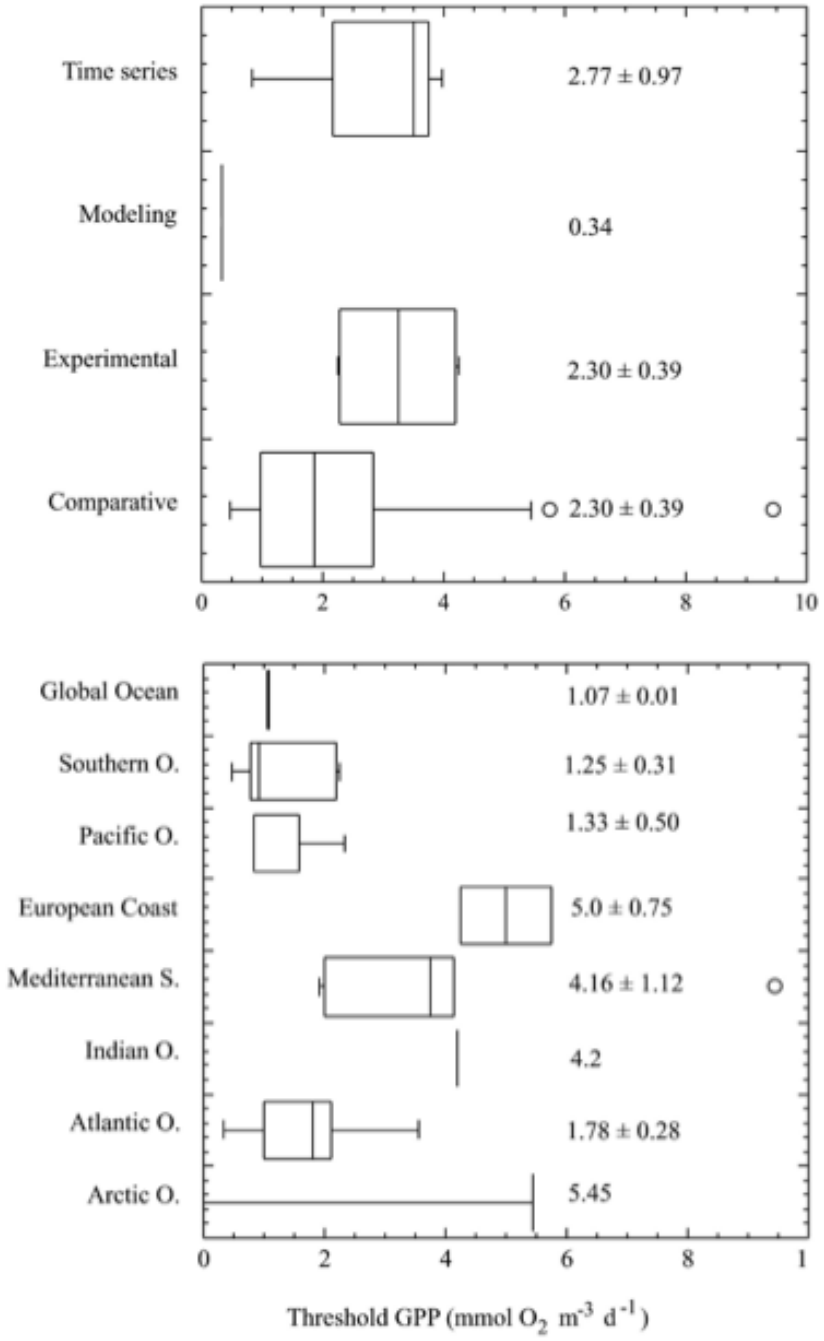

Figure 2.1. Box-plots showing the distribution of GPP thresholds for metabolic balance of planktonic communities depending on the method of assessment and the region from where the data were derived. The lines extend to range, the box extends from the 25th to the 75th percentile and the central line represents the median (50th percentile). Open circles identify outliers. When only one observation was available a vertical line is shown to indicate the corresponding value.

A significant threshold GPP separating heterotrophic from autotrophic marine planktonic communities was present in all except two of the reports, where the estimated thresholds were not significantly different from zero (t-test, df = 14 and 22, $p > 0.05$; Table 2.1). Whereas comparative analyses of planktonic metabolism in coastal and estuarine systems revealed very high thresholds of 50.60 mmol O_2 m^{-3} d^{-1} (Duarte and Agustí, 1998; Table 2.1; Fig. 2.1), all other empirical studies, pertaining to communities in the open-ocean and continental shelf showed small threshold GPP values with a 20-fold variation (Table 2.1) between the lowest threshold (0.45 mmol O_2 m^{-3} d^{-1}, reported for the subtropical NE Atlantic; Duarte *et al*., 2001) and the highest thresholds (9.45 mmol O_2 m^{-3} d^{-1}, reported for the Mediterranean Sea; R. Vaquer-Sunyer, unpubl.). The mean GPP threshold values derived from different approaches, including regional comparative studies, time series and experimental studies were very similar at ~ 2.3– 2.8 mmol O_2 m^{-3} d^{-1} (Table 2.1; Fig. 2.1) and did not differ significantly (t-test, df = 27, 3 and 4, respectively, $p > 0.05$) from one another.

The experimental assessments yielded somewhat higher GPP threshold estimates (Fig. 2.1), probably attributable to the fact that these were all conducted in coastal locations, where GPP threshold values tend to be higher than in open-ocean waters. The estimate of threshold GPP for Atlantic planktonic communities derived from modelling analysis (López-Urrutia *et al*., 2006) is the lowest of all 35 estimates compiled (Table 2.1; Fig. 2.1). The modelling approach used by López-Urrutia *et al*., (2006) carries considerable uncertainty because it is a semi-empirical approach that calculates organism-specific respiration and photosynthesis rates from water temperature and cell size and then integrates these estimates for the community, using experimentally determined size spectra of the planktonic communities, to derive community R and production, which was calibrated using ^{14}C incorporation into particles, which underestimates GPP. Although López-Urrutia *et al*., (2006) do not provide an assessment of error about their estimate, inspection of their calibration between measured and modelled R and P shows that the error involved is 3-fold for both these estimates. Hence, provided the uncertainties involved in the model construction (López-Urrutia *et al*., 2006) and the fact that modelled P should underestimate GPP, it is unlikely that this estimate be different from the value of 1.07 mmol O_2 m^{-3} d^{-1} indicated by the global comparative analysis. There was substantial variability in the threshold GPP for metabolic balance within basins (Table 2.1; Fig. 2.1), because estimates for the Atlantic Ocean, (the basin with most available estimates), ranged over 6-fold among

studies, possibly reflecting the compound effect of spatial and temporal differences in the metabolism of the communities. The European Coast showed the highest mean GPP threshold values, followed by the Indian Ocean, and the Arctic Ocean and the Mediterranean Sea, both semi-enclosed basins receiving substantial land-derived inputs (Fig. 2.1). The Atlantic Ocean, the Southern Ocean, and, particularly, the Pacific Ocean showed the lowest mean GPP threshold values (Fig. 2.1). Indeed, the GPP threshold estimate from the oligotrophic ALOHA (A Long-Term Habitat Assessment) time-series station in the subtropical Pacific was almost four-fold lower than those of time-series analysis in more productive coastal Mediterranean locations (Table 2.1). The two global syntheses of comparative analyses of open-ocean metabolism (Duarte and Agustí, 1998; Robinson and Williams, 2005) yielded remarkably similar estimates of the threshold GPP (1.06 mmol O_2 m^{-3} d^{-1} and 1.09 mmol O_2 m^{-3} d^{-1}, respectively; Table 2.1; Fig. 2.1).

Discussion

The meta-analysis reported here provides compelling evidence for the existence of a threshold GPP below which planktonic communities tend to be heterotrophic, because the earlier suggestion of Duarte and Agustí (1998) has been validated on the basis of multiple, independent comparative analyses, time-series analysis, and modelling exercises. Moreover, the existence of a threshold GPP for community metabolism is unlikely to derive from artifacts introduced by a particular approach, because it has been detected using standard light–dark bottle incubations, inverse solution analysis using mass balance considerations to improve the estimates of R and GPP, triple-oxygen isotope fields, and size-based metabolic models (Table 2.1). Two objections were initially raised to the inference of Duarte and Agustí (1998) of a threshold GPP of 1.09 mmol O_2 m^{-3} d^{-1} separating less productive, heterotrophic oceanic planktonic communities from more productive, autotrophic ones, that the result was a consequence of the choice of Type-I regression analysis, and that it was also a result of the use of volumetric rather than areally integrated metabolic rates by Williams and Bower (1999). The estimates reported here have been all derived using Type-II regression analysis, and thresholds of GPP below which planktonic communities tend to be heterotrophic have been since reported for areally integrated data as well (e.g., 94 mmol O_2 m^{-3} d^{-1} for the subtropical NE Atlantic, Duarte *et al.*, 2001; 500 mmol O_2 m^{-3} d^{-1} for estuaries, Hopkinson and Smith, 2005). Indeed, a regression analysis of NCP on GPP of the areally integrated data reported by Williams (1998) also suggests a threshold

GPP at 80.4 mmol O_2 m^{-3} d^{-1}. Indeed, the existence of a threshold GPP below which planktonic communities tend to be heterotrophic can be argued by considering what would be the respiration rate of an ideal planktonic community shaded, in a mental experiment, in a parcel of the ocean as to drive GPP to zero. The respiration rate will be expected to decline rapidly, as labile DOC is used up by bacteria, to proceed at a slow rate for months supported by semi-labile DOC (Carlson *et al*., 2004). In fact an analogue to this mental experiment, the long-term confinement of plankton communities in the dark, is the experimental approach used to operationally define and infer the size of the pools of labile and semi-labile dissolved organic carbon (DOC; Hopkinson *et al*., 2002). Additional evidence is derived from the observation that winter planktonic respiration is greater than zero in dark polar waters where there is no GPP (Sherr and Sherr, 2003). Provided R is not expected to be zero in the absence of GPP, the existence of a threshold GPP below which communities tend to be heterotrophic (i.e., R > GPP) is a given, the problem rests in elucidating the magnitude of the GPP required to balance planktonic metabolism. Whereas much of bacteria respiration, a major source of planktonic respiration in the ocean (Robinson and Williams, 2005), is sustained by freshly produced, labile organic carbon, there is an underlying, baseline respiration rate supported by the use of semi-labile DOC (Carlson *et al*., 2004). This semi-labile DOC is not necessarily produced locally, because it has ^{14}C ages spanning over decades (Bauer *et al*., 1992), over which the DOC must have been transported far away from the location where it was originated; therefore, its use represents use of organic carbon produced elsewhere in the ocean, thus allochthonous to the community actually using it. The background respiration rate at low GPP is, thus, expected to correspond to the background respiration sustained by semi-labile DOC in the ocean, which has been reported to be ~ 3 – 5 mmol C m^{-3} d^{-1} (Carlson *et al*., 2004), comparable to the threshold GPP estimates (Table 2.1; Fig. 2.1). Another set of drivers of the GPP threshold for metabolic balance is composed of the processes affecting the GPP : R ratio through effects on carbon use by primary producers. For instance, the fraction of gross primary production that may be available for bacterial respiration may be higher in less productive waters. Indeed, comparative analyses of the DOC release by phytoplankton show that the percent of the extracellular primary production release increases as primary production decreases (Teira *et al*., 2001; Hessen and Anderson, 2008). Hence, less productive planktonic communities are likely to support lower GPP : R ratios, because a higher proportion of primary production maybe readily available to be

respired, which will be conducive to higher GPP thresholds for metabolic balance. In addition, exposure to intense Light fields may lead to enhanced photorespiration by autotrophs (Raven and Beardall, 2005; Hessen and Anderson, 2008) and, as a consequence, a reduced GPP : R ratio, conductive to higher GPP thresholds for metabolic balance. High DOC release and high respiration by autotrophs, conducive to higher GPP thresholds for metabolic balance, are also more likely under nutrient limitation and hence, in oligotrophic, less productive systems, where organic carbon is produced in excess relative to nutrient availability (Hessen and Anderson, 2008). The examination of the partitioning of planktonic biomass between autotrophs and heterotrophs also supports the arguments provided here. A broad comparative analysis of the relationship between autotrophic biomass and heterotrophic biomass in marine planktonic communities (Gasol *et al*., 1997) showed that oligotrophic planktonic communities tend to support a higher heterotrophic biomass per unit autotrophic biomass than more productive ones, consistent with the high respiration relative to gross primary production expected at low GPP.

This analysis concluded that the dominant role of heterotrophs in the structure of oligotrophic planktonic systems should be reflected in a dominance of the carbon flow by heterotrophs therein (Gasol *et al*., 1997), consistent with arguments that less productive communities should be net-heterotrophic, supporting an excess community respiration over gross primary production at low GPP, resulting in the threshold GPP for metabolic balance reviewed here. The existence of a threshold GPP separating less productive, heterotrophic oceanic planktonic communities from more productive, autotrophic planktonic communities has been interpreted as evidence that less productive ocean communities often tend to be heterotrophic (Duarte and Agustí, 1998; Duarte *et al*., 2001; Duarte and Prairie, 2005). This assertion has proved controversial (Duarte *et al*., 1999; Williams and Bower, 1999; Karl *et al*., 2003), because it is indeed paradoxical that these less productive planktonic communities, claimed to be net heterotrophic, still export organic matter. Indeed, heterotrophic planktonic metabolism requires that excess respiration, which can be estimated as the threshold GPP (i.e., ~ 1–3 mmol C m^{-2} d^{-1}, on average, for open-ocean communities; Table 2.1; Fig. 2.1), and the organic carbon export (OC_{export}, mmol C m^{-2} d^{-1}), which in less productive communities reaches ~ 4 mmol C m^{-2} d^{-1} considering both particulate and dissolved export (Arístegui *et al*., 2005), be subsidized by inputs of allochthonous organic carbon (AOC_{input}, mmol C m^{-2} d^{-1}). Hence, the allochthonous organic inputs to the less productive regions of the

ocean, approximated as $AOC_{input} = GPP_{threshold} + OC_{export}$, must be in the order of 5–6 mmol C m^{-2} d^{-1} in order to support heterotrophic communities in less productive regions of the ocean. The role of allochthonous inputs in subsiding heterotrophy in less productive regions has been argued from the onset of the debate on the metabolic balance of the ocean (Duarte and Agustí, 1998; Williams and Bower, 1999; del Giorgio and Duarte, 2002). However, these arguments were speculative because no estimates of allochthonous carbon inputs to the open ocean were then available. The only component of allochthonous carbon inputs that has been considered in depictions of the global oceanic carbon cycle is that provided by lateral inputs from land and coastal regions, which a number of studies estimating organic carbon export estimate at ~ 3 Gmol C yr^{-1} per km of shelf break (Bauer *et al*., 2001; Hung *et al*., 2003; Dittmar *et al*., 2006). However, direct atmospheric organic carbon inputs to the ocean can be important. For instance, for the NE subtropical Atlantic Ocean, Dachs *et al*. (2005) and Duarte *et al*. (2006) reported organic carbon inputs with dry aerosol deposition to average 1 mmol C m^{-2} d^{-1} and that have been calculated to deliver 245 Tg C annually to the ocean (Jurado *et al*., 2008), and Dachs *et al*. (2005) reported a large air–sea exchange of volatile organic carbon, which could sustain an input of ~ 25–31 mmol C m^{-2} d^{-1} to the NE subtropical Atlantic Ocean. This high atmospheric organic carbon input is likely to represent upper values for the ocean, because the NE subtropical Atlantic is an area supporting particularly high atmospheric inputs (Jickels *et al*., 2005), but even input rates six-fold lower than those reported for the subtropical NE Atlantic will suffice to meet the required 5–6 mmol C m^{-2} d^{-1} required to simultaneously support excess respiration and organic carbon export in less productive regions of the ocean. These considerations suggest that allochthonous organic carbon inputs to the ocean may suffice to explain the apparent paradox of heterotrophic communities in the presence of organic carbon export in less productive regions of the ocean, a suggestion that must be measured against a sufficient empirical base yet to be developed. Hence, field estimates of GPP and NCP based on O_2 are not unrealistic and can be reconciled with biogeochemical mass balances once atmospheric inputs of organic carbon are considered. The metabolic threshold GPP values vary considerably, by a factor of 30, among individual studies of open-ocean communities. Some of this variability may represent uncertainties in the estimation of this threshold value in the presence of low rates, near the detection limit of metabolic methods. However, this variability may also be informative of differences across systems. For instance, a cross-comparative survey

of metabolism in coastal waters (Duarte and Agustí, 1998) point at a threshold GPP value about a factor of 10 or higher in these environments compared to open-ocean waters (Table 2.1), consistent with the high threshold value of 500 mmol C m^{-2} d^{-1} reported for whole-system metabolism of estuaries by Hopkinson and Smith (2005). These high-threshold GPP are consistent with the rationale that a minimum threshold GPP is set by the extent of allochthnous inputs, because estuarine waters receive large amounts of allochthonous carbon materials (Hopkinson and Smith, 2005). The reported threshold values for the Southern Ocean tend to be particularly low (Table 2.1), consistent with the absence of riverine inputs and with low atmospheric inputs there. Among the time-series studies, the threshold GPP inferred for the ALOHA station at the N. subtropical Pacific, the most oligotrophic area for which threshold GPP values have been inferred (Williams *et al*., 2004), showed a threshold GPP value 3–4-fold lower than those derived for oligotrophic coastal Mediterranean locations, but identical to that derived from cross comparative analysis at the same region (Table 2.1). In addition to allochthonous inputs, climate may also affect threshold GPP. The modelling analysis by López- Urrutia *et al.*, (2006), based on predictions derived from metabolic theory about temperature effects on respiration and photosynthesis rates, concluded that threshold GPP depends strongly on ambient temperature and is expected to increase from 1 mmol O_2 m^{-3} d^{-1} in cold environments to 4 mmol O_2 m^{-3} d^{-1} at temperatures of 15 ºC, encompassing the range observed here for open-ocean systems. Indeed, respiration rates are more sensitive than photosynthetic rates to temperature increase (Harris *et al*., 2006). A warming by 4 ºC is likely to be reached over the present century, expected to directly lead to a 16 % decrease in P : R ratios, and a corresponding increase in threshold GPP (Harris et al., 2006). These predictions await experimental confirmation, but suggest that climatic variability across the ocean and over time may be partially responsible for variability in threshold GPP estimates. These predictions suggest that the forecasted ocean warming is likely to elevate the threshold GPP for metabolic balance and, therefore, the extent of heterotrophic regions in the ocean.

In summary, the synthesis of threshold GPP estimates compiled here provides compelling evidence for existence of a threshold GPP of, on average, 1–3 mmol O_2 m^{-3} d^{-1} for open-ocean planktonic communities, separating less productive, heterotrophic communities from autotrophic ones. Allochthonous inputs of organic matter to the ocean appear sufficient to account for heterotrophy and concurrent downward organic carbon export in these heterotrophic regions of the ocean.

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References

Agustí S, Duarte CM (2005) Threshold of gross primary production for planktonic metabolic balance in the Southern Ocean: An experimental test. Limnol Oceanogr 50: 1334–1339

Agustí S, Satta MP, Mura MP (2004) Summer community respiration and pelagic metabolism in upper surface Antarctic waters. Aquat Microb Ecol 35: 197–205

Arístegui J, Agustí S, Middelburg JJ, Duarte CM (2005) Respiration in the mesopelagic and bathypelagic zones of the oceans. In del Giorgio PA and Williams PJleB (ed), Respiration in aquatic ecosystems, Oxford Univ Press, pp 181–205

Arístegui J, Harrison WG (2002) Decoupling of primary production and community respiration in the ocean: Implications for regional carbon studies. Aquat Microb Ecol 29: 199–209

Arístegui J, Montero MF, Ballesteros S, Basterretxea G, Van Lenning K (1996) Planktonic primary production and microbial respiration measured by ^{14}C assimilation and dissolved oxygen changes in coastal waters of the Antarctic Peninsula during the austral summer: Implications for carbon flux studies. Mar Ecol Prog Ser 132: 191–201

Bauer JE, Druffel ERM, Wolgast DM, Griffin S (2001) Sources and cycling of dissolved and particulate organic radiocarbon in the northwest Atlantic continental margin. Glob Biogeochem Cycles 15: 615–636

Bauer JE, Williams PM, Druffel ERM (1992) ^{14}C activity of dissolved organic carbon fractions in the northcentral Pacific and Sargasso Sea. Nature 357: 667–670

Carlson CA, Giovannoni SJ, Hansell DA, Goldberg SJ, Parsons R, Vergin K (2004) Interactions among dissolved organic carbon, microbial processes, and community structure in the mesopelagic zone of the northwestern Sargasso Sea. Limnol Oceanogr 49: 1073– 1083.

Dachs J, Calleja ML, Duarte CM, del Vento S, Turpin B, Polidori A, Herndl GJ, Agustí S (2005) High atmosphere–ocean exchange of organic carbon in the NE subtropical Atlantic. Geophys Res Lett 32: L21807, doi:10.1029/2005GL023799

del Giorgio PA, Duarte CM (2002) Respiration in the open ocean. Nature 420: 379–384

Dittmar T, Hertkorn N, Kattner G, Lara RJ (2006) Mangroves, a major source of dissolved organic carbon to the oceans. Glob Biogeochem Cycles 20: GB1012, doi:10.1029/ 2005GB002570

Duarte C, Agustí S (1998) The CO_2 balance of unproductive aquatic ecosystems. Science 281: 234–236

Duarte CM, Agustí S, del Giorgio PA, Cole JJ (1999) Regional carbon imbalances in the oceans. Science 284: 1735b

Duarte CM, Agustí S, Vaqué D (2004) Controls on planktonic metabolism in the Bay of Blanes, north-western Mediterranean littoral. Limnol Oceanogr 49: 2162–2170

Duarte CM, Arístegui J, González N, Agustí S, Anadón R (2001) Evidence for a heterotrophic subtropical NE Atlantic. Limnol Oceanogr 46: 425–428

Duarte CM, Dachs J, Llabrés M, Gasol JM, Tovar-Sánchez A, Sañudo-Wilhemy S, Agustí S (2006) Aerosol inputs enhance new production in the subtropical northeast Atlantic. J Geophys Res 111: G04006, doi:10.1029/2005JG000140

Duarte CM, Prairie YT (2005) Prevalence of heterotrophy and atmospheric CO_2 emissions from aquatic ecosystems. Ecosystems 8: 862–870

Gasol JM, del Giorgio PD, Duarte CM (1997) Biomass distribution in marine planktonic communities. Limnol Oceanogr 42: 1353–1363

Gonzaléz N, Anadon R, Marañón E (2002) Large-scale variability of planktonic net community metabolism in the Atlantic Ocean: Importance of temporal changes in oligotrophic subtropical waters. Mar Ecol Prog Ser 333: 21–30

Gonzaléz N, Anadon R, Mouriño B, Fernández E, Sinha B, Escánez J, De Armas D (2001) The metabolic balance of the planktonic community at the N. Atlantic Subtropiucal Gyre: The role of mesoscale instabilities. Limnol Oceanogr 46: 946–952

Harris LA Duarte CM, Nixon SW (2006) Allometric laws and prediction in estuarine and coastal ecology. Estuar Coasts 29: 340–344

Harrison WG, Arístegui J, Head EJH, Li WKW, Longhurst AR, Sameoto DD (2001) Basin-scale variability in plankton biomass and community metabolism in the subtropical North Atlantic Ocean. Deep-Sea Res II 48: 2241–2269

Hendricks MB, Bender ML, Barnett BA (2004) Net and gross O_2 production in the southern ocean from measurements of biological O_2 saturation and its triple isotope composition. Deep-Sea Res I 51: 1541–1561

Hessen, Anderson TR (2008) Excess carbon in aquatic organisms and ecosystems: Physiological, ecological, and evolutionary implications. Limnol Oceanogr 53: 1685–1696

Hopkinson Jr CS, Smith EM (2005) Estuarine respiration: An overview of benthic, pelagic and whole system respiration. In del Giorgio PA, Williams PJLeB (ed), Respiration in aquatic ecosystems. Oxford Univ Press pp 123–147

Hopkinson Jr CS, Vallino JJ, Nolin A (2002) Decomposition of dissolved organic matter from the continental margin. Deep- Sea Res II 49: 4461–4478

Hung J-J, Chen CH, Gong GC, Sheu D-D, Shiah FK (2003) Distribution, stoichiometric patterns and cross shelf exports of dissolved organic matter in the East China Sea. Deep-Sea Res II 50: 1127–1145

Jickells TD, An ZS, Andersen KK, Baker AR, Bergametti G, Brooks N, Cao JJ, Boyd PW, Duce RA, Hunter KA, Kawahata H, Kubilay N, laRoche J, Liss PS, Mahowald N, Prospero JM, Ridwell AJ, Tegen I, Torres R (2005) Global iron connections between desert dust, ocean biogeochemistry, and climate. Science 308: 67–71

Jurado E, Dachs J, Duarte CM, Simó R (2008) Atmospheric deposition of organic and black carbon to the global ocean. Atmospheric Environment 42: 7931–7939

Karl DM, Laws EA, Morris P, Williams PJLeB, Emerson S (2003) Metabolic balance of the open sea. Nature 426: 32

Kiddon J, Bender ML, Marra J (1995) Production and respiration in the 1989 North Atlantic Spring bloom—an analysis of irradiance dependent changes. Deep-Sea Res I 42: 553–576

Lefèvre D, Minas HJ, Minas M, Robinson C, Williams PJLeB, Woodward EMS (1997) Review of gross community production, primary production, net community production and dark community respiration in the Gulf of Lions. Deep-Sea Res II 44: 801–832

López-Urrutia A, San Martín E, Harris RP, Irigoyen X (2006) Scaling the metabolic balance of the oceans. Proc Natl Acad Sci USA 103: 8739–8744

Luz B, Barkan E (2000) Assessment of oceanic productivity with the triple-isotope composition of dissolved oxygen. Science 288: 2028–2031

McAndrew PM, Björkam KM, Church MJ, Morris PJ, Jachowski N, Willians PJLeB, Karl DM (2007) Metabolic response of oligotrophic plankton communities to deep water nutrient enrichment. Mar Ecol Prog Ser 332: 63–75

Navarro N, Agustí S, Duarte CM (2004) Plankton metabolism and dissolved organic carbon use in the Bay of Palma, NW Mediterranean Sea. Aquat Microb Ecol 37: 47–54

Odate T, Furuya EK, Fukuchi EM (2002) Photosynthetic oxygen production and community respiration in the Indian sector of the Antarctic Ocean during austral summer. Polar Biol 25: 859–864

Odum HT (1956) Primary production in flowing waters. Limnol Oceanogr 1: 112–117

Olsen Y, Agustí S, Andersen T, Duarte CM, Gismervik I, Heiskanen A-S, Hoell E, Kuuppo P, Lignell R, Reinertsen H, Sommer U, Stibor H, Tamminen T (2006) A comparative study of responses in plankton food web structure and function in contrasting European coastal waters exposed to experimental nutrient addition. Limnol Oceanogr 51: 488–503

Prentice I, and others. 2001. The carbon cycle and atmospheric carbon dioxide. In Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Xiaosi D (ed), Climate change 2001. The scientific basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Intergovernmental Panel on Climate Change, pp 183-237

Raven JA, Beardall J (2005) Respiration in aquatic photolithotrophs, In del Giorgio PA and Williams PJLeB (ed), Respiration in aquatic ecosystems. Oxford Univ Press. pp 36–46

Robinson C, Williams PJLeB (1999) Plankton net community production and dark respiration in the Arabian Sea during September 1994. Deep-Sea Res II 46: 745–766

Robinson C, Serret P, Tilstone G, Teira E, Zubkov MV, Rees AP, Woodward EMS (2002a) Plankton respiration in the Eastern Atlantic Ocean. Deep-Sea Res I 49: 787–813

Robinson C, Widdicombe CE, Zubkov MV, Tarran GA, Miller AEJ, Rees AP (2002b) Plankton community respiration during a coccolithophore bloom. Deep-Sea Res II 49: 2929–2950

Robinson C, Williams PJLeB (2005) Respiration and its measurement in surface waters. In del Giorgio PA, Williams PJLeB (ed), Respiration in aquatic ecosystems. Oxford Univ Press. pp 147–180

Schloss IR, Ferreyra GA, Ferrario ME, Almandoz GO, Codina R, Bianchi AA, Balestrini CF, Ochoa HA, Ruiz Pino D, Poisson A (2007) Role of plankton communities in sea–air variations in pCO_2 in the SW Atlantic Ocean. Mar Ecol Prog Ser 332: 93–106

Serret P, Fernandez E, Robinson C (2002) Biogeographic differences in the net ecosystem metabolism of the open ocean. Ecology 83: 3225–3234

Sherr BF, Sherr EB (2003) Community respiration/ production and bacterial activity in the upper water column of the central Arctic Ocean. Deep-Sea Res I 50: 529–542

Teira E, Pazo MJ, Serret P, Fernández E (2001) Dissolved organic carbon production by microbial populations in the Atlantic Ocean. Limnol Oceanogr 46:1370–1377

Williams PJLeB, Purdie PA (1991) In vitro and in situ derived rates of gross production, net community production and respiration of oxygen in the oligotrophic subtropical gyre of the North Pacific Ocean. Deep-Sea Res I 38: 891–910

Williams PJLeB (1998) The balance of plankton respiration and photosynthesis in the open ocean. Nature 394: 55–57

Williams PJLeB, Bower DG (1999) Determination of organic carbon balance in the oceans from field observations—A reevaluation. Science 284: 1735a

Williams PJLeB, Morris PJ, Karl DM (2004) Net community production and metabolic balance at the oligotrophic ocean site, station ALOHA. Deep-Sea Res I 51: 1563–1578

Williams PJLeB, del Giorgio PA (2005) Respiration in aquatic ecosystems: History and background. In del Giorgio PA, Williams PJLeB (ed), Respiration in aquatic ecosystems. Oxford Univ Press pp 1–17

Chapter 3

Regional and global variability in the pelagic metabolism in the ocean

1 - Patterns in late spring planktonic metabolism in the Mediterranean Sea

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Abstract

Planktonic gross community production (GPP), net community production (NCP) and community respiration (CR) across the Mediterranean Sea was examined in two cruises, THRESHOLDS 2006 and 2007, each crossing the Mediterranean from West to East to test for consistent variation along this longitudinal gradient in late spring to early summer. GPP averaged 2.4 ± 0.4 mmol O_2 m^{-3} d^{-1}, CR averaged 3.8 ± 0.5 mmol O_2 m^{-3} d^{-1}, and NCP averaged – 0.8 ± 0.6 mmol O_2 m^{-3} d^{-1} across the studied sections, indicative of a tendency for a net heterotrophic metabolism in late spring to early summer, prevalent across studied sections of the Mediterranean Sea as reflected in 70 % of negative NCP estimates. The median P/R ratio was 0.6, also indicating a strong prevalence of heterotrophic communities (P/R < 1) along the studied sections of the Mediterranean Sea. The communities tended to be net heterotrophic (i.e. P/R < 1) at GPP less than 2.8 mmol O_2 m^{-3} d^{-1}. The Western Mediterranean tended to support a higher gross primary production and community respiration than the Eastern basin did, but these differences were not statistically significant (t-test, $p > 0.05$). The net heterotrophy of the studied sections of the Mediterranean Sea indicates that allochthonous carbon should be important to subsidise planktonic metabolism during the late spring.

Introduction

The Mediterranean Sea represents an anomaly in the world ocean because it ranks amongst the most oligotrophic areas of the world while receiving significant land-derived inputs of both natural and anthropogenic materials. The Mediterranean Sea receives nutrient inputs through atmospheric deposition across the entire basin, from riverine inputs (Martin *et al*., 1989; Bethoux and Gentili, 1999; Guerzoni *et al*., 1999), and from inputs with Atlantic water entering the Western basin. Hence, nutrient inputs are highest in the Western basin, which receives the largest riverine discharge (e.g. Rhône, France) compared to the eastern basin. Accordingly, the Mediterranean Sea has been reported to show a decreasing gradient in primary production from West to East, with primary production three times lower in the Eastern basin compared to the North-western basin (Turley, 1999). While nutrient inputs stimulate primary production, most of these inputs are accompanied by organic inputs as well, which may also stimulate planktonic respiration. Hence, it is unclear whether the reported gradient in primary production may lead to a similar west-east gradient in net community production. Yet,

whether a West-East gradient in net community production exists in the Mediterranean Sea has not yet been resolved, due to a paucity of reports on planktonic metabolism in the Mediterranean Sea, particularly on the Eastern basin, as the bulk of the data available derive from the Western basin, with a dominance of studies in coastal waters (Gulf of Lions, González *et al*., 2008, Lefèvre *et al*., 1997; Bay of Blanes, Duarte *et al*., 2004, Lucea *et al*., 2005; Alboran Sea, Van Wambeke *et al*., 2004; Majorca Island, González *et al*., 2008, Gazeau *et al*., 2005, Navarro *et al*., 2004). Moreover, the magnitude of gross primary production and community respiration and the possible correlation between these processes in the Mediterranean Sea remains poorly resolved. Yet, the metabolic balance of planktonic communities is a key determinant of their role in biogeochemical cycle and, particularly, the role of planktonic communities as CO_2 sinks or sources affecting the atmosphere-sea CO_2 transfer (Duarte and Prairie, 2005).
Here we evaluate gross community production (GPP) and community respiration (CR) across the Mediterranean Sea in late spring and test the hypothesis that planktonic metabolism varies consistently along the West to East gradient in the Mediterranean Sea. We do so on the basis of two cruises across the Mediterranean Sea, THRESHOLDS 2006 and 2007, each crossing the Mediterranean from West to East and back. The first cruise covered a section from Majorca Island (Spain), Western Mediterranean, to the Black Sea, returning to Majorca Island, in June 2006, and the second cruise covered a section from Majorca Island to Alexandria (Egypt), returning to Majorca Island, in May 2007 (Fig. 3.1.1).

Materials and Methods

The study was conducted on board of the Spanish R/V Garcia del Cid, involving two cruises: THRESHOLDS-2006 (04/06/2006 – 04/07/2006) and THRESHOLDS-2007 (06/05/2007 – 01/06/2007) occupying 36 and 23 stations, respectively. At each station, vertical profiles for temperature, salinity and fluorescence were taken with a Seabird CTD attached to a Rosette sampling system. The metabolism of the planktonic communities was measured in the THRESHOLDS-2006 and THRESHOLDS-2007 at 7 and 14 stations, respectively (Fig. 3.1.1).

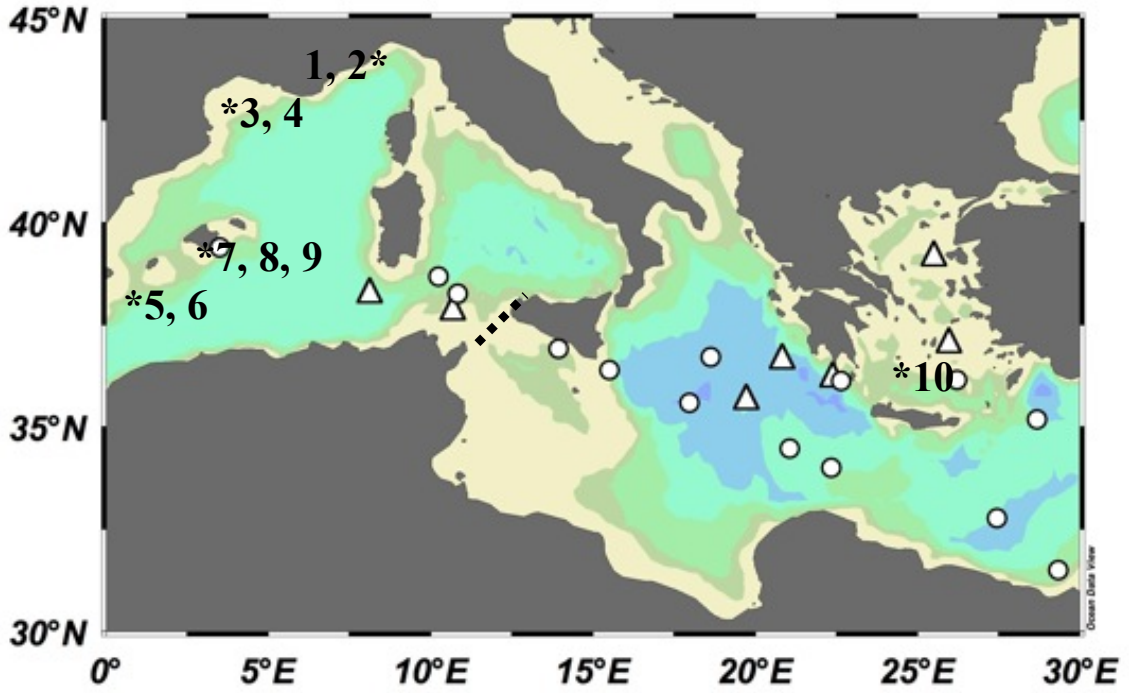

Figure 3.1.1. Distribution of the stations occupied for planktonic metabolism determinations during the THRESHOLDS-2006 (triangles) and THRESHOLDS-2007 (circles) cruises. The dotted line delimits the western and the eastern basin across the Sicily-Tunisia Strait (SIS). Also shown the location of previous studies of community metabolism, marked with asterisks (*) with the reference number of the studies shown in Table 3.1.3.

Community metabolism (gross primary production, community respiration and net community production) was determined from changes in oxygen over 24 h in water samples containing communities sampled from the surface layer (5 m), the Deep Chlorophyll Maximum (DCM, typically between 40 and 120 m), and at an intermediate depth (20 m or 50 m) at each station. Water samples collected from these depths using 10-L Niskin bottles attached to a Rosette sampler system were carefully siphoned into narrow-mouth Winkler bottles. The water samples were taken during the early morning and were protected by a dark screen to avoid exposure to solar irradiance before the onset of the incubation. The penetration of irradiance at depth was measured with a Satlantic™ OCP-100FF submarine irradiance profiler from surface to 100 m. The percent of the surface irradiance reaching to the different sampling depths was calculated and used to adjust the incubation irradiance for the "clear" bottles to that *in situ* using neutral density screens. Seven replicates were used to determine the initial oxygen concentration, and seven replicates bottles were incubated for 24 h in the "dark"

and in the "light". The Winkler bottles were incubated on deck at the water temperature corresponding to 5 m depth. The mean temperature difference observed between the surface layer and the DCM at the stations occupied was 3.8 ± 0.4 º C and the maximum difference was around 7.6 ºC. This difference may enhance somewhat metabolic rates of DCM samples when incubated at surface temperature. We calculated with the activation energy equation (Raven and Geider, 1988; López-Urrutia *et al*., 2006), Q_{10} values for R of 1.60 and NCP of 1.51, suggesting that the metabolic rates presented here for the DCM layer may be 10 % to 20 % higher, on average, than those at the *in situ* temperature for the Western and the Eastern basin, respectively. This is within the error of the estimates and, therefore, no correction was considered necessary.

Net community production (NCP) and community respiration were measured by monitoring oxygen concentration changes in the light and dark bottles along the incubation (Carpenter, 1965; Carritt and Carpenter, 1966). Oxygen concentrations were analysed by Winkler titration using a potentiometric electrode and automated endpoint detection (Mettler Toledo, DL28 titrator) (Oudot *et al*., 1988). CR and NCP were calculated from changes in dissolved oxygen concentration after incubation of samples under "dark" and "light" conditions, respectively and GPP was calculated by solving the mass balance equation GPP = NCP – CR. The integrated metabolism rates were calculated by the trapezoid method, from the surface layer to the DCM. Occasionally, metabolism experiments failed, yielding "negative" planktonic community respiration rates (i.e. oxygen in dark bottles higher than initial values at the end of the incubation). These estimates were not considered in the analysis. Therefore, the number of stations where GPP, NCP and CR rates have been presented here, are not exactly the same.

Samples of 200 ml for chlorophyll a determinations were filtered through Millipore GF/F filters (pressure < 0.3 kg cm^{-2}), frozen and then extracted for 24 hrs with 90 % acetone fluorometric determination (Turner Designs fluorometer) following Parsons *et al*. (1984).

Total bacterial abundance (BA) samples were determined by epifluorescence microscopy (Porter and Feig, 1980). Water subsamples of 4 and 10 ml were filtered through 0.2 μm polycarbonate black filters and stained with DAPI (4, 6-diamino-2 phenylindole) to a final concentration of 1 μg ml^{-1}. During the cruises, BA was determined by flow cytometry by FACSCalibur Flow Cytometer (Beckton Dickinson©) as described in Ortega-Retuerta *et al*. (2008).

Samples for dissolved organic carbon (DOC) concentration analyses were taken in duplicate by transferring a volume of 10 ml of sample into pre-combusted glass ampoules, which were then acidified with phosphoric acid to pH 2, heat sealed and preserved in the dark until analysis. At the laboratory, samples were analysed by High Catalytic Oxidation (HTOC) technique on a Shimadzu TOC 5000 analyser (for THRESHOLDS-2006 samples) and on a Shimadzu TOC 5050 analyser (for THRESHOLDS-2007 samples) (Benner and Strom, 1993). Standards provided by Dennis A. Hansell and Wenhao Chen (University of Miami, USA) of 2 μM and 45 μM TOC were used to assess the accuracy of the estimates.

Samples for nutrient (nitrate + nitrite, silicate and phosphate) analyses were collected at each depth and kept frozen until analyzed in a Bran Luebe AA3 autoanalyzer using standard methods (Hansen and Koroleff, 1999).

Volumetric metabolic rate estimates (GPP, CR and NCP) for the two different cruises were tested for normality and homogeneity of variances. GPP and NCP estimates were normally distributed ($p > 0.05$), in contrast with CR estimates, which deviated from normal distribution. Variances were homogeneous for GPP, CR and NCP estimates (Levene's test, $p < 0.05$). The Student t-test was used to compare variables distributed normally and the Kruskal-Wallis test was used to compare variables departing from normal distribution.

Results

Seawater temperature was relatively uniform across the Mediterranean, varying from 20 ºC to 23 ºC at 5 m depth, and from 10 ºC to 15 ºC at 100 m depth across the transects (data not shown). Chlorophyll a concentration was low, below 1.0 μg L^{-1} over the entire water column (5 to 200 m) across the studied section, except in the Balearic Sea, where chlorophyll a concentration increased up to 4.5 μg L^{-1} at 50 m depth during THRESHOLDS-2006 and up to 1.2 μg L^{-1} at 70 m depth in the Sicily-Tunisia Strait, during THRESHOLDS-2007 (Fig. 3.1.2). Total BA showed similar average values during THRESHOLDS 2006 ($5.9 \pm 1.1\ 10^5$ cell ml^{-1}) and THRESHOLDS 2007 ($5.0 \pm 0.3\ 10^5$ cell ml^{-1}, Table 3.1.1). BA showed higher values in the Eastern basin during THRESHOLDS 2006 ($7.6 \pm 1.2\ 10^5$ cell ml^{-1}) than during THRESHOLDS 2007 ($4.7 \pm 0.4\ 10^5$ cell ml^{-1}) and the opposite was observed in the Western basin, with BA higher during THRESHOLDS 2007 ($6.2 \pm 0.4\ 10^5$ cell ml^{-1}) than during THRESHOLDS 2006 ($2.4 \pm 1.3\ 10^5$ cell ml^{-1}).

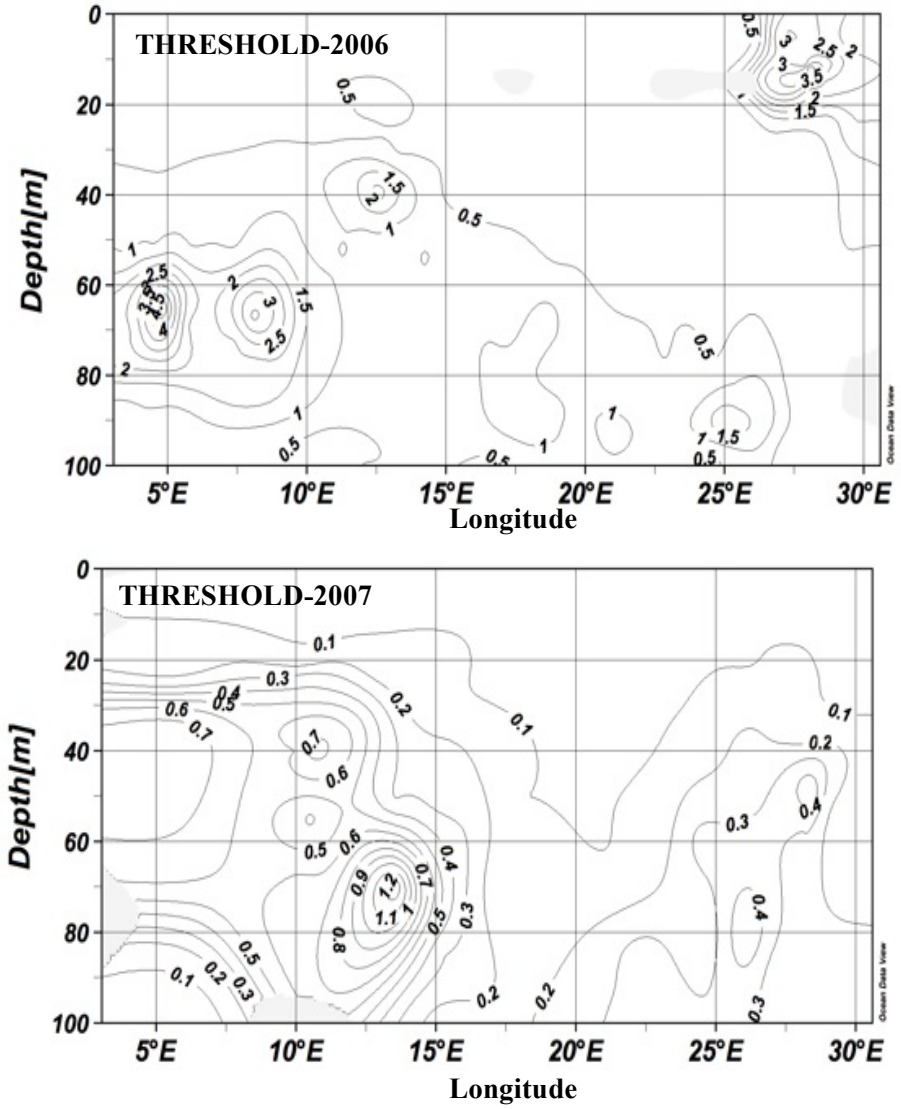

Figure 3.1.2. Chlorophyll a (mg m^{-3}) profiles across the Mediterranean Sea during the THRESHOLDS-2006 and THRESHOLDS-2007 cruises.

Nutrient concentrations were generally low (Table 3.1.1), particularly for phosphate, which was often below the detection limit (0.05 µmol P L^{-1}) of the analysis. Dissolved organic carbon ranged two fold within basins (Table 3.1.1), with DOC concentrations generally declining with depth. During THRESHOLDS 2006, seawater surface had an average DOC concentration of 120 µmol C L^{-1} and decreased to reach 50 µmol C L^{-1} at 100 m depth. A DOC concentration increase to 100 µmol C L^{-1} was observed at in Sicily Strait. During THRESHOLDS 2007, DOC concentrations showed an average of 100 µmol C L^{-1} above 50 m depth, and decreased with depth to a mean value of 75 µmol C L^{-1} at 100 m depth.

Table 3.1.1. Mean, SE, Range and number of estimates of volumetric gross primary production (GPP), community respiration (CR) and net community production (NCP) rates (mmol O_2 m^{-3} d^{-1}), DOC (Dissolved Organic Carbon, μmol C L^{-1}), nutrients concentrations (μmol L^{-1}) and bacterial abundance (10^5 cell ml^{-1}) in the western and eastern Mediterranean basins, during THRESHOLDS 2006 (1) and 2007 (2).

		Western Basin		Eastern Basin	
		1	2	1	2
	Mean	4.5	2.9	4.9	1.2
	SE	2.3	1.1	1.3	0.2
GPP	Minimun	2.1	0.6	1.1	0.1
	Maximum	9	8	15.1	2.9
	N	3	7	10	25
	Mean	6.4	6.2	4.8	2.4
	SE	3.4	2.3	0.8	0.4
CR	Minimun	2.4	0.6	0.9	0.1
	Maximum	13.1	16.9	8.9	8.2
	N	3	7	10	25
	Mean	-2.6	-2.7	0.22	-0.4
	SE	9.5	1.4	1.3	0.6
NCP	Minimun	-18.6	-8.9	-2.8	-6.4
	Maximum	11.1	1.4	11.8	8.1
	N	6	8	11	28
	Mean	76.9	84.3	88.6	78.9
	SE	8.2	4.8	5.9	2.2
DOC	Minimun	54	54.8	45	42.8
	Maximum	147	141.7	183	128.5
	N	13	18	34	66
	Mean	0.1	0.1	0.1	0.1
	SE	0	0	0	0
Phosphate	Minimun	0	0	0	0
	Maximum	0.13	0.2	0.2	0.2
	N	13	18	34	66
	Mean	0.6	1	0.7	0.8
	SE	0.1	0.2	0.1	0.1
Silicate	Minimun	0	0.3	0.2	0.1
	Maximum	1.7	3.3	1.4	4.1
	N	13	18	34	66
	Mean	0.8	1.1	0.5	0.7
	SE	0.3	0.4	0.1	0.1
Nitrite and Nitrate	Minimun	0	0.1	0	0.1
	Maximum	3.3	5.6	2.8	4.2
	N	13	18	34	66
	Mean	2.4	6.2	7.6	4.7
	SE	1.3	0.4	1.2	0.4
Bacterial Abundance	Minimun	0.2	5.2	4.7	0.5
	Maximum	6.2	8.5	16.6	11.1
	N	5	8	10	28

GPP averaged (± SE) 2.4 ± 0.4 mmol O_2 m^{-3} d^{-1} across the sections (Table 3.1.1) and remained below 10 mmol O_2 m^{-3} d^{-1} in the euphotic zone (Fig. 3.1.3), except for the subsurface maxima of the Aegean Sea (at 25.92 ºE) where GPP reached 15.1 mmol O_2 m^{-3} d^{-1}. GPP differed significantly between the THRESHOLDS 2006 and 2007 (t-test, p = 0.012) with higher rates observed in the THRESHOLDS 2006 cruise. GPP showed a diversity of vertical profiles, from lack of vertical structure to strong vertical heterogeneity with surface or deep maxima (Fig. 3.1.3). CR averaged 3.8 ± 0.5 mmol O_2 m^{-3} d^{-1} and also remained, for the majority of stations, below 10 mmol O_2 m^{-3} d^{-1} throughout the sections (Table 3.1.1). CR was significantly higher in THRESHOLDS 2006 than in THRESHOLDS 2007 (Kruskal-Wallis test, p = 0.031). CR also showed a diversity of vertical profile patterns across the stations, typically including a subsurface maximum (Fig. 3.1.3).

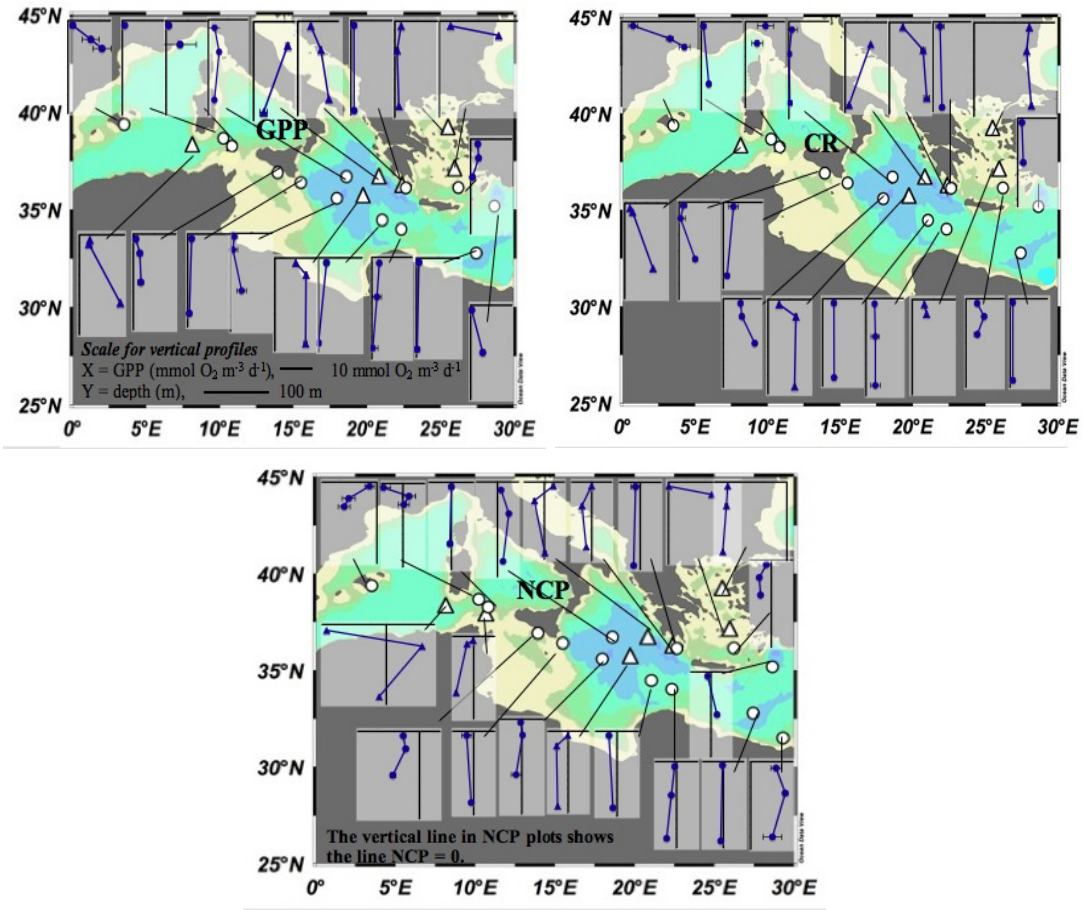

Figure 3.1.3. Vertical profiles of gross primary production (GPP, mmol O_2 m^{-3} d^{-1}), community respiration (CR, mmol O_2 m^{-3} d^{-1}) and net community production (NCP) (mmol O_2 m^{-3} d^{-1}) profiles at each station along the Mediterranean studies combined for the THRESHOLD-2006 (triangles) and 2007 (circles) cruises.

NCP averaged – 0.8 ± 0.6 mmol O_2 m^{-3} d^{-1} across the sections (Table 3.1.1) and showed contrasting vertical patterns (Fig. 3.1.3). NCP was similar between the THRESHOLDS 2006 and 2007 cruises and did not differ across the basins. NCP values were below 5 mmol O_2 m^{-3} d^{-1}, with a prevalence of negative values (70 % of the estimates) indicative of a prevalence of net heterotrophic communities during the two cruises. The median P/R ratio was 0.6 indicating also a strong prevalence of heterotrophic communities (P/R < 1) along the studied sections during late spring. The majority of the Mediterranean regions examined supported heterotrophic communities, except for the Ionian Sea with a P/R ratio of 1.35, where autotrophic communities prevailed. No significant relationships were observed between the metabolic rates (GPP, CR and NCP) and nutrient concentrations, DOC concentrations or bacterial abundance ($p > 0.05$).

The P/R ratio tended to increase significantly ($R^2 = 0.34$, $p < 0.05$) with increasing gross primary production (Fig. 3.1.4) implying that the studied communities tended to be net heterotrophic (i.e. P/R < 1) at low GPP and net autotrophic at high GPP. The volumetric GPP required for production to balance respiration (GPP at GPP = R) was 2.8 mmol O_2 m^{-3} d^{-1}, with the GPP threshold for the Western basin being more than 2-fold higher (GPP = 4.7 mmol O_2 m^{-3} d^{-1}) than that for the Eastern basin (GPP = 1.9 mmol O_2 m^{-3} d^{-1}).

Discussion

The two cruises presented here showed a broad range of planktonic metabolic rates across the Mediterranean. The volumetric GPP and CR, as well as the chlorophyll a concentration, were significantly higher during THRESHOLDS-2006 than THRESHOLDS-2007 (Kruskal-Wallis test, $p < 0.001$). Whereas GPP and NCP tended to be somewhat higher in the western compared to the eastern basin, these differences were not statistical significant, so no significant West-East gradient in planktonic metabolism was supported by our data.

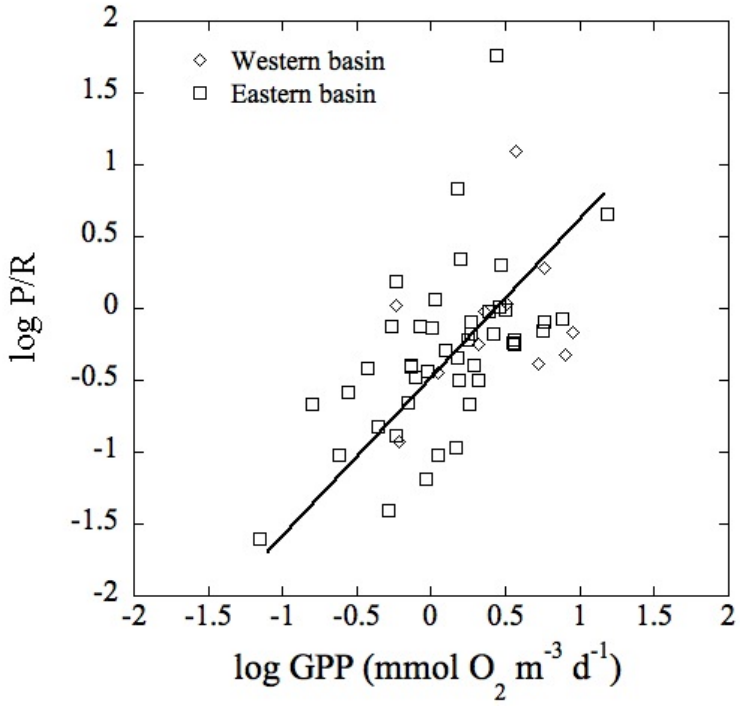

Figure 3.1.4. The relationship between log of gross primary production to community respiration ratio (P/R) and log of gross primary production (mmol O_2 m^{-3} d^{-1}) in the Western (diamonds) and Eastern (squares) basins of the Mediterranean Sea. The solid line shows the fitted linear regression model II equation (both basins): log P/R = 1.09 (± 0.12) log GPP - 0.48 (± 0.06) (R^2 = 0.34, $p < 0.0001$).

Planktonic communities across the studied sections during late spring tended to be heterotrophic, consistent with available reports of metabolic seasonality for the NW Mediterranean littoral (Duarte *et al*., 2004; Navarro *et al*., 2004; Satta *et al*., 1996). The prevalence of heterotrophic conditions during the studied period was consistent with the supersaturation in CO_2 of surface Mediterranean waters across the THRESHOLDS 2006 cruise (more than 20 stations), with the mean pCO_2 in surface waters exceeding atmospheric equilibrium by, on average, 40 ± 14 ppm (Vaquer-Sunyer, unpublished data). These data are in accordance with the data observed by D'Ortenzio et al. (2008) and Copin-Montégut *et al*. (2004) who showed surface Mediterranean seawaters to be supersaturated in pCO_2 during late spring-early summer. In contrast, the mean atmospheric pCO_2 during THRESHOLDS 2007 was 371 μatm (mean sea-air difference -18 ± 4 ppm, Álvarez, unpublished data), implying that the Mediterranean Sea acted as a sink for atmospheric CO_2, possibly a legacy from the late winter-early spring bloom preceding this cruise. Some published works reported the presence of late winter (February-March) phytoplankton blooms (Duarte *et al*., 2004; Navarro *et al*., 2004;

Agustí and Duarte, 2000; Lefèvre *et al*., 1997). Lefèvre *et al*. (1997) explained that in winter the Rhône River water moves rapidly westwards, providing fresh nutrients into the Gulf of Lion, and giving rise to a winter diatom bloom. Navarro *et al*. (2004) observed high values of GPP in February, coinciding with the late winter phytoplankton bloom when high chlorophyll a concentration was observed. Gazeau *et al*. (2005) observed also a phytoplankton bloom in March at Palma de Mallorca Bay. These observations, describing a late winter-early spring phytoplankton bloom, may account for the relatively low CO_2 values observed during THRESHOLDS 2007.

The P/R ratio tended to increase with increasing GPP (Fig. 3.1.4) indicating that the most productive areas, associated with the Sicily-Tunisia Strait separating the West and East basins, tend to support net autotrophic planktonic communities. Comparison of GPP rates between autotrophic (NCP > 0) and heterotrophic (NCP < 0) samples showed that the mean GPP tended to be higher, but not significantly so (t-test, $p > 0.05$), for autotrophic (GPP mean = 3.5 ± 1.1 mmol O_2 m^{-3} d^{-1}) than for heterotrophic (GPP mean = 2.2 ± 0.3 mmol O_2 m^{-3} d^{-1}) communities. However, there were significant differences (t-test, $p < 0.05$) in GPP between autotrophic and heterotrophic communities once the major differences in GPP among cruises were considered. Hence, planktonic communities tended to be net heterotrophic at low GPP and net autotrophic at high GPP within any one cruise.

Turley (2000) reported significant gradients between the western and the eastern basin in primary production (West to East ratio = 3.33, $p = 0.018$, t-test), bacterial production (West to East ratio = 1.87, $p = 0.029$) and bacterial growth rate (West to East ratio = 2.27, $p = 0.007$). Our data suggest a similar, but not significant ($p > 0.05$), trend across basins for GPP (West to East ratio = 1.37, t-test, $p = 0.68$) and for CR (West to East ratio = 1.74, t-test, $p = 0.37$), consistent with the enhanced bacterial abundance and activity in the Western basin reported by Turley (2000). Hence, NCP in the Western basin tended to be more negative than that in the Eastern Basin (Table 3.1.2). However, the important variability within basins rendered these differences in metabolic rates not statistically significant ($p = 0.88$, t-test). Although GPP seems to be enhanced in the less oligotrophic Western basin relative to the Eastern basin, CR is increased as well as riverine inputs are accompanied by important loads of organic matter (Lefèvre *et al*., 1997; Moutin *et al*., 1998; de Madron *et al*., 2002) that enhance community respiration. Accordingly, planktonic communities in the Western Mediterranean also tended to be heterotrophic in this study during late spring.

Table 3.1.2. Western to Eastern ratios of planktonic community components and processes integrated to the DCM (Deep Chlorophyll Maximum). Ratios for this study were calculated as the ration of the mean value for each basin.
* Mean net community production was negative, heterotrophic, so that the ratio > 1 implies NCP to be more negative in the Western than in the Eastern basin.

Variable	West:East	References
Bacteria biomass (mg C m^{-2})	0.75	Turley *et al*. (2000)
Bacterial production (mg C m^{-2} d^{-1})	1.87	Turley *et al*. (2000)
Bacterial growth rate (d^{-1})	2.27	Turley *et al*. (2000)
Net Primary Production (mg C m^{-2} d^{-1})	3.33	Turley *et al*. (2000)
Chlorophyll (mg m^{-2})	1.13	Turley *et al*. (2000)
Chlorophyll a (mg m^{-2})	1.55	This study
GPP (mmol O_2 m^{-2} d^{-1})	1.37	This study
CR (mmol O_2 m^{-2} d^{-1})	1.74	This study
NCP (mmol O_2 m^{-2} d^{-1})	1.46*	This study

This study reports the first assessment of planktonic community metabolism across the Mediterranean during late spring of two yearly consecutives cruises, as previous reports focussed on particular regions, mostly coastal areas in the NW Mediterranean (Table 3.1.3, Fig. 3.1.5). In addition to riverine inputs, atmospheric inputs, which are high across the Mediterranean (Guerzoni *et al*., 1999), are an important source of organic carbon (Dachs *et al*., 2005; Jurado *et al*., 2008), providing, along with riverine inputs, the allochtonous carbon required to support net heterotrophic communities.

The metabolic rates observed in the THRESHOLDS cruises were somewhat higher than previously reported rates (Table 3.1.3). This could be explained by the fact that most previous studies were conducted during the winter and/or fall, whereas planktonic metabolic rates are highest, both for CR and GPP, in early summer, when an increase in metabolic rate per unit autotrophic and heterotrophic biomass has been reported for the Mediterranean Sea (Satta *et al*., 1996; Duarte *et al*., 2004). Also some of the literature rates were derived from shallow littoral stations (Table 3.1.3), where vertically integrated metabolic rates were constrained by the water column depth available.

Table 3.1.3. Geometric mean of the integrated (euphotic zone) planktonic metabolic rates (mmol O_2 m^{-2} d^{-1}) and of the P/R ratio for different studies of planktonic communities metabolism in the Mediterranean Sea (Figure 3.1.1). The number of stations (N station) and number of individual volumetric estimates (N depth) in each study is also shown. We just took into account stations with metabolism analysed for 3 depths.
a: data reported in carbon units converted to oxygen units assuming a 1.25 molar stoichiometry between O_2 and C (Williams, 1979, Davies and Williams, 1984).
n.d. = not determined.

Ref.	Authors	Region	Date	Depth (m)	GPP	R	NCP	P/R	N station	N depth
1	Lefèvre *et al.* (1997)	Gulf of Lions	12/1988 – 03/1992	53	72.2	72.7	-0.5	1	19	83
2	González *et al.* (2008)	Gulf of Lions	10/2002; 12/2002; 03/2003; 06/2003	30	24.7	26.5	1.5	0.7	4	16
3	Duarte *et al.* (2004)	Bay of Blanes	03/1988 – 10/1994	5	12.9	23.4	-10.5	0.6	333	333
4	Lucea *et al.* (2005)	Bay of Blanes	01/1996 – 12/1997	15	28.3	41.3	-13.0	0.7	23	23
5	Lefèvre *et al.* (PANGEA 2001)	Alboran Sea	12/1997-01/1998	60	34.8	40.3	-5.5	0.9	8	40
6	VanWambeke*et al.* (2004)	Alboran Sea	12/2001 – 01/2002	80	25.9	33.0	-7.1	0.8	7	n.d.
7	Navarro *et al*. (2004)	Bay of Palma	06/2001 – 10/2002	7	23.2	27.9	-4.7	0.8	14	14
8	Gazeau *et al*. (2005)	Bay of Palma	03/2002 - 06/2002	26	68.0	54.0	15	1.3	4	32
9	González *et al*. (2008)	Bay of Palma	06/2002	20	46	58.1	-6.4	1.1	4	16
10	Robinson (2000)	Aegean Sea	06/1996; 09/1996; 06/1997	7	25.2	130.2	-105.0	0.2	10	16
	This study	Western basin	06/2006; 05/2007	54	195.9	370.3	-155.4	0.6	3	9
	This study	Eastern basin	06/2006; 05/2007	63	118.6	156.9	-82.9	1.3	9	27

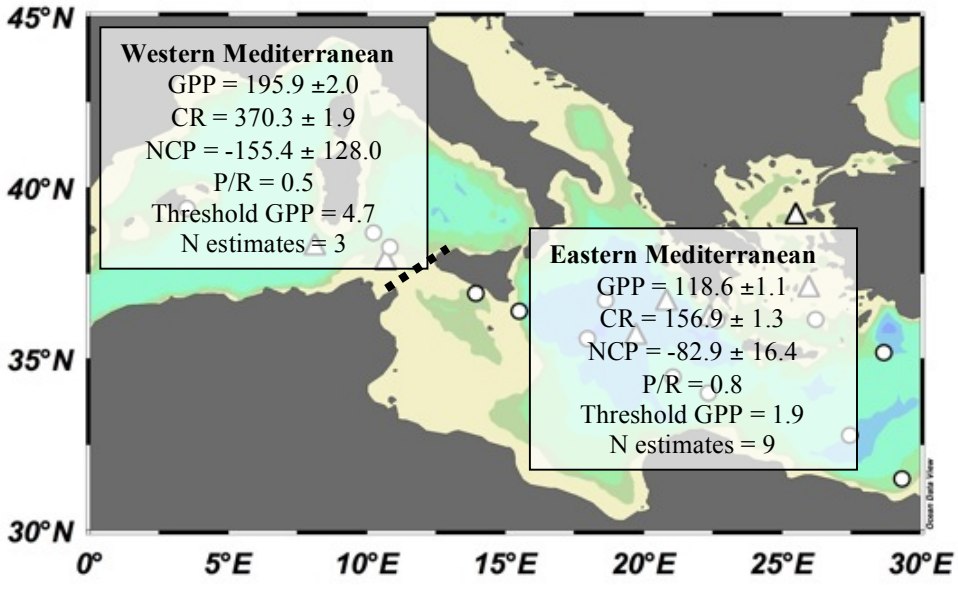

Figure 3.1.5. Integrated (0 – 100 m) geometric mean (± SE) metabolic rates (mmol O_2 m^{-2} d^{-1}) in the western and eastern basins (N = 22), along with the corresponding geometric integrated mean P/R ratio, threshold GPP for GPP = R, and number of estimates (N) for this study. The Geometric means were calculated for stations with metabolism analysed at 3 depths.

Our study shows that net heterotrophic communities prevailed at GPP rates < 4 mmol O_2 m^{-3} d^{-1} during late spring for the studied sections of the Mediterranean Sea. The GPP threshold for metabolic balance for this study is somewhat higher than those reported earlier for NW Mediterranean coastal areas (Bay of Palma: 2.8 mmol O_2 m^{-3} d^{-1}, Navarro *et al*., 2004; and Bay of Blanes: 3.8 mmol O_2 m^{-3} d^{-1}, Duarte *et al*., 2004) and well above that for the global ocean (1.1 mmol O_2 m^{-3} d^{-1}, Duarte and Regaudie-de-Gioux, 2009), implying that the GPP necessary to balance community respiration for Mediterranean communities during these studies is three times higher than that for the global ocean. This suggests that a higher gross primary production is required to compensate for the excess respiration supported by the high inputs of allochthonous organic carbon to the Mediterranean Sea during late spring.

In conclusion, the study presented here provides evidence that the planktonic communities of the studied regions during the late spring in the Mediterranean Sea tend to be net heterotrophic, as supported by previous reports from studies conducted mostly in coastal areas. Whereas the Western Mediterranean supports a higher gross primary production than the eastern basin does, it also supports higher community respiration rates, so that net community production tends to be more negative in the Western than in the Eastern basin during late spring. Planktonic metabolism in the Mediterranean Sea is likely to be very sensitive to changes in organic carbon inputs. Regulation of major rivers (Rhône, Ebro, Nile, Po) discharging in the Mediterranean, changes in the aerosol load over the Mediterranean, and increased human population in the basin may all have affected community metabolism and the role of planktonic communities in the CO_2 budget of the Mediterranean Sea. Whereas the data presented here represent the first evaluations of planktonic metabolism across the Mediterranean basin, our results are restricted to the late spring-early summer period and cannot resolve the annual metabolic balance of the communities. Indeed, resolving simultaneously the variability in planktonic metabolism across seasons and at the basin scale is a daunting task, which has not been completed as yet at the basin scale for any sea. The data presented here, although limited in their own right, provide a useful and unique resource to continue to improve and validate models, such as that presented by D'Ortenzio *et al*. (2008), that can be used, once properly validated, to integrate across scales. The combination of large-scale surveys, such as those presented here, and models may help resolve the metabolic balance of Mediterranean planktonic communities and its response to organic inputs delivered by river discharge and aerosol inputs.

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References

Benner R, Strom M (1993) A critical evaluation of the analytical blank associated with the DOC measurements by high-temperature catalytic oxidation. Mar Chem 41: 153-160

Bethoux JP, Gentili B (1999) Functioning of the Mediterranean Sea: past and present changes related to freshwater input and climate changes. J Mar Syst 20 (1-4): 33-47

Carpenter JH (1965) The accuracy of the Winkler method for dissolved oxygen analysis. Limnol Oceanogr 10: 135-140

Carrit DE, Carpenter JH (1966) Comparison and evaluation of currently employed modifications of the Winkler method for determining dissolved oxygen in sea-water. J Mar Res 24: 286-318

Claustre H, Marty J-C, Cassiani L (1989) Intraspecific differences in the biochemical composition of a diatom during a spring bloom in Villefrance-sur-mer Bay, Mediterranean Sea. J Exp Mar Biol Ecol 129: 17-32

Copin-Montégut C, Bégovic M, Merlivat L (2004) Variability of the partial pressure of CO2 on diel to annual time scales in the Northwestern Mediterranean Sea. Mar Chem 85: 169-189

Cruzado A, Velàsquez Z, Pérez MdelC, Bahamòn N, Grimaldo NS, Ridolfi F (2002) Nutrient fluxes from the Ebro river and subsequent across-shelf dispersion. Cont Shelf Res 22: 349-360

Dachs J, Calleja MLl, Duarte CM, del Vento S, Turpin B, Polidori A, Herndl G, Agustí S (2005) High atmosphere-ocean exchange of organic carbon in the NE Subtropical Atlantic. Geophys Res Lett 32: L21807 (10.1029/2005GL023799)

Davies JM, Williams PJleB (1984) Verification of 14C and O2 derived primary organic production measurements using an enclosed ecosystem. J Plankt Res 6(3): 457-474

de Madron XD, Denis L, Diaz F, Garcia N, Guieu C, Grenz C, Loÿe-Pilot M-D, Ludwig W, Moutin T, Raimbault P, Ridame C (2003) Nutrients and carbon budgets for the Gulf of Lion during the Moogli cruises. Oceanol Acta 26 (4): 421-433

D'Ortenzio F, Antoine D, Marullo S (2008) Satellite-driven modeling of the upper ocean mixed layer and air-sea CO2 flux in the Mediterranean Sea. Deep-Sea Res (1. Oceanogr Res Pap) 55: 405-434

Duarte CM, Agustí S (1998) The CO2 balance of unproductive aquatic ecosystems. Science 281: 234-236

Duarte CM, Agustí S, Vaqué D (2004) Controls on planktonic metabolism in the Bay of Blanes, northwestern Mediterranean littoral. Limnol Oceanogr 49 (6): 2162-2170

Duarte CM, Prairie YM (2005) Prevalence of heterotrophy and atmospheric CO2 emissions from aquatic ecosystems. Ecosystems 8: 862-870

Duarte CM, Regaudie-de-Gioux A (2009) Thresholds of Gross Primary Production for the Metabolic Balance of Marine Planktonic Communities. Limnol Oceanogr 54: 1015-102

Gazeau F, Duarte CM, Gattuso J-P, Barròn C, Navarro N, Ruiz S, Prairie YT, Calleja MLl, Delille B, Frankignoulle M, Borges AV (2005) Whole-system metabolism and CO2 fluxes in a Mediterranean Bay dominated by seagrass beds (Palma Bay, NW Mediterranean). Biogeosciences 2: 43-60

González N, Gattuso J-P, Middelburg JJ (2008) Oxygen production and carbon fixation in oligotrophic coastal bays and the relationship with gross and net primary production. Aquat Microb Ecol 52: 119-130

Guerzoni S, Chester R, Dulac F, Herut B, Loÿe-Pilot M-D, Measures C, Migon C, Molinaroli E, Moulin C, Rossini P, Saydam C, Soudine A, Ziveri P (1999) The role of atmospheric deposition in the biogeochemistry of the Mediterranean Sea. Prog Oceanogr 44: 147-190

Hansen K, Koroleff FF (1999) Determination of nutrients, in: Grasshoff K, Kremling K, Ehrhardt M (Eds): Methods of seawater analysis, Wiley-VCH, Germany, 159-228

Jurado E, Dachs J, Duarte CM, Simò R (2008) Atmospheric deposition of organic and black carbon to the global ocean. Atmos Environ 42(34): 7931-7939

Lefèvre D, Minas HJ, Minas M, Robinson C, Williams PJLeB, Woodward EMS (1997) Review of gross community production, primary production, net community production and dark community respiration in the Gulf of Lions. Deep-Sea Res (1. Oceanogr Res Pap) 44(3-4): 801-832

López-Urrutia Á, San Martin E, Harris RP, Irigoyen X (2006) Scaling the metabolic balance of the oceans. PNAS 103(23): 8739-8744

Lucea A, Duarte CM, Agustí S, Kennedy H (2005) Nutrient dynamics and ecosystem metabolism in the Bay of Blanes (NW Mediterranean). Biogeochemistry 73: 303-323

Martin J-M, Elbaz-Poulichet F, Guieu C, Loye-Pilot M-D, Hans G (1989) River versus atmospheric input of material to the Mediterranean Sea: An overview. Mar Chem 28 (1-3): 159-182

Morel A, André J-M (1991) Pigment distribution and primary production in the western Mediterranean as derived and modeled from Coastal Zone Color Scanner observations. J Geophys Res 96: 12685-12698

Moutin T, Raimbault P, Golterman HL, Coste B (1998) The input of nutrients by the Rhône river into the Mediterranean Sea: recent observations and comparison with earlier data. Hydrobiologia 373/374: 237-246

Navarro N, Agustí S, Duarte CM (2004) Plankton metabolism and dissolved organic carbon use in the Bay of Palma, NW Mediterranean Sea. Aquat Microb Ecol 37: 47-54

Ortega-Retuerta E, Reche I, Pulido-Villena E, Agustí S, Duarte CM (2008) Explorring the relationship between active bacterioplankton and phytoplankton in the Southern Ocean. Aquat Microb Ecol 52: 99-106

Oudot C, Gerard R, Morin P, Gningue I (1988) Precise Shipboard Determination of Dissolved-Oxygen (Winkler Procedure) for Productivity Studies with a Commercial System. Limnol Oceanogr 33(1): 146-150

Parsons TR, Maita Y, Lalli CM (1984) A manual of chemical and biological methods for seawater analysis.Pergamon Press, Oxford, 173 pp

Porter KG, Feig YS (1980) The use of DAPI for identifying and counting aquatic microflora. Limnol Oceanogr 25: 943-948

Raven JA, Geider RJ (1988) Temperature and algal growth. New Phytol 110: 441-461

Robinson C (2000) Plankton gross production and respiration in the shallow water hydrothermal systems of Miles, Aegean Sea. J Plankton Res 22(5): 887-906

Satta MP, Agustí S, Mura MP, Vaqué D, Duarte CM (1996) Microplankton respiration and net community metabolism in a bay on the NW Mediterranean coast. Aquat Microb Ecol 10: 165-172

Spyres G, Nimmo M, Worsfold PJ, Achterberg EP (2000) Determination of dissolved organic carbon in seawater using high temperature catalytic oxidation techniques. Trends in Anal Chem 19(8): 498-506

Turley CM (1999) The changing Mediterranean Sea - a sensitive ecosystem? Prog Oceanogr 44: 387-400

Turley CM, Bianchi M, Christaki U, Conan P, Harris JRW, Psarra S, Ruddy G, Stutt E D, Tselepides A, Van Wambeke F (2000) Relationship between primary producers and bacteria in an oligotrophic sea - the Mediterranean and biogeochemical implications. Mar Ecol Prog Ser 193: 11-18

Van Wambeke F, Lefèvre D, Prieur L, Sempéré R, Bianchi M, Oubelkheir K, Bruyant F (2004) Distribution of microbial biomass, production, respiration dissolved organic carbon and factors controlling bacterial production across a geostrophic front (Almeria-Oran, SW Mediterranean Sea). Mar Ecol Prog Ser 269: 1-15

Williams PJLeB, Raine RCT, Bryan JR (1979) Agreement between the ^{14}C and oxygen methods of measuring phytoplankton production: reassessment of the photosynthetic quotient. Oceanol Acta 2: 441-416

APPENDIX

Volumetric metabolism rates (GPP, CR and NCP) (mmol O_2 m^{-3} d^{-1}) and SE during the two studied cruises, Threshold-2006 and 2007.

n.d. not determined

Cruise	Station	Longitude (E)	Latitude (N)	Date	Depth (m)	GPP	SE	CR	SE	NCP	SE
Threshold-2006	2	8.0950	38.3087	6/4/06	5	n.d.	n.d.	n.d.	n.d.	-18.55	0.26
	2	8.0950	38.3087	6/4/06	19	n.d.	n.d.	n.d.	n.d.	11.06	0.09
	2	8.0950	38.3087	6/4/06	63	n.d.	n.d.	n.d.	n.d.	-2.23	0.08
	8	20.7867	36.6865	6/8/06	5					2.20	0.33
	8	20.7867	36.6865	6/8/06	24	3.63	0.17	6.06	0.12	-2.42	0.18
	8	20.7867	36.6865	6/8/06	91	1.05	0.71	0.90	0.62	0.15	0.41
	9	22.3462	36.2493	6/11/06	5	3.16	0.15	3.22	0.08	-0.06	0.14
	9	22.3462	36.2493	6/11/06	30	5.63	0.57	8.06	0.56	-2.43	0.11
	9	22.3462	36.2493	6/11/06	82	7.59	0.66	8.94	0.66	-1.35	0.03
	22	25.9245	37.0900	6/22/06	5	2.86	0.15	2.78	0.12	0.08	0.09
	22	25.9245	37.0900	6/22/06	15	15.13	0.08	3.30	0.11	11.83	0.11
	26	19.6943	35.7050	6/25/06	5	2.43	0.15	2.54	0.15	-0.11	0.06
	26	19.6943	35.7050	6/25/06	18	3.63	0.27	6.46	0.23	-2.83	0.16
	26	19.6943	35.7050	6/25/06	92	3.58	0.19	6.15	0.09	-2.57	0.18
	32	10.6443	37.8846	6/30/06	5	2.28	0.06	2.41	0.06	-0.13	0.02
	32	10.6443	37.8846	6/30/06	9	2.10	0.04	3.69	0.08	-1.59	0.07
	32	10.6443	37.8846	6/30/06	68	8.97	0.16	13.12	0.19	-4.15	0.16
Threshold-2007	1B	3.5387	39.3392	5/6/07	5	1.11	0.59	3.13	1.22	-2.02	1.26
	1B	3.5387	39.3392	5/6/07	20	5.31	1.98	12.98	0.95	-7.67	1.76
	1B	3.5387	39.3392	5/6/07	30	7.96	2.13	16.85	1.46	-8.89	1.60
	1B	10.8553	38.2322	5/11/07	5	0.61	1.01	5.11	2.02	-4.50	1.69
	1B	10.8553	38.2322	5/11/07	15					1.39	1.53
	1B	10.8553	38.2322	5/11/07	25	3.21	1.19	2.99	1.35	0.22	1.25
	3	15.5253	36.3603	5/12/07	5	0.93	0.19	2.57	1.17	-1.64	1.18
	3	15.5253	36.3603	5/12/07	85	0.37	0.28	0.96	0.31	-0.59	0.28
	4B	17.9757	35.5862	5/13/07	4	0.85	0.80	1.14	0.78	-0.29	0.33
	4B	17.9757	35.5862	5/13/07	20	0.58	1.14	0.38	1.14	0.20	0.24
	4B	17.9757	35.5862	5/13/07	70	2.65	1.16	3.97	0.52	-1.32	1.08
	5	21.0670	34.4652	5/14/07	5	1.86	0.46	2.80	0.42	-0.94	0.37
	5	21.0670	34.4652	5/14/07	90	0.07	0.31	2.82	0.23	-2.75	0.33
	6	22.3383	34.0013	5/15/07	5	1.84	0.33	2.27	0.33	-0.43	0.19
	6	22.3383	34.0013	5/15/07	35	1.26	1.11	2.47	1.11	-1.21	0.36
	6	22.3383	34.0013	5/15/07	80	0.24	1.27	2.50	1.27	-2.26	0.79
	8	27.4547	32.7683	5/16/07	5	0.54	0.16	0.72	0.16	-0.18	0.20
	8	27.4547	32.7683	5/16/07	110	0.16	0.39	0.74	0.39	-0.58	0.17
	10	29.3362	31.4962	5/17/07	5	n.d.	n.d.	n.d.	n.d.	5.97	1.27
	10	29.3362	31.4962	5/17/07	25	n.d.	n.d.	n.d.	n.d.	8.13	0.53
	10	29.3362	31.4962	5/17/07	60	n.d.	n.d.	n.d.	n.d.	5.14	2.18
	13	28.6765	35.1763	5/22/07	5	0.28	0.20	1.06	0.20	-0.78	0.39
	13	28.6765	35.1763	5/22/07	50	2.93	0.37	1.46	0.37	1.47	0.35
	15	26.2210	36.1525	5/25/07	5	1.75	0.36	2.88	0.36	-1.13	0.55
	15	26.2210	36.1525	5/25/07	20	1.92	0.39	4.74	0.39	-2.82	0.42
	15	26.2210	36.1525	5/25/07	40	0.44	0.82	2.95	0.82	-2.51	0.80
	17	22.6475	36.1253	5/26/07	5	0.73	0.52	1.85	1.03	-1.12	1.11
	17	22.6475	36.1253	5/26/07	95	0.79	0.36	2.37	0.46	-1.58	0.29
	19	18.6275	36.7097	5/27/07	5	1.56	1.43	0.70	1.41	0.86	0.28
	19	18.6275	36.7097	5/27/07	20	2.73	0.53	0.05	0.56	2.69	0.57
	19	18.6275	36.7097	5/27/07	50	1.51	0.45	0.22	0.45	1.29	0.27
	21	13.9397	36.9083	5/31/07	5	0.58	0.36	4.51	0.41	-3.93	0.28
	21	13.9397	36.9083	5/31/07	20	1.52	0.42	4.86	0.42	-3.34	0.41
	21	13.9397	36.9083	5/31/07	50	1.80	0.75	8.23	0.49	-6.44	0.63
	22	10.2410	38.6755	6/1/07	5	0.58	0.50	0.56	0.47	0.02	0.46
	22	10.2410	38.6755	6/1/07	70	1.56		1.84	0.35	-0.28	0.44

Chapter 3

Regional and global variability in the pelagic metabolism in the ocean

2 - Plankton metabolism in the Greenland Sea during the polar summer of 2007

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Abstract

The polar summer metabolism of the planktonic communities in the Greenland Sea was surveyed in July 2007. Planktonic metabolism showed great variability across the studied area, with on average, higher metabolic rates in the Fram Strait-Svalbard region than along the Greenland Current**.** A significant fraction (47 %) of the planktonic communities in the Fram Strait-Svalbard region were net heterotrophic, suggesting that increased respiration rates with further warming may lead the planktonic communities at this region to act as net CO_2 sources. The thresholds gross primary production for metabolic balance (i.e. gross primary production = community respiration) was much higher in the European sector of the Arctic than reported for the Southern Ocean, suggesting that heterotrophic metabolism is more prevalent in the European sector of the Arctic than in the Southern Ocean, indicating high allochthnous inputs in the Arctic region.

Introduction

The metabolic balance of planktonic communities refers to the balance between gross primary production (GPP) and community respiration (CR), defining whether plankton communities act as net CO_2 sources (CR > GPP) or sinks (CR < GPP) for the atmosphere. Although the metabolism of oceanic planktonic communities appears to be in approximate balance across large scales (GPP ≈ CR; Duarte and Agustí, 1998; Williams 1998; Duarte *et al*., 2001; del Giorgio and Duarte, 2002), allochthonous inputs of organic matter generate a potential for CR to exceed GPP (Smith and Hollibaugh, 1993; del Giorgio and Duarte, 2002). Whereas efforts to examine planktonic metabolic balance in the ocean have increased greatly in the recent past (del Giorgio and Williams, 2005), there is still a remarkable paucity of estimates of planktonic metabolism in the Arctic Ocean, limited to three published reports (Cota *et al*., 1996; Sherr and Sherr, 2003; Cottrell *et al*., 2006). Cota *et al*. (1996), working in the Chukchi Sea, observed that the respiratory activity in the upper mixed layer exceeded primary productivity at the deep-water stations, as it often does in summer oligotrophic conditions at lower latitudes. Sherr and Sherr (2003), working from the Canada Basin to the Mendeleyev Basin reported that the respiration rates were on average 3-fold lower during winter compared to summer, and documented an order-of-magnitude increase in activity of heterotrophic bacterioplankton from winter to summer. Bacterial activity has been reported to be highly variable in the Arctic Ocean (Rich *et al*., 1997; Kirchman *et al*.,

2009). Heterotrophic bacteria represent active components of the planktonic communities of the Arctic Ocean (Rich *et al*., 1997). Cottrell *et al*. (2006) observed that the planktonic communities at the majority of studied stations were net heterotrophic (67 % of the stations) in the Chukchi Sea during the polar summer 2004. These reports suggest that net heterotrophy may not be uncommon in the Arctic, as reported for the Southern Ocean (Agustí *et al*., 2005). However, such assessment may be premature, as it is based on a limited number of estimates. There is, therefore, a need to improve our empirical base and our understanding on the regulation of pelagic community metabolism in the Arctic.

The examination of planktonic metabolism in the Arctic Ocean is particularly pressing. The accelerating trend toward ice loss is leading to a growth of the ice-free surface in the polar summer (Arrigo and van Dijken, 2004; Arrigo *et al*., 2008), as well as warming of seawater (Hansell *et al*., 1998; Hassol, 2004). These changes have been predicted to enhance primary production and, thereby, the CO_2 sink capacity of Arctic plankton communities, implying an increased net community metabolism. The evaluation during the polar summer of the net community metabolism of Arctic plankton communities has become even more pressing as the open-water area increased with an important ice loss experienced in 2007 (Stroeve *et al*., 2007; Comiso *et al*., 2008). Surface waters in the Arctic Ocean have the highest loads of terrigenous dissolved organic matter of all ocean basins (Opsahl *et al*., 1999; Benner *et al*., 2005). Peterson *et al*. (2002) showed a strong positive correlation between the global surface air temperature and the Eurasian rivers discharge over 63 years. Cooper *et al*. (2005) showed that the dissolved organic carbon (DOC) concentration increased with runoff of Arctic rivers. Thus, warming is expected to increase the riverine inputs of organic matter to the Arctic Ocean (Lalande *et al*., 2009). High inputs of organic matter from increased primary production and riverine inputs may enhance the response of bacteria to warming, as the response of bacteria to temperature maybe affected by high demands for substrate in cold waters (Pomeroy and Wiebe, 2001). Warmer temperatures, inputs of organic matter derived from enhanced primary production and riverine inputs may further stimulate plankton respiration rates. Hence, a high primary production in the Arctic during the polar summer may not be necessarily favourable to an increased net community production as assumed earlier.

The goal of this study was to examine the metabolism of plankton communities in the Greenland Sea (Greenland to Svalbard Islands) during the polar summer. We

evaluated CR and GPP, as well as the net community production (NCP, defined as the net production of oxygen over 24 h at ambient light levels) of plankton communities during July 2007, and examined the relationships between CR and GPP.

Materials and Method

The study was conducted during the ATOS cruise, July 01 to 25, 2007, aboard the Spanish Oceanography Research vessel *Hespérides*. The ATOS cruise sampled the Greenland Current (GC, July 01- July 07) to enter the Arctic Ocean (AO, July 08- July 25) through the Fram Strait to occupy stations from 78° 00'72 N to 80° 83'28 N (Fig. 3.2.1).

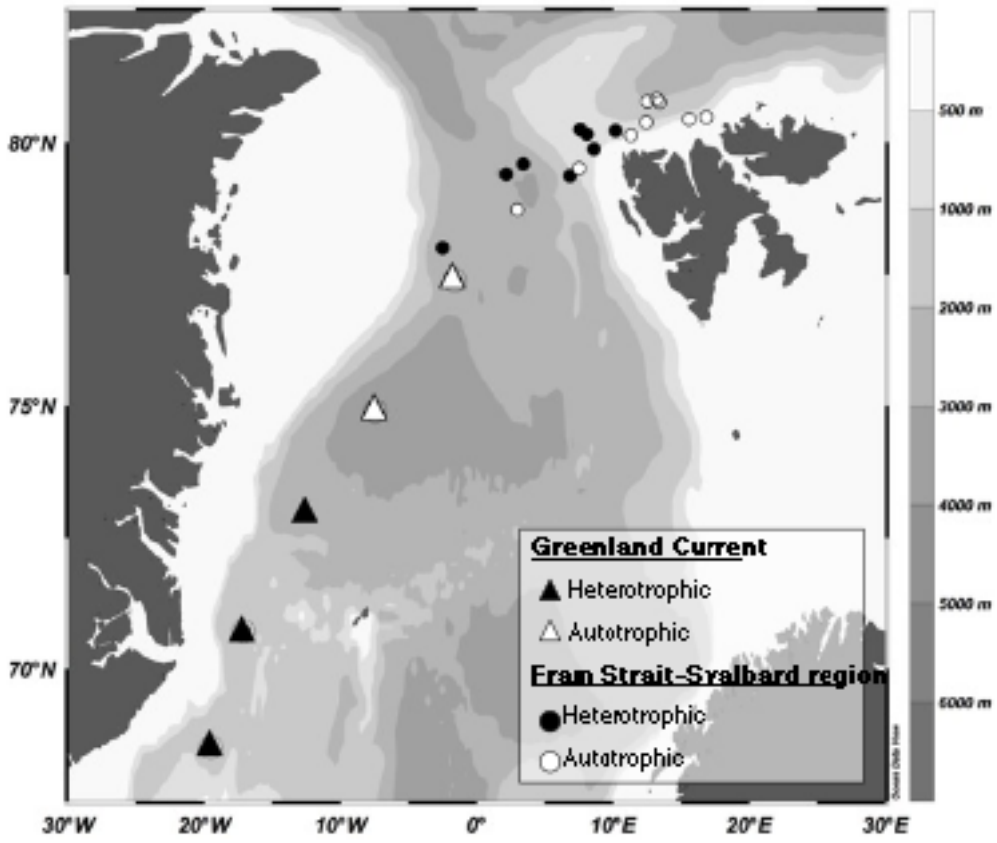

Figure 3.2.1. Distribution of the stations sampled during the cruise. Black and white circles represent heterotrophic and autotrophic depth-integrated community metabolism, respectively.

The gross primary production (GPP), the community respiration (CR) and the net community production (NCP) were determined at 22 stations from changes in oxygen of samples derived from the surface layer (1 m), the Chlorophyll Maximum (CM, on average 26 m), and at an intermediate depth (on average, 10 m) at each station.

The sill depth of the Arctic Ocean through the Fram Strait is on average 2,600 m depth. Six of a total of 22 stations sampled here were located at depths higher than 2,000 m depth and three of the stations were shallower than 250 m. We, thus, can consider that the majority of the stations sampled (sampled stations north of 78º00 N) were located in the Greenland Sea, rather than the Arctic basin. Water samples were collected from these depths using a 30 L Niskin bottle for 1 m samples, and 12 L Niskin bottles attached to a Rosette sampler system for the deeper layers. Samples were carefully siphoned from the Niskin bottles into 75 ml narrow mouth Winkler bottles. Seven replicates were used to determine the initial oxygen concentration, and seven replicate bottles were incubated for 24 h in the "dark" and in the "light". The bottles for "light" were incubated on deck at *in situ* temperature (temperature at 5 m depth), adjusting the incident natural irradiance to that received *in situ* using neutral density screens or in the dark, in the case of the seven replicate "dark" bottles. During the cruise, the thermocline was located deeper than the sampled depths, which showed a uniform temperature distribution, thereby avoiding temperature effects on metabolism rates during the incubation time. The mixed layer depth was calculated from the vertical profile of density following the criterion selected by de Boyer Montégut *et al*. (2004). The penetration of irradiance at depth was measured with a SatlanticTM OCP-100FF submarine irradiance profiler deployed from the surface down to 200 m. The percent of the surface irradiance reaching to the different sampled depths was calculated and used to adjust the incubation irradiance for the "clear" bottles to that in situ using neutral density screens. The measurements were conducted in borosilicate Winkler bottles. This material blocks UV-B radiation and may, therefore, bias rates, relative to those in situ when UVB radiation is high. However, UV-B radiation remained low during the ATOS cruise (daily mean UV = 0.96 kJ m^{-2}) (Coello-Camba and Agustí, submitted), and was, therefore, unlikely to affect metabolic rates in this study.

Oxygen concentrations were analysed by Winkler titration using a potentiometric electrode and automated endpoint detection (Mettler Toledo, DL28 titrator) (Oudot *et al*., 1988). CR and NCP were calculated from changes in dissolved oxygen concentration after incubation of samples under "dark" and "light" conditions, respectively, and GPP was calculated as NCP + CR. The integrated metabolic rates were calculated using the conventional trapezoid method down to the Chlorophyll Maxima (26 m ± 2 m depth). The limited number of sampled depths, forced by the large flow of samples associated with the daily nature of the measurements, implies that the

estimates of integrated rates presented carry considerable uncertainty. Hence integrated rates derived here (units mmol O_2 m^{-2} d^{-1}) are only reported to the nearest integer. The Chlorophyll Maxima depth was upper than the 1 % light depth (depth where reached 1 % surface irradiance) (see Appendix). We considered that the metabolic rates at the 1 % light depth were about the same range than at the Chlorophyll Maxima depth. We evaluated thus, the integrated metabolic rates down to the 1 % light depth and we compared with the integrated rates down to the Chlorophyll Maxima depth. We observed no significant differences between the integrated metabolic rates down to the Chlorophyll Maxima and to the 1 % light depth. We can so conclude that integrated rates are robusts, independently of the integrated depth and we decided so to present here the metabolic rates down to the Chlorophyll Maxima.

The initial oxygen concentration of the surface waters sampled during the cruise averaged (± SE) 329.1 ± 1.2 µmol O_2 l^{-1} (range 288.1 µmol O_2 l^{-1} and 385.7 µmol O_2 l^{-1}). The estimates of oxygen concentration were rather precise in the replicated initial, "clear" and "dark" measurements, with mean coefficients of variation for these measurements of 0.03 (mean oxygen concentration = 326.6 µmol O_2 l^{-1}), 0.02 (mean oxygen concentration = 327.1 µmol O_2 l^{-1}) and 0.02 (mean oxygen concentration = 321.71 µmol O_2 l^{-1}), respectively. The coefficients of variation of the metabolic rates (GPP, CR and NCP) were also calculated for each station at each depth. The GPP, CR and NCP rates had low coefficients of variation for each station at each sampled depth, with mean coefficient of variation of 0.04 (mean value = 6.02 mmol O_2 m^{-3} d^{-1}), 0.01 (mean value = 5.24 mmol O_2 m^{-3} d^{-1}) and 0.02 (mean value = 1.23 mmol O_2 m^{-3} d^{-1}), respectively. The coefficients of variation for the metabolic rates (GPP, CR and NCP) at the different sampled depth for each station were in general lower than 0.05.

Temperature and salinity at 1 m depth were determined using a Seabird CTD 19 deployed from a Zodiac and those at greater depths were determined from the Seabird SBE-25 CTD attached to the Rosette sampling system of the research vessel. Samples of 250 ml for chlorophyll *a* determinations were filtered through Millipore GF/F filters (pressure < 0.3 kg cm^{-2}), frozen and then extracted for 24 hrs with 90% acetone. Fluorescence of the extracts was measured using a Shimadzu RF-5301 fluorometer (Yentsch and Menzel, 1963).

Results

The cruise encompassed ice-free stations and stations with up to 60 % ice cover, with very dynamic changes in ice cover in the studied area. Indeed, the cruise was conducted in July 2007, when unprecedented ice melting occurred in the Arctic (Stroeve *et al*., 2007). The incident solar radiation was relatively low, due to fog and cloud cover during the cruise, averaging 1.28 watt cm^{-2}. Some of the stations presented a shallow pycnolcine at about 2 m depth, with rather uniform properties below this pycnocline, where the water column remained uniform until, on average (±SE) 11.5 ± 1.1 m. The nutricline was located even deeper at an average (±SE) depth of 84.3 ± 8.1 m (data not shown). Nutrient concentrations within the mixed layer were low for phosphate (mean 0.18 µmol P L^{-1}) and intermediate for other nutrients (mean nitrate + nitrite 1.85 µmol N L^{-1}, mean silicate 1.75 µmol Si L^{-1}) and mean DOC (Dissolved Organic Carbon) values were relatively high (mean 91 µmol C L^{-1}) for oceanic waters (Duarte, unpubl. results).

The stations sampled along the Greenland Current had colder waters (mean 0.48 ± 0.01 º C) but similar salinity (mean 34.83 ± 0.004 º C) as the waters in the stations sampled along the Eastern Fram Strait-Svalbard region (2.53 ± 0.013 º C and salinity 34.87 ± 0.003) (Fig. 3.2.2). However, the waters sampled in the Eastern Fram Strait-Svalbard region were more variable in temperature (range-1.79 to 7.07 ºC) and salinity (30.57 to 35.33) than those sampled along the Greenland Current (-1.47 to 4.37 º C, salinity range 31.27 to 35.07) (Fig. 3.2.2).

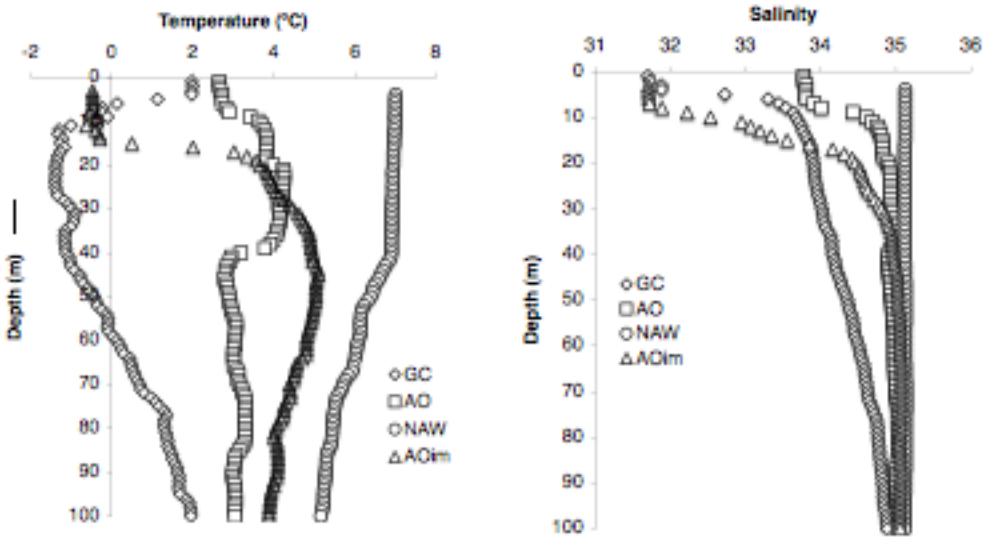

Figure 3.2.2. Temperature and salinity profiles of four sampled stations representative of the research are in the study area: one station sampled in the Greenland Current (GC), one station in the Arctic Ocean (AO), one station in the Arctic Ocean affected by the ice-melt (AOim) and one station sampled in the Arctic Ocean characterized by the water masses of the Norwegian Atlantic Water (NAW).

Planktonic metabolic rates showed great variability across the study area (see Appendix), which included the Greenland Current and the Eastern Fram Strait-Svalbard region. Metabolic rates were more variable in the Eastern Fram Strait-Svalbard region than they were in the Greenland Current (Table 3.2.1), consistent with the greater hydrographic variability in the Eastern Fram Strait-Svalbard region. GPP (both volumetric and integrated) and CR (volumetric) rates differed significantly between these two regions (Kruskal Wallis test, $p < 0.05$), with the rates being higher south of 78º00 N (Table 3.2.1). Both regions had more than 40 % heterotrophic stations (Table 3.2.1 and Figure 3.2.1). Furthermore, bacterial abundance was significantly higher in the Eastern Fram Strait-Svalbard region ($1.28\ 10^6$ cell ml^{-1}) compared to that in the Greenland Current ($0.82\ 10^6$ cell ml^{-1}, t-test, $p < 0.05$). These results are in accordance with the significant difference observed for the volumetric CR between the two regions. Some of the high variability in metabolic rates observed in the study maybe attributable to temporal changes, confounded here with spatial variability, as the study was not a synoptic one. Limited sampling effort along the Greenland Current (5 stations) precludes further examination if any significant relationship exists between metabolic rates and other environmental properties (temperature and salinity).

Table 3.2.1. Median, mean, SE, range and number of estimates of net community production (NCP), community respiration (CR), gross primary production (GPP) and P/R ratio, volumetric (mmol O_2 m^{-3} d^{-1}) and integrated rates (mmol O_2 m^{-2} d^{-1}) in the stations sampled in the Greenland Current and in the Fram Strait-Svalbard region. The percentage of autotrophic stations is also indicated for the two studied areas.

		Greenland Current				Fram Strait-Svalbard Region			
		NCP	**CR**	**GPP**	**P/R**	**NCP**	**CR**	**GPP**	**P/R**
Volumetric rates	Median	0.39	2.11	2.12	1.40	1.00	3.42	5.57	1.37
	Mean	1.15	2.10	3.57	2.13	1.25	6.23	6.73	1.96
	SE	1.02	0.29	1.09	0.50	1.13	0.87	0.80	0.31
	Min	-4.20	0.24	0.05	0.01	-21.71	1.01	0.05	0.04
	Max	10.55	3.74	13.89	6.87	22.71	29.20	25.24	9.99
	N	15	15	14	14	51	48	48	48
Integrated rates	Median	-5	54	49	1	28	136	127	1
	Mean	9	53	66	1	5	172	153	2
	SE	31	6	26	1	42	37	21	0
	Min	-68	39	22	0	-303	35	56	0
	Max	122	74	164	4	389	578	382	6
	N	5	5	5	5	17	16	16	16
		40 % autotrophic stations				53 % autotrophic stations			

The volumetric GPP increased significantly with increasing Chl *a*, as well as with increasing salinity and water temperature (Fig. 3.2.3 and 3.2.4).

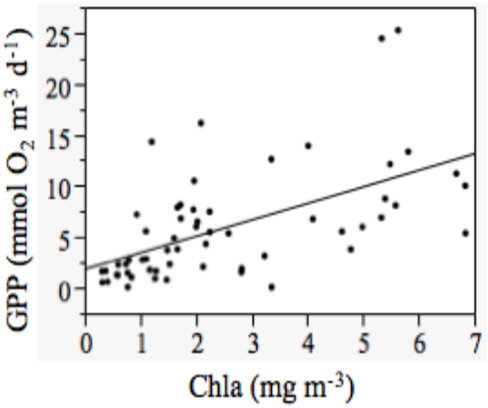

Figure 3.2.3. The relationship between GPP (mmol O_2 m^{-3} d^{-1}) and the chlorophyll *a* concentration (mg Chl *a* m^{-3}) in the Fram Strait-Svalbard region. The solid line represents the fitted regression: (GPP = 2.32 (± 1.24) + 1.58 (± 0.38) Chl *a*, $R^2 = 0.29$, $p < 0.05$).

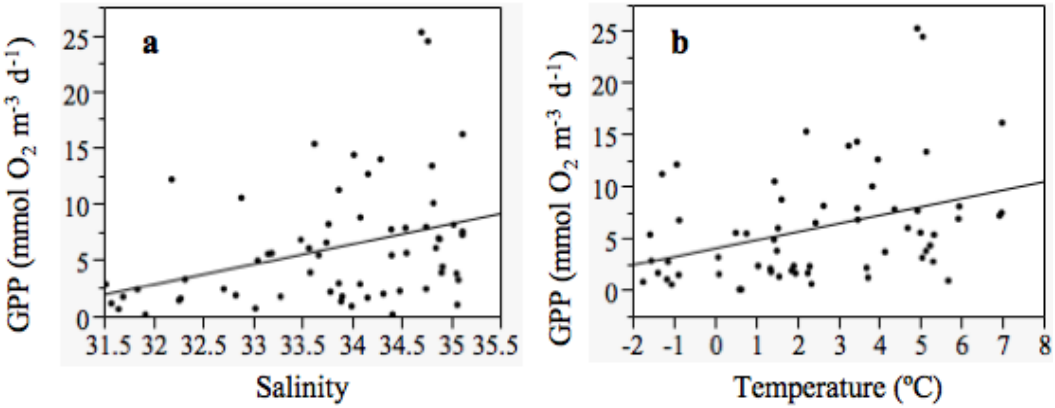

Figure 3.2.4. The relationship between GPP (mmol O_2 m^{-3} d^{-1}) and salinity ([a]) and seawater temperature (T, ºC) ([b]) in the Fram Strait-Svalbard region. The solid lines represent the fitted regressions: a), GPP = -55.72 (± 24.00) + 1.84 (± 0.71) S, $R^2 = 0.13$, $p < 0.05$; and b), GPP = 4.88 (± 1.07) + 0.70 (± 0.29) T, $R^2 = 0.12$, $p < 0.05$.

No significant relationship was observed between CR or NCP and Chl *a* concentration, temperature or salinity. The volumetric NCP increased with the volumetric GPP across the two oceanic regions (Fig. 3.2.5) implying the studied communities tend to be heterotrophic (i.e. NCP < 0) at low GPP and net autotrophic at high GPP. The volumetric GPP required for GPP to balance respiration (GPP at GPP = R) was 6.4 mmol O_2 m^{-3} d^{-1} in the Fram Strait-Svalbard region.

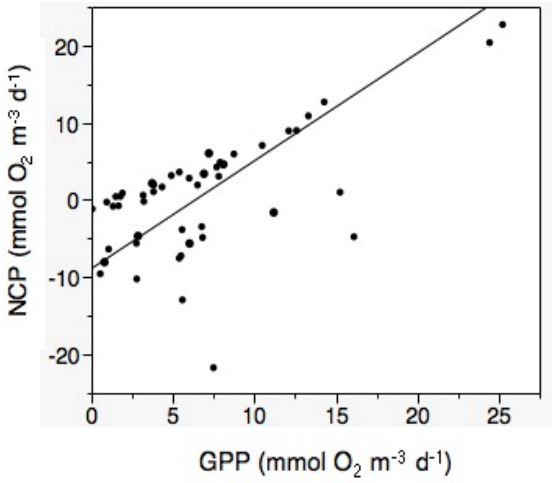

Figure 3.2.5. The relationship between NCP (mmol O_2 m^{-3} d^{-1}) and GPP (mmol O_2 m^{-3} d^{-1}) in the Fram Strait-Svalbard region. The solid line shows the fitted linear regression model II equation: NCP = -8.88 (± 1.38) +1.39 (± 0.16) GPP, $R^2 = 0.40$, $p < 0.05$.

Discussion

Planktonic metabolism showed considerable variation, with somewhat higher metabolic rates in the stations sampled at the highest latitudes (Table 3.2.1). The Fram Strait connects the Arctic Ocean and the Atlantic Ocean (Rudels *et al*., 2000), and presents a complex hydrography with multiple water masses differing greatly in thermohaline characteristics (Arctic Intermediate Water, Canadian Basin Deep Water, Greenland Sea, Norwegian Atlantic Current, and West Spitsbergen Current waters, Rudels *et al*., 2000) (Fig. 3.2.2). The low salinity and low temperature waters observed in the Fram Strait correspond to Polar Sea Water (PSW) affected by freshwater discharge from ice melting (Rudels *et al*., 2005). The high salinity (> 34) and high temperature (> 4 ºC) waters in the eastern margin Fram Strait region corresponds to the Norwegian Atlantic Current (NAC) and the West Spitsbergen Current (WSC, Rudels *et al*., 2005). The low salinity and low temperature waters observed in the Fram Strait correspond to Polar Sea Water (PSW) affected by freshwater discharge from ice melting (Rudels *et al*., 2005). The high salinity (> 34) and high temperature (> 4 ºC) waters in the eastern margin Fram Strait region corresponds to the Norwegian Atlantic Current (NAC) and the West Spitsbergen Current (WSC, Rudels *et al*., 2005). The greater hydrographic variability in the Eastern Fram Strait-Svalbard region resulted in a higher variability in metabolic rates than those observed along the Greenland Current. Indeed, the Eastern Fram Strait-Svalbard region is a hydrographically complex region, where multiple water masses occur, from cold Arctic waters to warm Atlantic-influenced waters, and from high salinity waters to surface waters diluted with freshwater derived from ice melting. Our results indicate that this variability also affects metabolic rates,

which differ in mean values and variability, among the two regions, consistent with the differences in biological communities related to hydrographic variability in the region (Hamilton *et al*., 2008).

In this study, the volumetric and integrated GPP were much higher in the Fram Strait-Svalbard sector than in the Greenland Current for the same autotrophic biomass (data not shown here). During the cruise, *Phaeocystis pouchetti*, present in its colonial form, dominated in the sampled stations in the Eastern Fram Strait-Svalbard region (Lasternas and Agustí, submitted), while diatoms dominated in the stations sampled along the Greenland Current (S. Lasternas, unpubl. results). Smith *et al*. (1991) observed an important bloom of *Phaeocystis pouchetti* across much of the Greenland Sea during the spring 1989. *Phaeocystis* blooms may occur earlier in the Greenland sector than in the Eastern Fram Strait-Svalbard region of the Arctic Ocean. Hodal and Kristiansen (2008) showed the important role of small-celled phytoplankton in supporting primary production in the Arctic, and Li *et al*. (2009) reported an increase in the smallest phytoplankton (picoplankton) with increasing temperature in the Arctic Ocean, parallel to a decline in the abundance of larger phytoplankton cells (nanoplankton). A shift towards small-celled phytoplankton as dominant contributors of primary production in the Arctic may result in a higher community respiration, as the P/R ratio of planktonic communities has been shown to decline with an increasing dominance of photosynthetic picoplankton (Teira *et al*., 2001).

The integrated mean metabolic rates determined here for the plankton communities sampled in the Eastern Fram Strait- Svalbard were very close to published reports for the European sector of the Arctic Ocean, which collectively showed that integrated CR tends to be significantly higher in the European sector of the Arctic than the rates reported for the Chukchi Sea (Kruskal Wallis test, $p < 0.05$, Table 3.2.1, Table 3.2.2). The output of Arctic water through the Fram Strait and Barents Sea is on average more than 5 times larger than inflow of Pacific waters through Bering Strait (Carmack *et al*., 2006) and is, therefore, compensated by riverine inputs. Currents are cyclonic around the European sector of the Arctic Ocean, which receives riverine waters discharged mainly by the Yenisey river (620 km^3 y^{-1}) and the Obi river (429 km^3 y^{-1}). In contrast, currents in the Chukchi Sea sector tend to be anticyclonic, and this sector receives discharge from the Mackenzie river (330 km^3 y^{-1}) and the Yukon river (195 km^3 y^{-1}) (Carmack et al., 2006). The Lena river, one of the largest rivers discharging in the Arctic Ocean (525 km^3 y^{-1}), distributes its riverine inputs between the Nansen basin

and the Chukchi Sea sector. The distribution of riverine discharge and subsequent circulation implies that the European sector of the Arctic Ocean receives higher riverine inputs, which may help explain the high respiration rates observed there compared to those reported for the Chukchi Sea.

The Arctic communities investigated were in rather close metabolic balance overall, with average GPP and CR not differing significantly from one another (Table 3.2.2). Yet, these estimates were derived in the Arctic during the polar summer, with a daily radiation (continuous radiation along the day) allowing phytoplankton to photosynthesize throughout the entire day. Despite these favourable conditions, many (47 %) of the stations examined supported heterotrophic communities, as a result of very high respiration rates. Furthermore, our results, along with published reports, show that during the polar summer, mean GPP and CR in the Arctic Ocean (Table 3.2.2) are comparable to global mean values reported for oceanic communities (GPP = 137.3 mmol O_2 m^{-2} d^{-1} and CR = 140.2 mmol O_2 m^{-2} d^{-1}, Robinson and Williams 2005). Indeed, Smetacek and Nicol (2005) pointed out that the daily radiation available for photosynthesis during the polar summer is about the same as that in the tropics, partially accounting for the similarity in GPP between the Arctic and the global ocean.

Whereas the mean GPP measured here was remarkably similar to the mean GPP reported for planktonic communities in the Southern Ocean, the mean summer CR of Arctic planktonic communities tended to be higher than that reported for the Southern Ocean ($p > 0.05$, Kruskal Wallis test, Table 3.2.2). As a consequence, the median P/R ratio of Arctic planktonic communities was much lower than that for Southern Ocean communities (Kruskal Wallis test, $p < 0.05$, Table 3.2.2), suggesting that net heterotrophic communities are more prevalent in the Arctic than in the Southern Ocean. As planktonic CR tends to be higher for a given GPP in the Arctic compared to the Southern Ocean, the threshold GPP for metabolic balance (i.e. GPP = CR) was much higher in the European sector of the Arctic (this study, GPP = 6.4 mmol O_2 m^{-3} d^{-1}), during the early polar summer than the values reported for the Southern Ocean (GPP mean = 1.1 mmol O_2 m^{-3} d^{-1}, Duarte and Regaudie-de-Gioux, 2009). This observation further confirms that heterotrophic metabolism is more prevalent in the European sector of the Arctic than in the Southern Ocean, consistent with previous reports (Duarte and Regaudie-de-Gioux, 2009).

Table 3.2.2. Mean (± SE) integrated metabolism rates (GPP, NCP and CR) (mmol O_2 m^{-2} d^{-1}), median (±SE) P/R ratio and threshold of GPP (mmol O_2 m^{-3} d^{-1}), in the European sector of the Arctic Ocean, Chukchi Sea and Southern Ocean. Data for the European sector of the Arctic Ocean are from the compilation of our data and of the BODC data. Data for the Chukchi Sea are from the compilation of Cottrell *et al*., 2006, Cota *et al*., 1996. Data for the Southern Ocean are the compilation from Regaudie-de-Gioux, A, unpublished data, Duarte et al., 2009, Lefèvre *et al*., 2008, Reuer *et al*., 2007, Bender, 2003 (PANGAEA data), Serret, 2003 (PANGAEA data), Dickson and Orchado, 2001, Bender *et al*., 2000, Boyd *et al*., 1995, Robinson and Williams, 1993. n.d. not determined.
*Data held at the British Oceanographic Data Center (BODC); *' Data also held at the Published Network for Geoscientific and

Oceans		Regions	References	GPP	NCP	CR	P/R	n observations
Arctic Ocean	June 1999	European sector	BODC data*	106 ± 13	- 5 ± 11	110 ± 14	1.0 ± 0.3	9
	July 2007	European sector	This study	127 ± 21	28 ± 42	136 ± 37	1.2 ± 0.4	17
		Total		*141 ± 19*	*17 ± 31*	*143 ± 25*	*1.6 ± 0.3*	*26*
	July-Agust 2002; May-June 2004	Chukchi Sea	Cottrell et al., 2006	228 ± 74	25 ± 25	108 ± 55	3.0 ± 0.7	10
	Agust 1993	Chukchi Sea	Cota et al., 1996	50 ± 14	n.d.	78 ± 15	0.7 ± 0.2	6
		Total		*172 ± 54*	*25 ± 25*	*95 ± 33*	*2.1 ± 0.5*	*16*
Total				***157 ± 25***	***21 ± 19***	***114 ± 21***	***1.8 ± 0.3***	***42***
Southern Ocean	January-February 2009	Antarctic Peninsula	Regaudie-de-Gioux, unpubl. data	79 ± 14	88 ± 28	45 ± 8	2.4 ± 0.4	23
	compiled data	*compiled data*	Duarte *et al.,* 2009	145 ± 16	20 ± 4	124 ± 14	1.4 ± 0.1	54
	January-February 2005	Kerguelen Plateau	Lefèvre *et al.*, 2008	66 ± 17	0 ± 32	55 ± 17	1.4 ± 0.4	7
	September 1997-October 2003	Southern Ocean	Reuer *et al.*, 2007	188 ± 16	20 ± 2	n.d.	n.d.	47
	December 1997; February-March 1999 January-February 1997	Southern Ocean	Bender, 2003*'	163 ± 21	58 ± 16	63 ± 8	3.0 ± 0.4	24
	December 1995-January 1996	Bellingshaussen Sea	Serret, 2003*'	203± 84	134 ± 62	70 ± 26	3.7 ± 1.3	4
	December 1997-January 1998 February-March 1998	Antarctic Front Polar	Dickson *et al*., 2001	130 ± 27	78 ± 13	52 ± 6	3.1 ± 0.6	14
	November 1996;January-February 1997	Ross Sea	Bender *et al.*, 2000	109 ± 26	88 ± 16	88 ± 19	3.2 ± 0.7	9
	November-December 1992	Bellingshaussen Sea	Boyd *et al.*, 1995	162 ± 14	71 ± 27	88 ± 18	1.8 ± 0.6	4
	February 1991	Weddell Sea	Robinson *et al.*, 1993	97 ± 1	-9 ± 26	100 ± 3	1.9 ± 0.0	2
Total				***143 ± 8***	***47 ± 5***	***82 ± 6***	***2.2 ± 0.1***	***188***

The finding of increased respiration rates in Arctic planktonic communities compared to those in the Southern Ocean is consistent with high allochthonous carbon supply to the Arctic Ocean. The Arctic Ocean receives a riverine discharge of 2472 km^3 y^{-1} (1182 km^3 y^{-1} and 1290 km^3 y^{-1} to the Chukchi-Beaufort and Nansen basins of the Arctic Ocean, respectively) (Duarte, 2007). In contrast, however, there are no riverine inputs and no significant terrestrial organic inputs to the Southern Ocean. Indeed, dissolved organic carbon concentrations in the surface waters of the Arctic Ocean examined here (mean DOC = 92.8 ± 1.3 μmol C L^{-1}, C.M. Duarte, unpubl. data) were almost twice as high as those typically reported for the upper mixed layer in the Southern Ocean (51.3 ± 3.8 μmol C L^{-1}; Kähler *et al*., 1997; Wiebinga and de Baar, 1998; Ogawa *et al*., 1999) or the World's Ocean (67.5 ± 0.4 μmol C L^{-1}; Arístegui *et al*., 2002), indicative of high DOC inputs to the Arctic Ocean. Hansell *et al*. (2004) concluded that planktonic communities use only a fraction of this allochthonous inputs to the Arctic Ocean, but this subsidy may be sufficient to explain why Arctic planktonic communities support higher respiration rates for a given GPP and are net heterotrophic more often than Southern Ocean ones. Indeed, the threshold GPP for planktonic metabolism has been argued to indicate the level of allochthonous inputs (Duarte and Regaudie-de-Gioux, 2009), so that the high threshold GPP for planktonic metabolic balance in the Arctic Ocean compared to the Southern Ocean signals at high allochthnous inputs.

The Arctic Ocean is undergoing rapid change that may further impact on the metabolic balance of its planktonic communities. Warming may change planktonic metabolism, as indicated by the significant positive relationships between water temperature and GPP, and between salinity, which may be reduced due to increased ice melt in a warmer Arctic, and GPP (Fig. 3.2.4). The increase in GPP with increasing water temperature is consistent with metabolic theory (Brown, 2004). However, this theory predicts that CR should increase faster than GPP. Yet, no significant relationship between community respiration rates and water temperature was observed in this study. The absence of a relationship between community respiration rates and temperature may be derived from the differences in substrate availability, which was not evaluated here, as Pomeroy and Wiebe hypothesised that the response of bacteria to temperature in cold waters maybe affected by high demands for substrate (Pomeroy and Wiebe, 2001).

The results presented here portray the Arctic Ocean as supporting during the early polar summer than in the Southern Ocean, including higher respiration rates than observed in the Southern Ocean. A significant fraction (47 %) of the planktonic communities investigated during the sampled cruise were net heterotrophic, suggesting that further enhancement of respiration rates may render the planktonic communities at the European sector of the Arctic Ocean net CO_2 sources. Surface Arctic waters are typically undersaturated in CO_2, acting as sinks for atmospheric CO_2, (Takahashi *et al*. 2002; Bates *et al*. 2006; Else *et al*. 2008), consistent with observations during the ATOS cruise (Álvarez, unpubl. data). Our results suggest that the CO_2 deficit observed must be a signal from a bloom preceding our study, as we did not observe a prevalence of autotrophic metabolism in the planktonic communities studied. The capacity of planktonic communities to act as CO_2 sinks is weakened when respiration rates are high, as reported here for the European sector of the Arctic Ocean.

Climate warming may elevate community respiration directly, by enhancing metabolic rates, and indirectly through increased allochthonous inputs derived from increased runoff and permafrost melting (Peterson *et al*., 2002; Benner *et al*., 2005; Cooper *et al*., 2005; Wassmann, 2008). Whereas reduced ice loss may enhance primary production in the Arctic Ocean during the polar summer, it may also increase respiration rates, rendering the response of net community production, and, consequently, the role of Arctic plankton communities in CO_2 fluxes, uncertain.

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References

Agusti S, Duarte, CM (2005) Threshold of gross primary production for planktonic metabolic balance in the Southern Ocean: An experiment test. Limnol Oceanogr 50: 1334-1339

Arístegui J, Duarte CM, Agustí S, Doval M, Álvarez–Salgado XA, Hansell DA (2002) Dissolved organic carbon support of respiration in the dark ocean. Science 298: 1967

Arrigo KR, van Dijken G (2004) Annual cycles of sea ice and phytoplankton in Cape Bathurst polynya, southeastern Beaufort Sea, Canadian Arctic. Geophys Res Lett 31. doi: 10.1029/2003GL018978

Arrigo KR, van Dijken G, Pabi S (2008) Impact of a shrinking Arctic ice cover on marine primary production. Geophys Res Lett 35 (19). doi: 10.1029/2008GL035028

Bates NR, Moran SB, Hansell DA, Mathis JT (2006) An increasing CO_2 sink in the Arctic Ocean due to sea-ice loss. Geophys Res Lett 33. doi: 10.1029/2006GL027028

Bender ML, Dickson ML, Orchardo J (2000) Net and gross production in the Ross sea as determined by incubation experiments and dissolved O_2 studies. Deep Sea Res Pt II 47: 3141-3158

Benner R, Louchouarn P, Amon RMW (2005) Terrigenous dissolved organic matter in the Arctic Ocean and its transport to surface and deep waters of the North Atlantic. Glob Biogeochem Cycles 19. doi: 10.1029/2004GB002398

Boyd PW, Robinson C, Savidge G, Williams PJleB (1995) Water column and sea-ice primary production during Austral spring in the Bellingshaussen Sea. Deep Sea Res Pt II 42(4-5): 1177-1200

Brown JH (2004) Toward a metabolic theory of ecology. Ecology 85(7): 1771-1789

Carmack E, Wassmann P (2006) Food webs and physical-biological coupling on pan-Arctic shelves: Unifying concepts and comprehensive perspectives. Prog Oceanogr 71(2-4): 446-477

Carpenter JH (1965) The accuracy of the Winkler method for dissolved oxygen analysis. Limnol Oceanogr 10: 135-140

Carrit DE, Carpenter JH (1966) Comparison and evaluation of currently employed modifications of the Winkler method for determining dissolved oxygen in sea-water. J Mar Res 24: 286-318

Coello-Gamba A, Agustí S (2010) Arctic and Antarctic phytoplankton community responses to increased temperature and synergy with UVR. Polar Biol (submitted)

Comiso JC, Parkinson CL, Gersten R, Stock L (2008) Accelerated decline in the Arctic sea ice cover. Geophys Res Lett 35. doi:10.1029/2007GL031972

Cooper LW, Benner R, McClelland JW, Peterson BJ, Holmes RM, Raymond PA, Hansell DA, Grebmeier JM, Codispoti LA (2005) Linkages among runoff, dissolved organic carbon, and the stable oxygen isotope composition of seawater and other water mass indicators in the Arctic Ocean. J Geophys Res 110. doi: 10.1029/2005JG000031

Cota GF, Pomeroy LR, Harrison WG, Jones EP, Peters F, Sheldon Jr WM, Weingartner TR (1996) Nutrients, primary production and microbial heterotrophy in the southeastern Chukchi Sea: Arctic summer nutrient depletion and heterotrophy. Mar Ecol Prog Ser 135: 247-258

Cottrell MT, Malmstrom RR, Hill V, Parker AE, Kirchman DL (2006) The metabolic balance between autotrophy and heterotrophy in the western Arctic Ocean. Deep Sea Res Pt I 53: 1831-1844

De Boyer Montégut C, Madec G, Fischer AS, Lazar A, Iudicone D (2004) Mixed layer depth over the global ocean: An examination of profile data and a profile-based climatology. J Geophys Res 109. doi:10.1029/2004JC002378

del Giorgio PA, Duarte CM (2002) Respiration in the open ocean. Nature 420: 379-384

del Giorgio PA, Williams PJleB (2005) Respiration in Aquatic Ecosystems. Oxford University Press.

Dickson MJ, Orchado J (2001) Oxygen production and respiration in the Antarctic Polar Front region during the austral spring and summer. Deep Sea Res Pt II 48: 4101-4126

Duarte CM, Agusti S (1998) The CO_2 balance of unproductive aquatic ecosystems. Science 281

Duarte CM, Agusti S, Arìstegui J, Gonzàlez N, Anadòn R (2001) Evidence for a heterotrophic subtropical northeast Atlantic. Limnol Oceanogr 46(2): 425-428

Duarte CM (2007) Impactos del calentamiento global sobre los ecosistemas polares. Fundación BBVA, Bilbao

Duarte CM, Regaudie-de-Gioux A (2009) Thresholds of Gross Primary Production for the Metabolic Balance of Marine Planktonic Communities. Limnol Oceanogr 54: 1015-1022

Else BGT, Papakyriakou TN, Granskog MA, Yackel JJ (2008) Observations of sea surface fCO_2 distributions and estimated air-sea CO_2 fluxes in the Hudson Bay region (Canada) during the open water season. J Geophys Res 113. doi: 10.1029/2007JC004389

Hamilton AK, Lovejoy C, Galand PE, Ingram RG (2008) Water masses and biogeography of picoeukaryote assemblages in a cold hydrographically complex system. Limnol. Oceanogr. 53(3): 922-935

Hansell RIC, Malcolm JR, Welch H, Jefferies RL, Scott PA (1998) Atmospheric change and biodiversity in the Arctic. Environ Monit Assess 49: 303-325

Hansell DA, Kadki D, Bates NR (2004) Degradation of terrigenous dissolved organic carbon in the western Arctic Ocean. Science 304: 858-861

Hassol SJ (2004) Impacts of warming Arctic: Arctic climate impact assessment. Cambridge University Press, Cambridge

Hodal H, Kristiansen S (2008) The importance of small-celled phytoplankton in spring blooms at the marginal ice zone in the northern Barents Sea. Deep-Sea Res Pt II 55:2176-2185

Kähler P, Bjørnsen PK, Lochte K, Antia A (1997) Dissolved organic matter and its utilization by bacteria during spring in the Southern Ocean. Deep-Sea Res Pt II 44(1-2): 341-353

Kirchman DL, Hill V, Cottrell MT, Gradinger R, Malmstrom RR, Parker A (2009) Standing stocks, production, and respiration of phytoplankton and heterotrophic bacteria in the western Arctic Ocean. Deep-Sea Res. II 56: 1237-1248

Lalande C, Forest A, Barber DG, Gratton Y, Fortier L (2009) Variability in the annual cycle of vertical particulate organic carbon export on Arctic shelves: Contrasting the Laptev Sea, Northern Baffin Bay and the Beaufort Sea. Cont Shelf Res 29: 2157-2165

Lasternas S, Agustí S (2010) Phytoplankton community structure during the record arctic ice-melting of summer 2007. Polar Biol (submitted)

Lefèvre D, Guigue C, Obernosterer I (2008) The metabolic balance at two contrasting sites in the Southern Ocean: The iron-fertilized Kerguelen area and HNLC waters. Deep Sea Res Pt II 55(5-7): 766-776

Li WKW, McLaughlin FA, Lovejoy C, Carmack EC (2009) Smallest algae thrive as the Arctic Ocean freshens. Science 326: 539

Ogawa H, Fukuda R, Koike I (1999) Vertical distributions of dissolved organic carbon and nitrogen in the Southern Ocean. Deep Sea Res Pt I 46(10): 1809-1826

Opsahl S, Benner R, Amon RMW (1999) Major flux of terrigenous dissolved organic matter through the Arctic Ocean. Limnol Oceanogr 44(8): 2017-2023

Oudot C, Gerard R, Morin P, Gningue I (1988) Precise Shipboard Determination of Dissolved-Oxygen (Winkler Procedure) for Productivity Studies with a Commercial System. Limnol Oceanogr 33(1): 146-150

Pomeroy LR, Wiebe WJ (2001) Temperature regulation of bacterial activity during the spring bloom in Newfoundland coastal waters. Science 233: 359-361

Peterson BJ, Holmes RM, McClelland JW, Vörösmarty CJ, Lammers RB, Shiklomanov AI, Shiklomanov IA, Rahmstorf S (2002) Increasing river discharge to the Arctic Ocean. Science 298: 2171-2173

Rich J, Gosselin M, Sherr E, Sherr B, Kirchman D (1997) High bacterial production, uptake and concentrations of dissolved organic matter in the Central Arctic Ocean. Deep-Sea Res. II 44(8): 1645-1663.

Robinson C, Williams PJleB (1993) Temperature and Antarctic plankton community respiration. J Plankton Res 15(9): 1035-1051

Rudels B, Meyer R, Fahrbach E, Ivanov VV, Østerhus S, Quadfasel D, Schauer U, Tverberg V, Woodgate RA (2000) Water mass distribution in Fram Strait ando ver the Yermak Plateau in summer 1997. Ann. Geophysicae 18: 687-705

Rudels B, Björk G, Nilsson J, Winsor P, Lake I, Nohr C (2005) The interaction between waters from the Arctic Ocean and the Nordic Seas north Fram Strait anda long the East Greenland Current: results from the Arctic Ocean-02 Oden expedition. J Mar Syst 55: 1-30

Sakshaug E, Skoldal H (1989) Life at the ice edge. Ambio 18: 60-67

Sherr BF, Sherr EB (2003) Community respiration/production and bacterial activity in the upper water column of the central Arctic Ocean. Deep Sea Res Pt I 50(4): 529-542

Smetacek V, Nicol S (2005) Polar ocean ecosystems in a changing world. Nature 437(7057): 362-368

Smith WO, Codispoti LA, Nelson DM, Manley T, Buskey EJ, Niebauer HJ, Cota GF (1991) Importance of *Phaeocystis* blooms in the high-latitude ocean carbon cycle. Nature 352, 514-516

Smith SV, Hollibaugh JT (1993) Coastal metabolism and the oceanic organic carbon balance. Rev Geophys 31: 75-93

Stroeve J, Holland MM, Meier W, Scambos T, Serreze M (2007) Arctic sea ice decline: Faster than forecast. Geophys Res Lett 34. Doi: 10.1029/2007GL029703

Takahashi T, Sutherland SC, Sweeney C, Poisson A, Metzl N, Tilbrook B, Bates N, Wanninkhof R, Feely RA, Sabine C, Olaffson J, Nojiri Y (2002) Global sea-air CO_2 flux based on climatological surface ocean pCO_2, and seasonal biological and temperature effects. Deep-Sea Res. II 49: 1601-1622

Teira E, Serret P, Fernández E (2001) Phytoplankton size-structure, particulate and dissolved organic carbon production and oxygen fluxes through microbial communities in the NW Iberian coastal transition zone. Mar. Ecol.Progr. Ser. 219: 65-83

Wassmann P (2008) Impacts of global warming on Arctic pelagic ecosystem and processes. In: Duarte CM (2007) Impactos del calentamiento global sobre los ecosistemas polares, BBVA Foundation, pp 111-138

Wiebinga CJ, de Baar HJW (1998) Determination of the distribution of dissolved organic carbon in the Indian sector of the Southern Ocean. Mar Chem 61(3-4): 185-201

Williams PJleB (1998) The balance of plankton respiration and photosynthesis in the open oceans. Nature 394: 55-57

Yentsch CS, Menzel DW (1963) A method for determination of chlorophyll and phaeophytin by fluorescence. Deep-Sea Res 10, 221-231

APPENDIX

Volumetric (mmol O_2 m^{-3} d^{-1}) and integrated (mmol O_2 m^{-2} d^{-1}) metabolism rates and their standard errors, 1 % light depth (m), temperature (ºC) and salinity for each sampled station during ATOS-cruise.

n.d. not determined

Date	Longitude E	Latitude N	Depth (m)	1 % light depth (m)	Temperature (°C)	Salinity	NCP ± SE (mmol m-3 d-1)	NCP ± SE (mmol m-2 d-1)	CR ± SE (mmol m-3 d-1)	CR ± SE (mmol m-2 d-1)	GPP ± SE (mmol m-3 d-1)	GPP ± SE (mmol m-2 d-1)
07/02/11	-19.5105	68.5140	1	36	2.4	33.0	0.16 ± 0.61		0.43 ± 0.59		0.59 ± 0.26	
			15		3.7	33.9	0.68 ± 0.59		0.54 ± 0.38		1.23 ± 0.54	
			30		0.6	34.4	-3.70 ± 1.64	-16.7 ± 25.10	3.74 ± 1.07	39.0 ± 17.6	0.05 ± 1.48	22.3 ± 20.1
07/03/11	-17.1252	70.7192	1	45	2.0	31.7	1.40 ± 0.31		0.24 ± 0.25		1.64 ± 0.33	
			10		-0.3	33.4	-4.20 ± 0.88		2.96 ± 0.46		n.d.	
			30		-1.4	33.9	-1.28 ± 0.31	-67.5 ± 17.4	2.95 ± 0.64	73.5 ± 14.1	1.67 ± 0.68	24.1 ± 20.9
07/04/11	-12.6535	72.9622	1	50	2.3	31.8	0.69 ± 0.36		1.61 ± 0.33		2.20 ± 0.32	
			10		1.4	33.8	0.10 ± 0.28		1.98 ± 0.59		2.08 ± 0.58	
			26		0.1	34.2	-1.16 ± 0.75	-5.0 ± 11.2	2.71 ± 0.65	53.7 ± 14.1	1.55 ± 0.81	48.7 ± 15.1
07/05/11	-7.4473	74.8955	1	49	1.9	32.7	0.39 ± 0.26		1.94 ± 0.32		2.34 ± 0.29	
			10		3.7	34.5	1.16 ± 0.27		1.00 ± 0.57		2.15 ± 0.59	
			32		1.1	34.8	-0.77 ± 0.81	11.2 ± 14.3	3.11 ± 0.36	58.4 ± 14.3	2.34 ± 0.84	69.7 ± 19.8
07/06/11	-1.6192	77.3825	1	19	2.7	33.8	6.04 ± 0.32		2.11 ± 0.22		8.15 ± 0.32	
			5		3.3	34.3	10.54 ± 0.60		3.35 ± 0.28		13.89 ± 0.59	
			15		3.8	34.8	7.23 ± 2.55	122.0 ± 17.6	2.78 ± 0.46	41.6 ± 4.7	10.01 ± 2.54	163.6 ± 17.5
07/07/11	-2.5103	78.0072	1	36	3.5	34.8	4.87 ± 0.57		3.03 ± 0.52		7.89 ± 0.64	
			20		3.5	34.9	-4.86 ± 0.33		11.68 ± 0.28		6.82 ± 0.35	
			36		4.1	35.1	2.15 ± 0.74	-21.6 ± 17.1	1.57 ± 0.31	245.7 ± 12.3	3.72 ± 0.68	224.0 ± 17.6
07/08/11	2.9745	78.7287	1	30	3.5	34.0	12.68 ± 0.59		1.60 ± 1.16		14.28 ± 1.27	
			5		2.5	33.8	1.93 ± 1.48		4.58 ± 1.21		6.51 ± 0.90	
			15		5.0	35.1	0.61 ± 1.14	41.9 ± 17.2	2.56 ± 0.24	48.0 ± 12.0	3.17 ± 1.13	90.0 ± 14.5
07/09/11	7.4953	79.5163	1	38	1.5	32.9	7.06 ± 0.34		3.42 ± 0.33		10.48 ± 0.25	
			5		4.0	34.2	8.99 ± 1.02		3.59 ± 0.43		12.58 ± 1.09	
			10		4.4	34.5	3.06 ± 2.02	62.2 ± 10.3	4.75 ± 0.60	34.9 ± 4.1	7.81 ± 2.06	97.1 ± 10.6
07/10/11	11.3265	80.1407	1	37	4.9	34.7	22.71 ± 0.66		2.53 ± 0.23		25.24 ± 0.66	
			5		5.1	34.8	20.37 ± 0.25		4.07 ± 0.31		24.44 ± 0.29	
			20		5.1	34.8	10.88 ± 2.65	320.6 ± 23.6	2.43 ± 0.32	61.9 ± 5.9	13.31 ± 2.66	382.5 ± 24.1
07/11/11	15.5753	80.4495	1	23	1.5	33.6	1.97 ± 0.52		1.86 ± 0.53		3.82 ± 0.29	
			5		1.5	33.1	3.16 ± 0.29		1.74 ± 0.38		4.90 ± 0.33	
			27		5.1	34.9	1.08 ± 0.44	56.9 ± 9.7	2.73 ± 1.16	56.4 ± 18.8	3.81 ± 1.13	113.2 ± 17.4
07/12/11	16.8647	80.4858	2	20	1.6	33.6	2.82 ± 3.72		3.18 ± 0.69		6.00 ± 3.77	
			12		1.6	34.1	5.94 ± 0.26		2.80 ± 0.33		8.74 ± 0.35	
			25		1.9	34.3	0.89 ± 0.54	88.2 ± 25.1	1.01 ± 0.31	54.7 ± 9.3	1.90 ± 0.47	142.9 ± 26.0
07/13/11	10.1887	80.2328	1	42	0.1	32.3	-0.18 ± 0.25		3.39 ± 0.25		3.21 ± 0.31	
			10		2.2	33.6	1.00 ± 0.70		14.26 ± 0.78		15.26 ± 0.85	
			25		4.7	34.9	-5.63 ± 0.66	-31.1 ± 14.5	11.65 ± 1.68	273.8 ± 23.1	6.02 ± 1.80	242.7 ± 25.1
07/14/11	6.8260	79.3695	1	n.d.	5.3	34.1	-10.23 ± 2.50		13.00 ± 2.71		2.78 ± 0.24	
			10		5.3	34.4	-7.54 ± 1.79		12.92 ± 1.94		5.38 ± 1.05	
			24		5.9	34.9	3.39 ± 0.52	-109.0 ± 35.5	3.51 ± 1.53	231.7 ± 45.2	6.90 ± 1.60	122.7 ± 24.4
07/15/11	8.0897	80.1653	1	27	1.6	32.3	-0.82 ± 0.32		2.14 ± 0.18		1.32 ± 0.33	
			15		5.0	34.6	-12.94 ± 2.193		18.52 ± 4.15		5.58 ± 0.60	
			27		6.0	35.0	4.61 ± 1.50	-146.2 ± 65.0	3.48 ± 0.36	276.6 ± 57.4	8.09 ± 1.51	130.4 ± 19.2
07/16/11	8.5997	79.8785	1	24	7.0	35.1	-4.77 ± 1.153		20.88 ± 1.06		16.11 ± 7.98	
			15		7.0	35.1	-21.72 ± 1.88		29.20 ± 1.81		7.49 ± 0.64	
			30		6.9	35.1	6.04 ± 0.72	-302.9 ± 89.0	1.164 ± 0.72	578.3 ± 39.1	7.21 ± 0.48	275.4 ± 68.8
07/18/11	12.4338	80.3900	1	29	2.3	33.3	-0.75 ± 0.43		2.41 ± 0.31		1.66 ± 0.47	
			10		4.9	34.4	4.26 ± 0.41		3.42 ± 0.39		7.68 ± 0.39	
			22		5.7	35.1	-0.27 ± 0.63	39.7 ± 10.0	1.21 ± 0.56	54.0 ± 8.8	0.93 ± 0.49	93.7 ± 9.2
07/19/11	13.4255	80.7700	1	31	0.6	32.3	12.67 ± 0.36		n.d.		n.d.	
			14		3.6	34.1	14.33 ± 0.49		n.d.		n.d.	
			30		3.2	34.7	12.37 ± 0.44	389.0 ± 13.0	n.d.	n.d.	n.d.	n.d.
07/20/11	13.2315	80.8328	1	38	0.7	31.9	-1.16 ± 1.06		1.20 ± 0.68		0.05 ± 0.94	
			5		1.4	32.8	0.46 ± 0.46		1.31 ± 0.57		1.79 ± 0.56	
			32		5.2	34.9	1.68 ± 0.56	27.5 ± 16.8	2.65 ± 2.25	58.6 ± 40.6	4.33 ± 2.26	86.1 ± 41.0
07/21/11	12.5307	80.7875	1	51	-0.9	32.3	0.43 ± 0.56		1.05 ± 0.52		1.48 ± 0.55	
			10		-0.9	32.2	8.94 ± 0.83		3.16 ± 1.60		12.11 ± 1.77	
			20		-1.6	33.7	3.60 ± 1.57	104.9 ± 18.3	1.79 ± 0.59	43.7 ± 20.4	5.39 ± 1.60	148.6 ± 27.3
07/23/11	7.5769	80.2535	1	30	0.8	33.2	-7.23 ± 0.58		12.72 ± 0.66		5.50 ± 0.60	
			10		0.5	33.2	-3.84 ± 1.39		9.40 ± 1.23		5.56 ± 1.51	
			20		-1.3	33.9	-1.62 ± 1.23	-77.1 ± 21.9	12.81 ± 1.55	210.6 ± 22.4	11.19 ± 1.96	133.5 ± 26.8
07/24/11	3.4043	79.5929	1	50	-1.0	31.7	-9.56 ± 0.51		10.10 ± 0.53		0.54 ± 0.21	
			14		-0.9	33.5	-3.45 ± 0.47		10.22 ± 0.37		6.76 ± 0.39	
			32		-1.7	34.0	-8.05 ± 0.42	-188.1 ± 14.3	8.85 ± 0.38	303.6 ± 12.6	0.80 ± 0.31	115.5 ± 10.3
07/25/11	2.1683	79.4005	1	28	-1.1	31.5	-5.61 ± 0.58		8.36 ± 0.86		2.76 ± 0.78	
			10		-1.2	31.6	-6.37 ± 0.41		7.42 ± 0.47		1.05 ± 0.54	
			30		-1.5	33.9	-4.67 ± 0.79	-164.3 ± 16.4	7.52 ± 1.31	220.5 ± 23.8	2.85 ± 1.45	56.2 ± 25.8

Chapter 3

Regional and global variability in the pelagic metabolism in the ocean

3 - Plankton metabolism in the Antarctic Peninsula during Austral summer

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Abstract

The Antarctic Peninsula is considered for climatologists and oceanographers as a particular and special region. Indeed, it is considered as one of the three areas of recent rapid regional (RRR) warming and as a confluence zone where two distinct water masses are coming from Weddell and Bellingshaussen Seas. The goal of this study was to examine the austral summer metabolism of planktonic communities in the Antarctic Peninsula, thereby adding to previous analyses to assess the role of plankton communities in carbon cycling in this region and the possible effect of increase temperature on the metabolic balance. The planktonic metabolic rates showed a great variation across the study areas, ranging over 600-fold among stations. Heterotrophic planktonic communities composed less than 6 % of the total sampled stations indicating the prevalence of autotrophic planktonic communities. The metabolism of planktonic communities in the Antarctic Peninsula seemed to be dependent of the distinct water masses. Temporal evolution of the metabolic balance was observed for planktonic communities in the Antarctic Peninsula.

Introduction

The Antarctic Peninsula is considered as one of the three areas experiencing recent rapid regional (RRR) warming, where the rates of warming far exceed global average warming rates (Houghton *et al*., 2001) with a substantial warming of 2.5 ºC from 1945 to 1990 (King, 1994; Cox *et al*., 2000). Temperature records from Antarctica are particularly robust, as they are free from confounding effects of increase concentration of short-lived sulphate aerosols or urban contamination that may mask the warming due to greenhouse effect at other locations (Vaughan *et al*., 2003). The Antarctic Peninsula has a particular climate regime (Vaughan *et al*., 2003) characterised by relatively warm temperatures and a contrast between the east and west coasts due to the presence of unbroken mountain chains (1400-2000 m) that form climatic barriers and result in temperatures 7 ºC warmer on the west coast of the Peninsula (Bellingshaussen Sea) than at similar latitudes and elevations on the east coast (Weddell Sea) (Reynolds, 1981; Morris and Vaughan, 1994). Temperature increase in this, naturally warmer, Antarctic region is expected to have a considerable effect on the ecosystem and particularly on the planktonic metabolic balance.

The Antarctic Peninsula is hydrographically complex, with the confluence of distinct water masses from the Weddell and Bellingshaussen Seas (-0.75 ºC and 34.5 ‰

and 2.75 ºC and 33 ‰, respectively) in a frontal region separating these water masses in the Bransfield Strait (Huntley *et al*., 1991; Niler *et al*., 1991; Capella *et al*., 1992). This region is relatively iron-sufficient (Sañudo-Wilhelmy *et al*. 2004; Tovar-Sánchez *et al*. 2007; Agustí *et al*., 2009) due to high inputs from submarine volcanoes (Petersen *et al*., 2004) and ash deposits derived from surface eruptions of the volcano at Deception Island (Deheyn *et al*., 2005). The waters around the Antarctic Pensinsula are, thus, characterised by intense biological activity and the development of important phytoplankton blooms (Holm-Hansen *et al*., 1989). The role of this biological activity as a CO_2 pump depends, however, on the balance between primary production and respiratory CO_2 production.

The metabolic balance of planktonic communities refers to the balance between gross primary production (GPP) and community respiration (CR), defining whether plankton communities act as net sources (CR > GPP) or sinks (CR < GPP) of CO_2. Despite an important increase in efforts to examine planktonic metabolic balance in the Southern Ocean (13 published reports over the past 10 years), estimates of planktonic metabolism around the Antarctic Peninsula are still limited (Arístegui *et al*., 1996; Serret *et al*., 2001; Agustí *et al*., 2004), including experimental manipulations (Agustí *et al*., 2005).

The goal of this study was to examine the summer metabolism of plankton communities in the Antarctic Peninsula, thereby adding to previous analyses to assess the role of plankton communities in carbon cycling in this region. We did so on the basis of two different cruises evaluating CR and GPP, as well as the net community production (NCP = GPP - CR) of plankton communities across the Antarctic Peninsula, ICEPOS (January and February 2005) and ATOS-Antarctica (January and February 2009), both encompassing the Bellingshaussen Strait, the Bransfield Strait, the Antarctic Strait and the Weddell Sea. We then combined these data with previous reports of plankton metabolism in the Antarctic Peninsula to test for relationships between water temperature and plankton metabolism in this rapidly warming area of the ocean.

Materials and Method

Sampling was carried out during January and February 2005 and 2009, in the ICEPOS and ATOS-Antarctica oceanographic cruises across the Bellingshaussen Strait, the Bransfield Strait, the Antarctic Strait and the Weddell Sea (Fig. 3.3.1). The ICEPOS

cruise took place from 26 January to 26 February 2005 and the ATOS-Antarctic cruise from 26 January to 28 February 2009, both aboard the Spanish Oceanography Research vessel *Hespérides*.

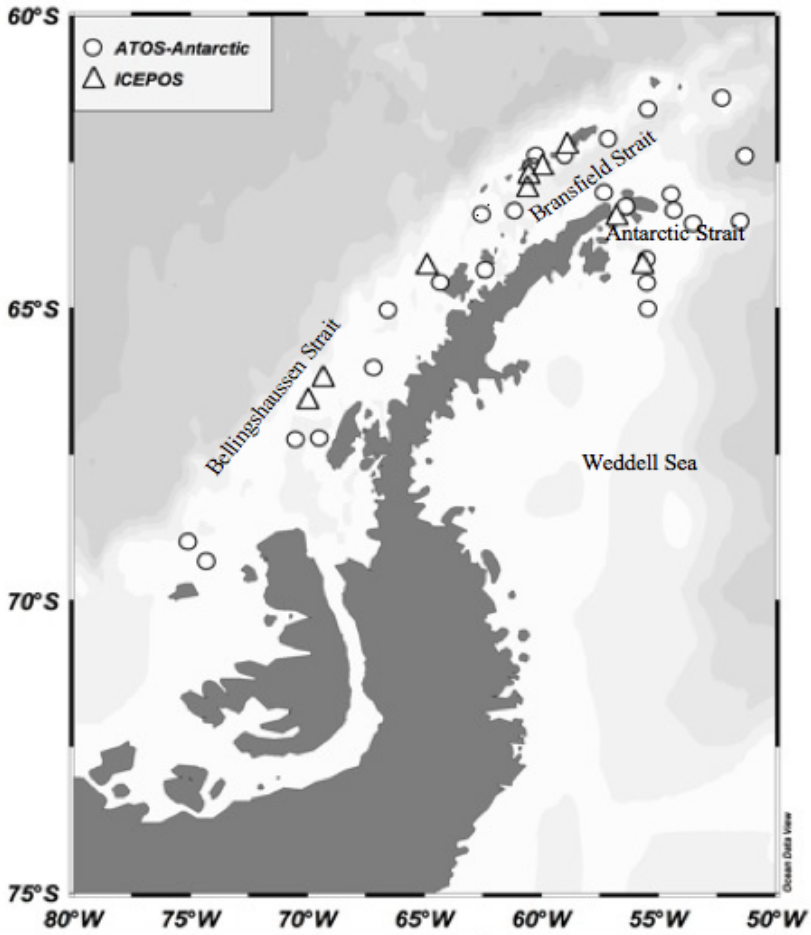

Figure 3.3.1. Distribution of stations sampled for planktonic metabolism determinations during the ICEPOS (triangles) and ATOS-Antarctic (circles) cruises.

The metabolism of planktonic communities was measured during ICEPOS and ATOS-Antarctic cruises at 9 and 25 stations, respectively (Fig. 3.3.1). At each station, vertical profiles for temperature, salinity and fluorescence were taken with a Seabird CTD attached to a Rosette sampling system. During ICEPOS cruise, 3 to 4 depths were sampled to determine the metabolism rates of the planktonic communities, from surface waters (5 m) to mid-depth layers (65 m on average), below the deep chlorophyll maximum (DCM), located between 15 and 35 m depth. During ATOS-Antarctic cruise, 3 depths were sampled to determine the metabolism rates of the planktonic communities, from surface waters (1 m) to the DCM (around 28 m depth).

Water samples were collected from these depths using a 30 L Niskin bottle for 1 m samples, and 12 L Niskin bottles attached to a Rosette sampler system for the deeper layers. Samples were carefully siphoned from the Niskin bottles into 100 ml narrow mouth Winkler bottles. Seven replicates were used to determine the initial oxygen concentration, and seven replicated bottles were incubated for 24 h on deck at 5 m depth temperature in the "dark" and in the "light". The bottles for "light" were incubated, adjusting the incident natural irradiance to that received *in situ* using neutral density screens. The water samples were taken during the early morning and were protected by a dark screen to avoid exposure to solar irradiance before the onset of the incubation. The penetration of irradiance at depth was measured with a Satlantic OCP-100FF submarine irradiance profiler and the percent of the surface irradiance reaching to the different sampling depths was calculated and used to adjust the incubation irradiance for the "clear" bottles to that *in situ* using neutral density screens.

Oxygen concentrations were analysed by Winkler titration using a potentiometric electrode and automated endpoint detection (Mettler Toledo, DL28 titrator) (Oudot *et al*., 1988). CR and NCP were calculated from changes in dissolved oxygen concentration after incubation of samples under "dark" and "light" conditions, respectively, and GPP was calculated as NCP – CR. Metabolism rates were vertically integrated using the trapezoid method, from the surface layer to the mean depth of the deep chlorophyll maxima (30 ± 5 m), with this closure depth corresponding to, on average, 4.0 ± 0.7 % of the irradiance incident below the surface. Integrated rates derived here are only reported to the nearest integer.

Temperature and salinity were determined from the Seabird SBE-25 CTD attached to the Rosette sampling system of the research vessel. Samples of 250 ml for chlorophyll a determinations were filtered through Millipore GF/F filters (pressure < 0.3 kg cm^{-2}), frozen and then extracted for 24 hrs with 90 % acetone. Fluorescence of the extracts was measured using a Shimadzu RF-5301 fluorometer (Yentsch and Menzel, 1963). During the two cruises, bacterial abundance was estimated by FACSCalibur flow cytometry (Beckton Dickinson©) of samples stained with SYTO13 (Gasol and del Giorgio, 2000).

Results

Chlorophyll a concentrations varied greatly along the Antarctic Peninsula (Table 3.3.1). Chlorophyll a concentration was somewhat higher during the 2009 cruise (Table

3.3.1), but not significantly so (Kruskal-Wallis test, $p > 0.05$), whereas bacterial abundance was four fold higher (mean ± SE = 16.6 ± 2.9 10^5 cell ml^{-1}) during the 2005 cruise compared to that during the 2009 cruise (mean ± SE = 4.4 ± 0.3 10^5 cell ml^{-1}, Kruskal-Wallis test, $p < 0.05$).

Table 3.3.1. Mean, SE, range and number of volumetric (mmol O_2 m^{-3} d^{-1}) GPP, CR and NCP, chlorophyll a concentration (Chl a, mg m^{-3}) and bacterial abundance (BA,

		ATOS-Antarctic 2009	ICEPOS 2005
	Mean	5.2	4.9
	SE	0.8	0.9
GPP	**Min**	0.3	0.2
	Max	45.1	16.8
	N	70	33
	Mean	1.9	1
	SE	0.2	0.2
CR	**Min**	0	0
	Max	8.2	4
	N	70	33
	Mean	3.7	3.9
	SE	0.8	0.8
NCP	**Min**	-2.5	-0.6
	Max	38.7	15.5
	N	77	33
	Mean	4.1	2
	SE	0.8	0.3
Chl a	**Min**	0.1	0.1
	Max	31.7	5.4
	N	69	33
	Mean	4.4	16.6
	SE	0.3	2.9
BA	**Min**	0.2	0.2
	Max	11.4	54
	N	70	33

Planktonic metabolic rates showed important variation across the study areas (Table 3.3.1, Fig. 3.3.2). The integrated metabolic rates (GPP, NCP and CR) were relatively uniform in the Bellingshaussen Sea, while the integrated metabolic rates

showed considerable variation across the Bransfield Strait, Antarctic Strait and Weddell Sea, ranging over 600-fold among stations (Fig. 3.3.2).

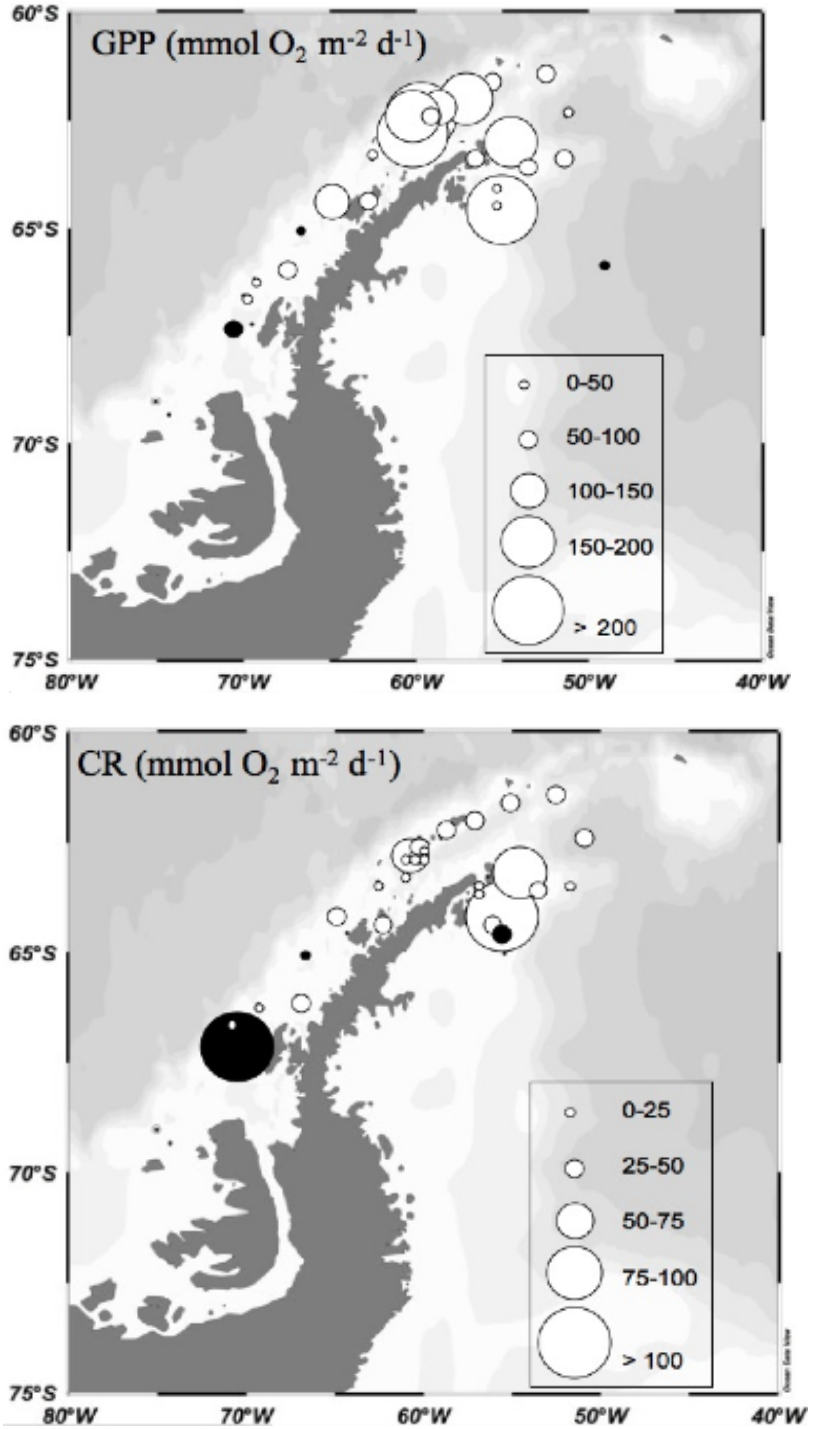

Figure 3.3.2. Integrated metabolic rates (GPP, CR and NCP, mmol O_2 m^{-2} d^{-1}) for the stations sampled during ICEPOS and ATOS-Antarctic cruises. The symbol size is scaled to the range reported at each cruise. Open circles represent autotrophic stations and full circles represent heterotrophic stations.

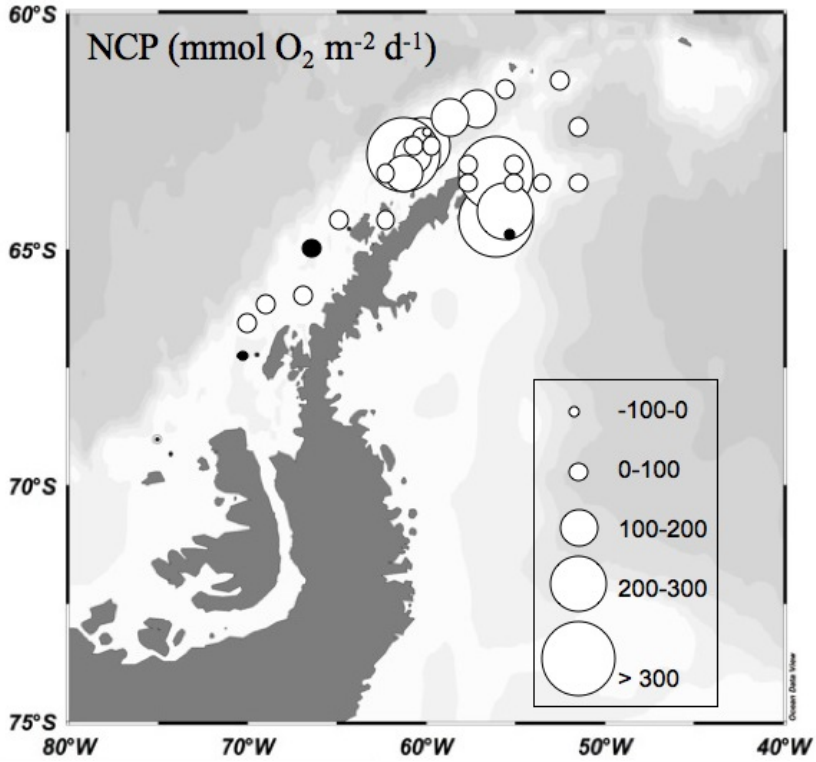

Figure 3.3.2. (*continued*) Integrated metabolic rates (GPP, CR and NCP, mmol O_2 m^{-2} d^{-1}) for the stations sampled during ICEPOS and ATOS-Antarctic cruises. The symbol size is scaled to the range reported at each cruise. Open circles represent autotrophic stations and full circles represent heterotrophic stations.

Volumetric and integrated metabolic rates were not significantly different (Kruskal-Wallis test, $p > 0.05$) between the ICEPOS and ATOS-Antarctic cruises, expect for volumetric CR rates which were significantly higher in ATOS-Antarctic than in ICEPOS (Kruskal-Wallis test, $p < 0.05$). Less than 12 % of the volumetric NCP rates were negative and only three of the 34 stations sampled supported net heterotrophic metabolism (integrated NCP < 0), representing < 9 % of the total sampled stations. Hence, the communities were strongly autotrophic along the study. Indeed, the mean gross primary production observed (GPP = 105.6 ± 20.3 mmol O_2 m^{-2} d^{-1}) was more than two-fold above the mean community respiration observed (CR = 40.4 ± 6.8 mmol O_2 m^{-2} d^{-1}, Table 3.3.2).

Table 3.3.2. Mean (± SE) integrated metabolism rates (GPP, NCP and CR, mmol O_2 m^{-2} d^{-1}) in the Antarctic Ocean derived from published reports for different regions of the Antarctic Ocean (Antarctic Peninsula: Arístegui *et al*., 1996; Serret *et al*., 2001; Agustí *et al*., 2004; Bellingshaussen Sea: Boyd *et al*., 1995; Ross Sea: Bender *et al*., 2000; Antarctic Circumpolar Current: Robinson *et al*., 1993; Dickson *et al*., 2001; Odate *et al*., 2002; Bender *et al*., 2003[a]; Hendricks *et al*., 2004; Reuer *et al*., 2007; Robinson, unpublished data[b]) and this study.
[a] Data collected from the publishing network PANGAEA
[b] Data from the data collection of Robinson and Williams, 2005.

Regions	Number of references	Number of observations	GPP	NCP	CR
Antarctic Peninsula	**This study**	**34**	105.6 ± 20.3	97.6 ± 26.7	40.4 ± 6.5
Antarctic Peninsula	**3**	**8**	189.9 ± 52.3	116.2 ± 32.8	66.3 ± 18.9
Bellingshaussen Sea	**1**	**5**	166.4 ± 11.3	71 ± 27.1	88.2 ± 17.9
Ross Sea	**1**	**21**	108.6 ± 25.6	88.0 ± 15.8	88.3 ± 18.8
Antarctic Circumpolar Current	**7**	**140**	160.1 ± 9.3	34.5 ± 4.3	93.2 ± 8.4
Global Antarctic Ocean	**13**	**208**	144.6 ± 7.6	50.1 ± 5.4	79.8 ± 5.8

Volumetric GPP and NCP rates increased significantly with increasing chlorophyll a concentrations (Fig. 3.3.3, R^2 = 0.29, $p < 0.0001$ and R^2 = 0.34, $p < 0.0001$, respectively). Volumetric GPP and CR rates increased significantly with increasing salinity (Fig. 3.3.4, $p < 0.05$) and increased with increasing temperature to decline at 3 ºC (Fig. 3.3.5, $p < 0.05$).

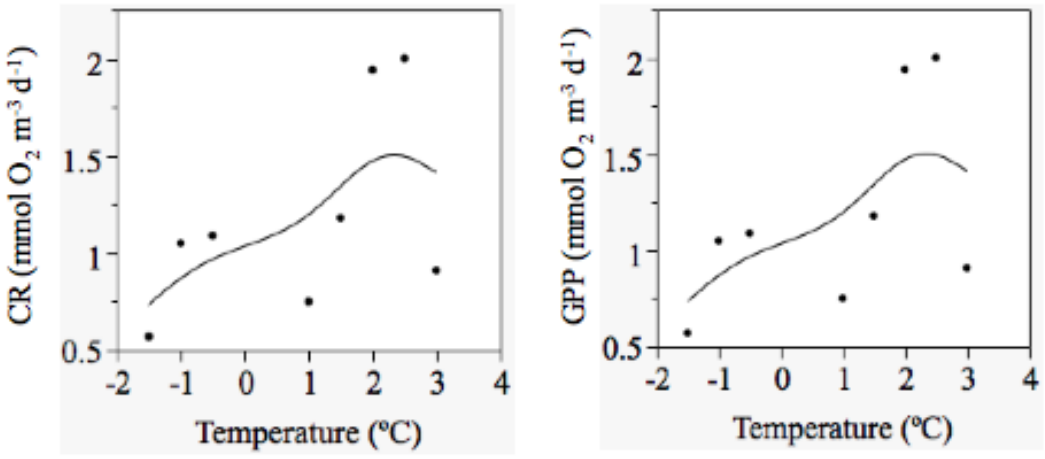

Figure 3.3.3. The relationship between the volumetric metabolic rates (CR and GPP, mmol O_2 m^{-3} d^{-1}) and the water temperature (T, ºC). Mean ± SE of estimates binned by 0.5 º C intervals shown. The solid lines represent the fit Spline (λ = 1) and with for CR and GPP, R^2 = 0.46 and 0.37, respectively.

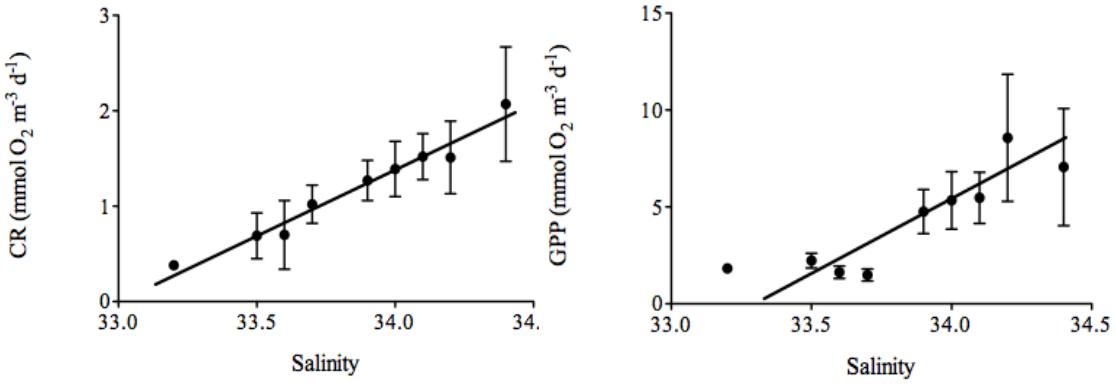

Figure 3.3.4. The relationship between the volumetric metabolic rates (CR and GPP, mmol O_2 m^{-3} d^{-1}) and the water temperature (T, ºC). Mean ± SE of estimates binned by 0.5 º C intervals shown. The solid lines represent the fit Spline (λ = 0.01).

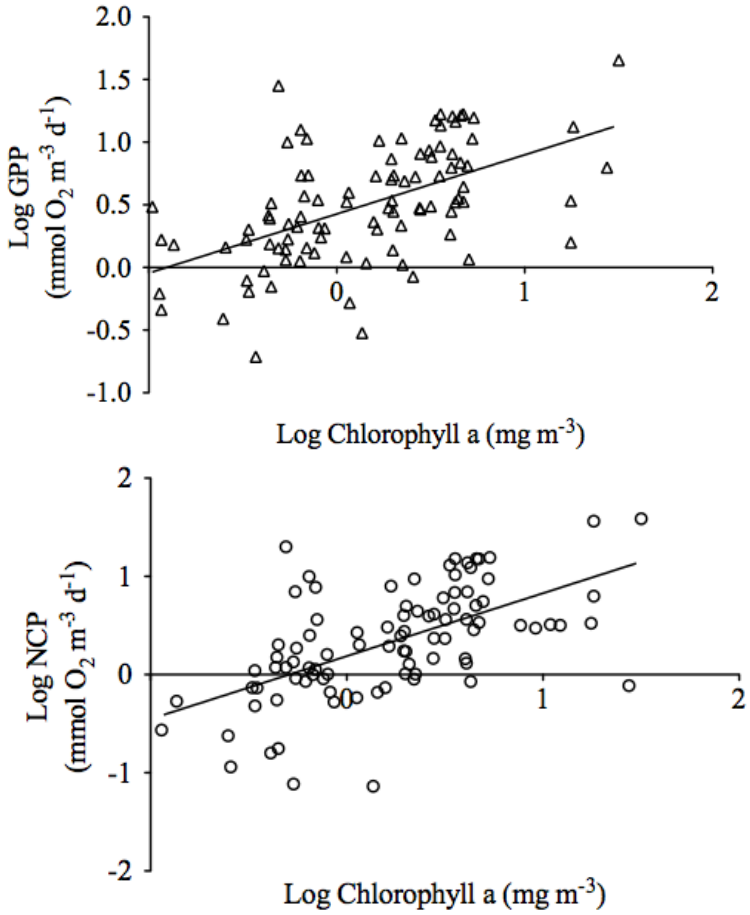

Figure 3.3.5. The relationship between the volumetric metabolic rates (CR and GPP, mmol O_2 m^{-3} d^{-1}) and salinity (S). The solid lines represent the fitted orthogonal regression with equations: CR = -45.85 (± 3.2) + 1.39 (± 0.1) S, R^2 = 0.97, $p < 0.0001$; GPP = -228.25 (± 41.8) + 6.87 (± 1.2) S, R^2 = 0.77, p = 0.0018. Mean ± SE of estimates binned by 0.1 units intervals shown.

Discussion

Summer planktonic metabolic rates showed considerable variability across the Antarctic Peninsula with particularly intense rates in the Weddell Sea. There was also important variability in chlorophyll a concentration and bacterial abundance, with significant phytoplankton blooms occurring in the Weddell Sea in both cruises. Across the Bransfield Strait, the Antarctic Strait and the Weddell Sea, the integrated metabolic rates ranged over 600-fold among stations (NCP ranged to 6.8 to 577.7 mmol O_2 m^{-2} d^{-1} in the Bransfield Strait). The Antarctic Peninsula region is relatively iron-sufficient (Sañudo-Wilhelmy *et al*. 2004; Tovar-Sánchez *et al*., 2007; Agustí *et al*., 2009), due to high inputs from submarine volcanoes (Petersen *et al*., 2004) and ash deposits derived from surface eruptions of the volcano at Deception Island (Deheyn *et al*., 2005). The waters around the Antarctic Peninsula are, thus, characterised by intense biological activity and the development of important phytoplankton blooms (Holm-Hansen *et al*., 1989). The variability in metabolic rates observed was partially attributable to variability in phytoplankton biomass, as reflected in the positive relationship between GPP and NCP and chlorophyll a concentrations, but also to differences in water masses, as reflected in the positive relationship between GPP and CR and salinity.

Plankton metabolic rates tended to be particularly intense in the Weddell Sea, including very high GPP rates (up to 45.1 mmol O_2 m^{-3} d^{-1}), consistent with high chlorophyll a concentrations and very low pCO_2 (minimum pCO_2 238.5 and 185 μatm in ICEPOS and ATOS cruises, respectively) in the Weddell Sea. The Weddell Sea is the Antarctic region supporting the most intense phytoplankton blooms (El-Sayed, 1978) and where the highest phytoplankton biomass has been reported (El-Sayed and Tagushi, 1981; Comiso *et al*., 1990; Estrada and Delgado, 1990; Nothig *et al*., 1991). The results presented identify the plankton community in the Weddell Sea as an intense CO_2 sink. What are the processes that sustain this important carbon sink capacity are, however, not resolved as yet. The most distinctive feature of the region where high NCP was observed in the Weddell Sea is the high cover by large icebergs, which may act as important iron sources, enhancing biological productivity (Raiswell *et al*., 2008). The Weddell Sea is also characterised by the presence of permanent cyclonic gyres (Knox, 2007) that may also enhance biological productivity, helping explain the high GPP of Weddell Sea communities.

Regional differences in integrated metabolic rates were examined further by pooling our estimates with those derived from previous studies across the Antarctic

Ocean (Arístegui *et al*., 1996; Agustí *et al*., 2004; Serret *et al*., 2001). Integrated NCP and CR rates were significantly lower in the Antarctic Peninsula than in the Antarctic Circumpolar Current. The integrated GPP rates observed during the two studied cruises were significantly lower (Kruskal-Wallis test, $p < 0.05$) than those observed in the past around the Antarctic Peninsula, but were comparable to those reported in the past for the Bellingshaussen Sea and the Ross Sea (Tukey test, $p > 0.05$, Table 3.3.2). The integrated CR rates observed during our cruises were also significantly lower than those observed in the Bellingshaussen and the Ross Sea in the past (Kruskal-Wallis, $p < 0.05$). The integrated metabolic rates (GPP, NCP and CR) were significantly lower than those observed in the Antarctic Circumpolar Current from previous published reports (Tukey test, $p < 0.05$, Table 3.3.2). The pooled data also showed that the mean annual community respiration, but not the GPP ($R^2 = 0.40$, $p = 0.17$, Fig. 3.3.6) in the Antarctic Peninsula region increased significantly with increasing water temperature ($R^2 = 0.69$, $p = 0.04$, Fig. 3.3.6).

The results presented showed that metabolic rates tend to increase with water temperature to reach a maximum at about 2.5 ºC, and decline abruptly at warmer temperatures. We tested further the positive relationship between metabolic rates and water temperature in the Antarctic Peninsula by extracting mean summer GPP, CR and water temperature by pooling all available studies for this region. Indeed, this analysis confirmed the positive relationship between mean summer GPP and CR and water temperature across years, which was stronger for CR than for GPP (Fig. 3.3.6). These relationships are consistent with predictions from metabolic theory (Brown *et al*., 2004), which predicts a steeper response of CR than GPP to temperature (Harris *et al*., 2006; López-Urrutia *et al*., 2006). The existence of a threshold temperature of about 3 ºC above which plankton metabolic rates decline in the Antarctic Ocean suggested by our results should be explored further, using also experimental approaches, as - if confirmed - this would have important consequences in a context of rapid warming of the Antarctic Peninsula region.

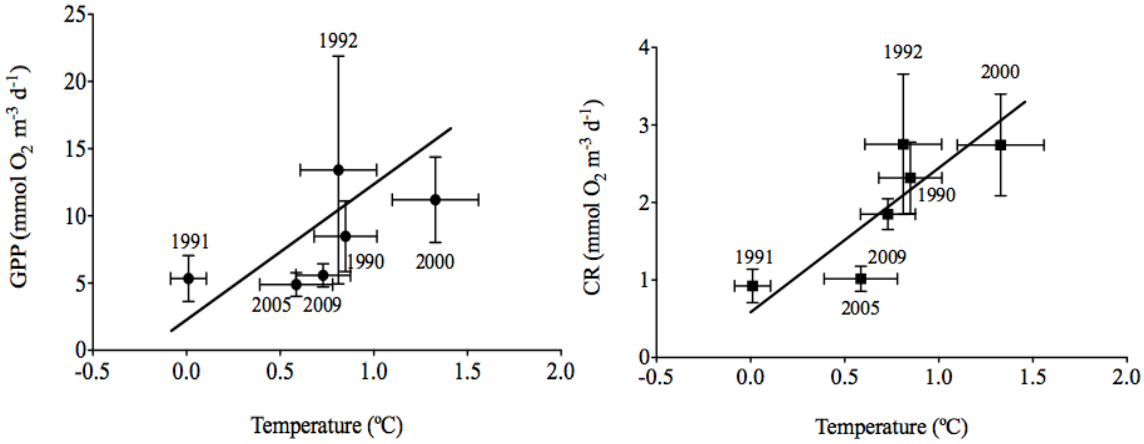

Figure 3.3.6. The relationship between the mean (± SE) GPP and CR (mmol O_2 m^{-3} d^{-1}) for surveys conducted in different years in the Antarctic Peninsula and water temperature (ºC). The solid line represents the fitted orthogonal regression with equations: GPP = 2.22 (± 2.61) + 8.24 (± 3.19) T, R^2 = 0.40, p = 0.17; CR = 0.56 (± 0.43) + 1.91 (± 0.53), R^2 = 0.69, p = 0.04.
Here are resumed 60 data from Serret *et al*., 2001; Arístegui *et al*., 2004; Agustí *et al*., 2004 and Agustí *et al*., 2005 and this study.

The results presented showed a strong positive relationship between metabolic rates and salinity, although the causes for this relationship are uncertain, as the relationship may simply reflect regional differences in metabolism with lower rates in low-salinity areas, rather than a casual relationship between salinity and metabolic rates. Indeed, freshwater inputs from melting icebergs are expected to enhance, rather than suppress, plankton metabolism. Freshwater released by melting icebergs enhances vertical stability (Wilson *et al*., 1986), an effect enhanced by the effect of the presence of a dense cover of icebergs, such as that characteristic of the Weddell Sea, in dumping mixing. Moreover, Sancetta (1992) suggested that icebergs enhance primary production by both physical (i.e. stratification) and biogeochemical mechanisms, as nutrient and iron supply with melting waters (Blain *et al*., 2007)

Polar basins rank among the most productive oceanic regions. Indeed, the mean GPP observed here around the Antarctic Peninsula is comparable to the mean GPP reported for Arctic planktonic communities (149.1 ± 22.8 mmol O_2 m^{-2} d^{-1}, Regaudie-de-Gioux and Duarte, in press). However, the mean CR mean observed in this study was much lower than that reported for the Arctic planktonic communities (111.5 ± 18.8 mmol O_2 m^{-2} d^{-1}, Regaudie-de-Gioux and Duarte, in press), resulting in contrasting P/R ratios between Antarctic (median P/R ratio 2.4) and Arctic (median P/R ratio 1.2)

communities. The striking difference in P/R between these plankton communities among Polar Regions may be partially accounted for by the lack of any significant terrestrial organic inputs into the Antarctic Ocean compared to the high inputs into the Arctic Ocean (Duarte, 2007; Regaudie-de-Gioux and Duarte, in press). This difference is also reflected in a much lower dissolved organic carbon concentrations in the surface waters of the Antarctic Ocean (51.3 ± 3.8 μmol C L^{-1}, Ogawa et *al*., 1999; Wiebinga and de Baar, 1998; Kähler et *al*., 1997) compared with those in the Arctic Ocean (93.8 ± 4.5 μmol C L^{-1}, Tovar-Sánchez *et al*., 2010).

The results presented here portray the Antarctic Peninsula as a region supporting intense net autotrophic planktonic metabolism (Table 3.3.2), although there are no reports of planktonic metabolism between March and November, so our understanding of seasonal dynamics is incomplete. Metabolic rates may be rising due to rapid warming of the Antarctic Peninsula. Whereas the direct effect of temperature on metabolic rates is greater for CR than for GPP, increased ice melting with warming may also contribute, with the fertilizer role of iceberg melting (Sancetta 1992; Blain *et al*., 2007), to enhance GPP, so the response of net community metabolism to warming remains uncertain and should be further examined.

Acknowledgements

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References

Agustí S, Duarte CM, Llabrés M, Agawin NSR, Kennedy H (2009) Response of coastal Antarctic phytoplankton to solar radiation and ammonium manipulation: an *in situ* mesocosm experiment. J Geophys Res 114: G01009

Agustí S, Duarte CM (2005) Threshold of gross primary production for planktonic metabolic balance in the Southern Ocean: An experiment test. Limnol Oceanogr 50(4): 1334-1339

Agustí S, Satta MP, Mura MP (2004) Summer community respiration and pelagic metabolism in upper surface Antarctic waters. Aquat Microb Ecol 35(2): 197-205

Arístegui J, Montero MF, Ballesteros S, Basterretxea G, VanLenning K (1996) Planktonic primary production and microbial respiration measured by ^{14}C assimilation and dissolved oxygen changes in coastal waters of the Antarctic Peninsula during austral summer: implications for carbon flux studies. Mar Ecol Prog Ser 132(1-3): 191-201

Blain S, Quéguiner B, Armand L, Belviso S et al (2007) Effects of natural iron fertilization on carbon sequestration in the Southern Ocean. Nature 446: 1070–1074

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. Ecology 85(7): 1771-1789

Capella JE, Ross RM, Quetin LB, Hofmann EE (1992).A note on the thermal structure of the upper ocean in the Bransfield Strait-South Shetland Islands region. Deep-Sea Res. 39 (7/8): 1221-1229

Comiso JC, Maynard NG, Smith WOJr, Sullivan CW (1990) Satellite ocean colour studies of Antarctic ice edges in summer and autumn. J Geophys Res 95(C6): 9481–9496

Cox PM, Betts RA, Jones CD, Spall CA, Totterdell IJ (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408: 184-187

Deheyn DD, Gendreau P, Baldwin RJ, Latz MI (2005) Evidence for enhanced bioavailability of trace elements in the marine ecosystem of Deception Island, a volcano in Antarctica. Mar Environ Res 60: 1–33

del Giorgio PA, Williams PJleB (2005) Respiration in Aquatic Ecosystems. Oxford University Press, 315 pp., New York

Duarte CM, Regaudie-de-Gioux A (2009) Thresholds of Gross Primary Production for the Metabolic Balance of Marine Planktonic Communities. Limnol Oceanogr 54: 1015-1022

Duarte CM (2007) Impactos del calentamiento global sobre los ecosistemas polares. Fundación BBVA, Bilbao

El-Sayed SZ (1978) Primary productivity and estimates of potential yields on the Southern Ocean, in Polar Research: To the Present and the Future, AAAS

Selected Symposia 7, Whinnie MA Ed., American Association for the Advancement of Science, Washington, DC, 141–160

El-Sayed SZ, Taguchi S (1981) Primary production and standing crop of phytoplankton along the iceedge in the Weddell Sea. Deep-Sea Res 28(A): 1017–1032

Estrada M, Delgado M (1990) Summer phytoplankton distribution in the Weddell Sea. Polar Biol 10: 413–422

Harris LA, Duarte CM, Nixon SW (2006) Allometric laws and prediction in estuarine and coastal ecology. Estuaries Coasts 29: 340-344

Holm-Hansen O, Mitchell BG, Hewes CP, Karl DM (1989) Phytoplankton blooms in the vicinity of Palmer Station. Polar Biol 10: 49–57

Houghton JT, Ding Y, Griggs DJ, Noguer M, van den Linden PJ, Dai X, Maskell K, Jonson CA (2001) Climate change 2001: The scientific basis. Cambridge University Press, Cambridge, 881 pp

Huntley M, Karl DM, Niler P, Holm-Hansen O (1991) Research of Antarctic Coastal Ecosystems Rates (RACER): an interdisciplinary field experiment. Deep-Sea Res 38: 911-941

Kähler P, Bjørnsen PK, Lochte K, Antia A (1997) Dissolved organic matter and its utilization by bacteria during spring in the Southern Ocean. Deep-Sea Res Pt II 44(1-2): 341-353

King JC (1994). Recent climate variability in the vicinity of the Antarctic peninsula. Int J. Climatol. 14: 357-369

Morris, E. M., Vaughan, D. G. (1994). Snow surface temperatures in West Antarctica. Ant Sci 6: 529-535.

Niler PP, Amos A, Hu JH (1991) Water masses and 200 m relative geostropic circulation in the western Bransfield Strait region. Deep-Sea Res 38: 943-959

Nöthig E-M, von Bodungen B, Sui Q (1991) Phyto- and protozooplankton biomass during austral summer in surface waters of the Weddell Sea and vicinity. Polar Biol 11: 293–304

Ogawa H, Fukuda R, Koike I (1999) Vertical distributions of dissolved organic carbon and nitrogen in the Southern Ocean. Deep Sea Res Pt I 46(10): 1809-1826

Ortega-Retuerta E, Reche I, Pulido-Villena E, Agustí S, Duarte CM (2008) Explorring the relationship between active bacterioplankton and phytoplankton in the Southern Ocean. Aquat Microb Ecol 52: 99-106

Oudot C, Gerard R, Morin P, Gningue I (1988) Precise Shipboard Determination of Dissolved-Oxygen (Winkler Procedure) for Productivity Studies with a Commercial System. Limnol Oceanogr 33(1): 146-150

Petersen S, Herzig PM, Schwarz-Schampera U, Hannington MD, Jonasson IR (2004) Hydrothermal precipitates associated with bimodal volcanism in the central Bransfield Strait, Antarctica. Miner Deposita 39: 358–379

Porter KG, Feig Y S (1980) The use of DAPI for identifying and counting aquatic microflora. Limnol Oceanogr 25: 943-948

Reynolds J (1981) The distribution of mean annual temperatures in the Antarctic Peninsula. Br. Antarct Surv Bull 54: 123-133

Sancetta C (1992) Primary production in the glacial North Atlantic and North Pacific oceans. Nature 360: 249-251

Sañudo-Wilhelmy SA, Olsen KA, Scelfo JM, Foster TD, Flegal AR (2002) Trace metal distribution off the Antarctic Peninsula in theWeddell Sea. Mar Chem 77: 157–170

Serret P, Fernandez E, Añadon R, Varela M (2001) Trophic control of biogenic carbon export in Bransfield and Gerlache Straits, Antarctica. J Plank Res 23(12): 1345-1360

Sullivan CW, Arrigo KR, McLain CR, Comiso JC, Firestone J (1993) Distribution of phytoplankton blooms in the Southern Ocean. Science 262: 1832–1837

Sverdrup U (1953) On conditions for the vernal blooming of phytoplankton. J Mar Sci 287-295

Tovar-Sánchez A, Duarte CM, Hernández-León S, Sañudo-Wilhelmy SA (2007) Krill as a central node for iron cycling in the Southern Ocean. Geophys Res Lett 34: L11601

Tovar-Sánchez A, Duarte CM, Alonso JC, Lacorte S, Tauler R, Galbán-Malagón C (2010) Impacts of metals and nutrients released from melting multiyear Arctic sea ice. J Geophys Res 115: C07003

Vaughan DG, Marshall GJ, Connolley WM, Parkinson CL, Mulvaney R, Hodgson DA, King JC, Pudsey CJ, Turner J (2003) Recent rapid regional climate warming on the Antarctic Peninsula. Clim Change 60: 243-274

Wiebinga CJ, de Baar HJW (1998) Determination of the distribution of dissolved organic carbon in the Indian sector of the Southern Ocean. Mar Chem 61(3-4): 185-201

Wigley TML, Raper SCB (2001) Interpretation of high projections for global-mean warming. Science 293(5529): 451-454

Wilson DL, Smith WOJr, Nelson DM (1986) Phytoplankton bloom dynamics of the western Ross Sea ice edge – I. Primary productivity and species-specific production. Deep-Sea Res 33(10): 1375-1387

Yentsch CS, Menzel DW (1963) A method for determination of chlorophyll and phaeophytin by fluorescence. Deep-Sea Res 10, 221-231

Chapter 3

Regional and global variability in the pelagic metabolism in the ocean

4 - Global patterns in oceanic planktonic metabolism

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Abstract

The rates gross primary production (GPP) and respiration (CR) of plankton communities in the ocean were evaluated here on the basis of a data set comprising 3597 estimates of GPP and CR by plankton communities within the euphotic zone. The data were extracted from 72 reports collected between 1984 and 2009, from open ocean and Mediterranean Sea. Metabolic differences were observed among the different oceanic regions, latitudinal bands and hemispheres. Despite the improvement relative to previous assessments, the data set on plankton metabolism represents less than 20 % of the ocean surface with a dominance of measurements in chlorophyll-rich, coastal waters and North Atlantic waters. Planktonic communities increased metabolic rates in coastal locations compared to open-ocean ones due to high nutrients concentration and organic carbon inputs. High respiration was observed in the Northern Hemisphere compared to that in the Southern Hemisphere due to the prevalence in the North to great human activity and river discharge. The results presented here shows that the scaling between GPP and CR is not universal across the ocean with a variability to 5 to 10-fold in the mean CR expected for any given GPP among oceanic basins. Heterotrophic communities were prevalent in the continental shelf stations and in the Northern Hemisphere, which receives relative high allochthonous inputs of organic carbon. Our estimates suggested a negative metabolic balance for the upper ocean, suggestion that has to be taken with caution due to the sparse coverage of estimates of metabolic rate in the ocean.

Introduction

Marine pelagic ecosystems contribute approximately half of the Earth's photosynthetic production (Falkowski, 1994; Field *et al*., 1998), supported by only 2 % of the Earth's photosynthetic biomass. In contrast to the dominance of autotrophic biomass on land, this small photosynthetic biomass supports a comparatively larger biomass of heterotrophs in the ocean (Gasol *et al*., 1997), which is associated with a high heterotrophic activity in oceanic plankton communities (Duarte and Cebrián, 1996; Duarte and Agustí, 1998; del Giorgio and Williams; 2005). Indeed, planktonic respiration may exceed primary production in individual plankton communities, particularly in the oligotrophic ocean (Duarte and Agustí 1998; Duarte *et al*., 2001; Duarte and Prairie, 2005; Duarte and Regaudie-de-Gioux, 2009). The suggestion that heterotrophic communities may prevail in oligotrophic ocean ecosystems raised

considerable debate (cf. Williams and Bower, 1999; Duarte *et al*., 2000; del Giorgio and Duarte, 2002; Karl *et al*., 1993). However, this controversy proved positive, in that is stimulated much-needed research to expand the meager empirical basis (Williams and del Giorgio, 2005) upon which these debates were originally based (Duarte *et al*., 1999; Williams and Bower, 1999; del Giorgio and Duarte, 2002).

A review of marine plankton metabolism in 2005 identified 957-paired observations of volumetric plankton metabolism and respiration (Robinson and Williams, 2005). These data were dominated by estimates derived from mid latitudes in the Atlantic Ocean, with very few estimates available for the rest of the ocean (cf. Figs. 9.2 and 9.12 in Robinson and Williams, 2005). The limited cover of the ocean then available precluded a robust evaluation of global and regional patterns in planktonic metabolism. Both are necessary, because much of the variance in global patterns in planktonic metabolism may derive from regional differences.

The prevalence of heterotrophy in some oceanic communities requires allochthonous inputs of organic carbon (del Giorgio and Duarte, 2002; Duarte and Prairie, 2005), which may derive from riverine inputs and atmospheric deposition (del Giorgio and Duarte, 2002). Riverine inputs enter the ocean through the coastal margins and are not evenly distributed in the ocean, with the Arctic Ocean receiving about 3000 km^3 y^{-1} of freshwater runoff, and the Equatorial Western Atlantic receiving 70140 km^3 y^{-1} of freshwater just from the Amazon and Orinoco rivers. Likewise, atmospheric inputs of organic carbon are highest in the Tropical Ocean, particular in the Eastern Atlantic Ocean (Dachs *et al*., 2005; Jurado *et al*., 2008). In addition, respiratory activity is likely to be elevated relative to primary production in warm tropical ocean waters (López-Urrutia *et al*., 2006). Hence, plankton metabolism is expected to exhibit significant variability across the ocean.

Here we examine global patterns in planktonic metabolic rates in the ocean. We do so on the basis of an expanded data set including 3597 volumetric estimates of planktonic metabolism in the photic layer of the ocean, more than twice as large as the data set compiled by Robinson and Williams (2005). We examined the distribution of volumetric and depth-integrated planktonic gross primary production (GPP), community respiration (CR), net community production (NCP = GPP – CR) and the ratio of GPP to CR (P/R ratio), examine the relationships between CR and GPP for the global data set and test for possible differences between coastal and open ocean

communities, between communities in different hemispheres and latitudinal bands, and between communities in different ocean basins.

Methods

A database containing volumetric and depth-integrated estimates of GPP, CR and NCP across the photic zone of the ocean was composed by compounding the data set compiled by Robinson and Williams (2005), with recently published data and our own unpublished data. The data was extracted from 72 individual reports collected between 1984 and 2009, from stations across the open ocean, including the Mediterranean Sea (Table 3.4.1). Most of the observations, 78 % of the GPP data and 98 % of the CR data were derived using the Winkler method (Carpenter, 1966; Carrit and Carpenter, 1966), 14 % of the GPP data and 2 % of the CR data were derived using the ^{18}O-labeled H_2O method (Grande *et al*., 1982; Bender *et al*., 1987), and 5 % and 3 % of the GPP data were derived from, respectively, the ^{14}C method (Steeman Nielsen, 1952) and triple oxygen isotope (Luz *et al*., 2000) methods. Depth-integrated rates, calculated using a conventional trapezoid method, were estimated for stations where rates were available for at least three depths within the euphotic layer. Carbon units were converted to oxygen-based values assuming a 1.25 molar stoichiometry between O_2 and C (Williams, 1979; Davies and Williams, 1984). Concurrent measurements of chlorophyll a concentration and bacterial abundance were also included in the data set where available.

Table 3.4.1. Sources of data to the database on plankton metabolism in the upper ocean, including the with number of observations (n data).

Reference	n data	Oceans	Reference	n data
		Mediterranean Ocean		
Cota, G.F., et al. (1996)	43		Duarte, C.M., et al. (2000)	3
Cottrell, M.T., et al. (2006)	112		Duarte, C.M., et al. (2004)	334
Holligan, P. M., et al. (1984)	7		Gonzalez, N., et al. (2008)	32
Regaudie-de-Gioux, A. and Duarte, C.M., in press	66		Lefevre, D. Unpublished data held at Robinson, C. Database (2005)	41
Robinson, C., et al. (2002) (1)	35		Lefevre, D., et al. (1997)	83
Vaquer-Sunyer, R. Unpublished data	59		Lucea, A., et al. (2005)	24
			Navarro, N., et al. (2004)	15
Aristegui, J. and Harrison, W. G. (2002)	40		Regaudie-de-Gioux, A., et al., Submitted	69
Aristegui, J. Unpublished data held at Robinson, C. Database (2005)	13		Robinson, C. (2000)	17
Aristegui, J., et al. (2004)	22		Satta, M. P., et al. (1996)	25
Gonzalez, N., et al. (2001)	64		VanWambeke, F., et al. (2004)	8
Gonzalez, N., et al. (2002)	117	**Antarctic Ocean**		
Gonzalez, N., et al. (2003)	12		Agusti et al., (2004)	197
Kiddon, J., et al. (1995)	46		Agusti, S., Duarte, C.M. (2005).	4
Lowry, R.K. (2004) (2)	151		Aristegui, J., et al. (1996)	22
Maixandeau, A., et al. (2005)	242		Bender, M.L. (2003) (2)	144
Moran, X.A.G., et al. (2004)	36		Bender, M.L., et al. (2000)	71
Navarro, et al., unpublished data (2003)	80		Blight, S. Unpublished data PhD thesis University of Wales; Bangor	17
Regaudie-de-Gioux, A. and Duarte, C.M., in press	71		Bouquegneau, J.M., et al. (1992)	14
Robinson, C. Unpublished (1)	13		Boyd, P. W., et al. (1995)	8
Robinson, C. Unpublished data held at Robinson, C. Database (2005)	4		Boyd, P.W., et al. (1995)(1)	8
Serret, P., et al. (1999)	45		Dickson, M.L, Orchado, J. (2001a)	125
Serret, P., et al. (2001b)	20		Hendricks, M.B., et al. (2004)	50
Serret, P., et al. (2001b); Robinson, C., et al. (2002)(1)	118		Lefèvre, D., et al. (2008)	42
Serret, P., et al. (2006)	87		Navarro, et al., unpublished data (2005)	33
Teira, E., et al. (2001)	31		Odate, T., et al. (2002)	12
Williams, P.J.leB. (1998); Williams, P.J.leB. (2000) (1)	143		Regaudie-de-Gioux, A. Unpublished data	77
			Reuer, M.K., et al. (2007)	47
Bender, M.L., et al. (1999)	109		Robinson, C. and Williams, P.J.LeB. (1993);Biscoe, J. (1991)	11
Duarte, C.M., Unpublished data	18		Robinson, C. Unpublished data held at Robinson, C. Database (2005)	11
Hashimoto, S., et al. (2005)	21		Serret, P. (2001) (2)	20
Juranek, L.W. and Quay, P.D. (2005)	20	**Indian Ocean**		
Karl, D., Church, M., et al. unpublished data (2007-2009)	18		Dickson, M.L., et al. (2001b)	117
MacAndrew, P.M., et al. (2007)	9		Lowry, R.K. (2004) (2)	27
Williams, P.J.LeB. and Purdie, D.A. (1991)	15		Robinson, C. (2003) (2)	40
Williams, P.J.LeB., et al. (2004)	55		Robinson, C. and Williams, P.J.leB. (1999)(1)	40
		3597		

Data also held at the British Oceanographic Data Centre (www.bodc.ac.uk)
Data held at PANGEA data collection
Data held at CMORE data collection

The resulting database contained 3597 estimates of volumetric metabolic rates derived from 1004 stations, for which these estimates were vertically integrated. The database is available from the digital repository of the Spanish Council for Scientific Research CSIC at https://digital.csic.es.xxx where the data set will be maintained and expanded in the future. This database provides an improved global coverage of planktonic metabolism, allowing the examination of global and regional patterns in planktonic metabolism (Table 3.4.1, Figs. 3.4.1 and 3.4.2). Most (40 %) of the observations in the data base derive from the Atlantic Ocean (Figs. 3.4.1 and 3.4.2) with a relatively high-density of data also available for the Antarctic Peninsula in the Southern Ocean, Eastern Arctic Ocean and the Mediterranean Sea, largely derived from our own research (Table 3.4.1, Figs. 3.4.1 and 3.4.2). In contrast, there is a remarkable paucity of data in the Pacific Ocean and the Indian Ocean (Figs. 3.4.1 and 3.4.2). The research effort on planktonic metabolism in the ocean increased greatly in the early 1990's, reaching around 626 observations reported between 1989 and 1992, and declined thereafter to a minimum of 181 reported between 2004 and 2007, with a subsequent increase to reach 344 observations reported between 2007 and 2009 (Fig. 3.4.3).

Global maps of the sampling locations were represented in geographic coordinate systems by using the WGS-1984 geocentric ellipsoid projection plotted using ArcGis 9.3 Geographic Information System software (ESRI). We imposed an 800 km x 800 km grid (with a total of 1113 gridboxes in the world's ocean) and sampling stations were assigned to the corresponding grid boxes. The goal of this assignment to a grid system was to calculate a maximum estimate of the ocean area encompassed by existing metabolic rate estimates, and produce similar calculations for individual basins, thereby allowing evaluation of the geographic spread of sampling efforts. In order to calculate the ocean surface encompassed within each gridbox, we used the projection "World Cylindrical Equal Area" for the Pacific Ocean, Atlantic Ocean, Indian Ocean and the Mediterranean Sea. For higher latitudes, we used "North Pole Lambert Azimuthal Equal Area" and "South Pole Lambert Azimuthal Equal Area" for areas north of 60 ºN and south of 60 ºS, respectively. The goal of the different grid system used was to minimize the distortion caused by the projection of the Earth surface.

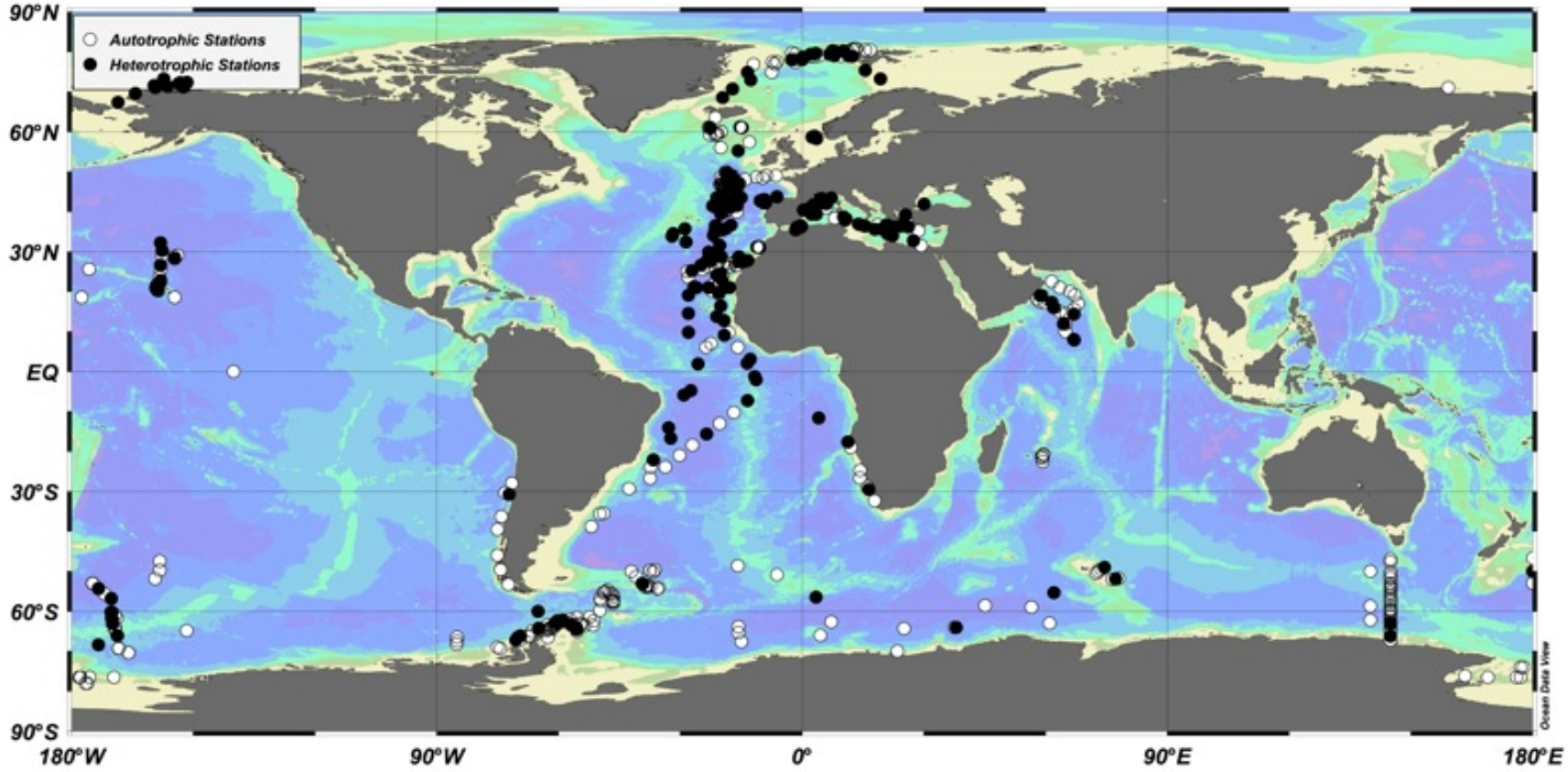

Figure 3.4.1. Map of the global database of planktonic metabolism observations. Black points represent heterotrophic stations and white points, autotrophic stations.

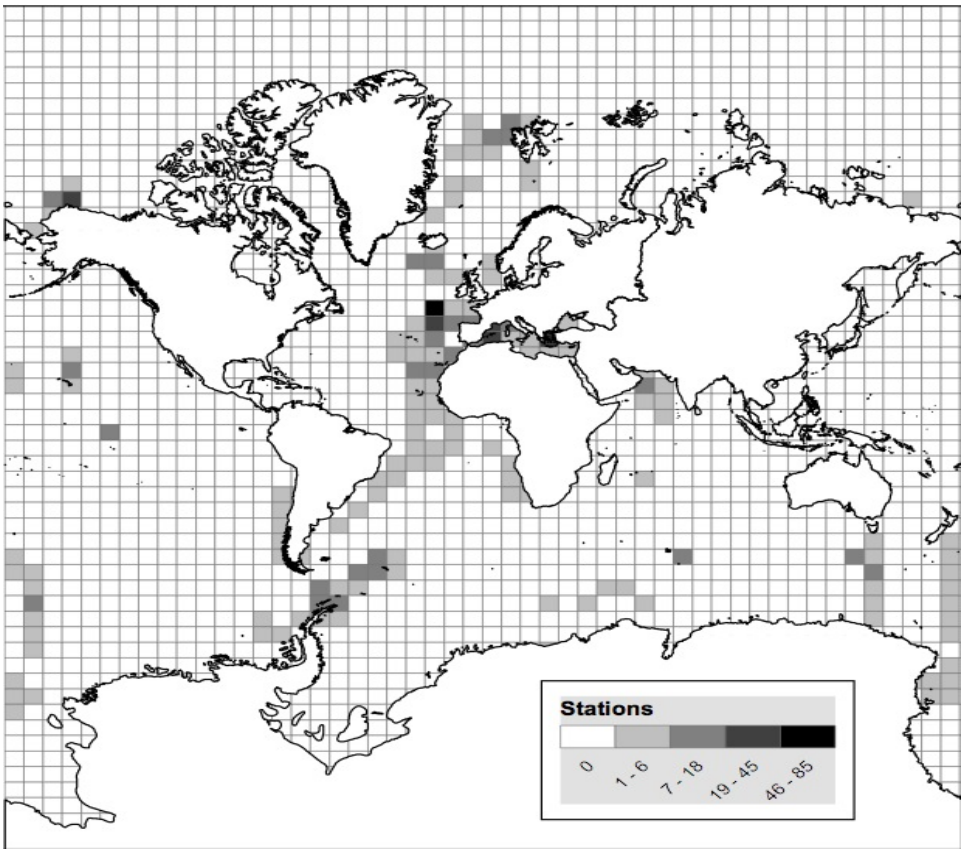

Figure 3.4.2. Geographic distribution of stations where planktonic metabolism have been studied. Grey scale indicates the number of stations per gridbox (64 000 km^2).

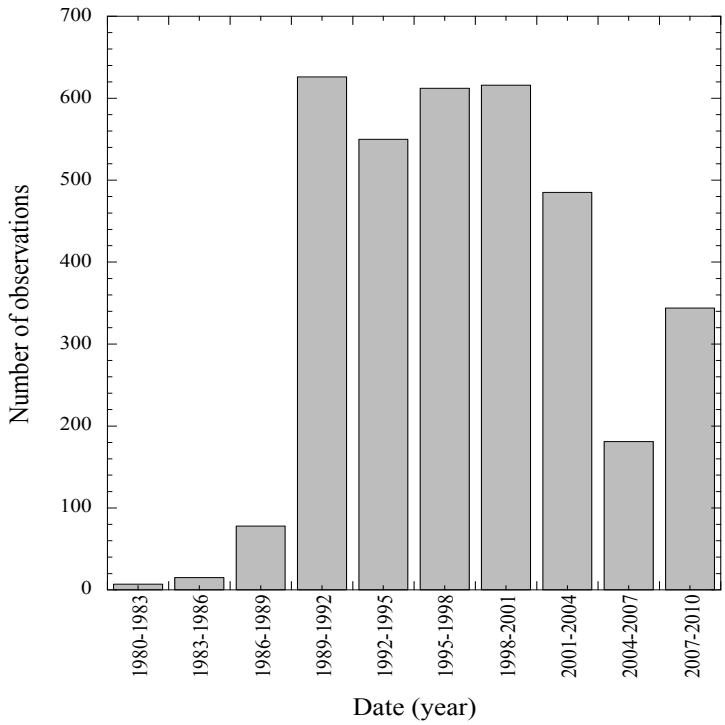

Figure 3.4.3. Yearly distribution of the number of observations of planktonic metabolism in the open ocean.

Regional analyses were conducted for the Atlantic Ocean, Arctic Ocean, Southern Ocean, Pacific Ocean and Indian Ocean, and the Mediterranean Sea, as well as for latitudinal bands: Polar (latitude 60º to 90º), Temperate (30 º to 60 º), Subtropical (10º to 30 º) and Tropical (10º N and 10º S) Oceans, and Hemispheres. Longhurst (1998) proposed an operational division of the Global Ocean in different biogeochemical provinces taking into account biogeochemical characteristics and seasonal cycles in phytoplankton growth, the optical field and the vertical transport of nutrients, and evaluated their primary production (PP). For each of those provinces where stations of our database were located, mean depth-integrated metabolic rates (GPP, CR and NCP) were evaluated (see Appendix). For those provinces, a strong correlation ($R^2 = 0.50$, $p < 0.05$, data not shown here) was observed between Longhurst's PP (Longhurst *et al*., 1995) and our mean GPP rates. This relationship suggested that metabolic rates for biogeochemical provinces where plankton metabolism has not yet been evaluated can be approximated from the integrated rates of the provinces supporting the closest PP for which data on plankton metabolism is available.

Mean values and parametric statistics were used to report statistics for variables normally distributed in the data set, and non-parametric statistics were used otherwise. The central tendency of the P/R ratio was represented by the median value, since the mean value is biased towards values > 1 (e.g. the mean P/R of two communities, one where GPP= 2 CR, and another one where GPP = ½ CR is 1.25). Model II regression was used to represent the relationship between variables, which were log-transformed when necessary to comply with the requirements of the analysis.

Results

The highest chlorophyll a concentrations (> 1.5 mg Chl a m^{-3}) in the data set were observed in the communities in Polar Oceans and the lowest ones in tropical and subtropical latitudes and in the communities studied in the Mediterranean Sea and Indian Ocean (< 0.75 mg m^{-3}, Table 3.4.2). The highest bacterial abundance (> 10^6 cell ml^{-1}) was observed in the communities studied in Polar basins and the lowest ones (< 6 10^5 cell ml^{-1}) in tropical and subtropical latitudes and the Mediterranean Sea (Table 3.4.2).

Table 3.4.2. Means ± SE (number of observations) of the integrated GPP, CR, NCP, Chlorophyll a concentration, bacterial abundance and P/R ratio medians ± SE (number of observations) for five different oceans, the Mediterranean Sea, and the percentage of heterotrophic stations for each oceanic region. We evaluated also the percentage of analysed area for each oceanic basin and for the global ocean. n.d. not determined

	Global Ocean	**Atlantic Ocean**	**Pacific Ocean**	**Indian Ocean**	**Arctic Ocean**	**Southern Ocean**	**Mediterranean Sea**
GPP	121.3 ± 4.6	107.9 ± 6.6	120 ± 13.7	169.3 ± 16.8	128.4 ± 24.5	138.2 ± 7.7	104.5 ± 23.4
(mmol O_2 m^{-2} d^{-1})	*650*	*239*	*52*	*37*	*61*	*209*	*65*
CR	97.9 ± 4.5	113.5 ± 7.6	91.0 ± 12.2	133.4 ± 9.9	100.5 ± 19.9	78.6 ± 5.9	78.2 ± 14.4
(mmol O_2 m^{-2} d^{-1})	*658*	*235*	*27*	*47*	*74*	*162*	*113*
NCP	18.6 ± 4.0	3.6 ± 5.9	48.8 ± 11.3	39.1 ± 18.2	20.0 ± 18.5	45.3 ± 5.1	-9.3 ± 15.2
(mmol O_2 m^{-2} d^{-1})	*805*	*311*	*42*	*46*	*78*	*211*	*117*
P/R	1.2 ± 0.1	1.2 ± 0.1	1.0 ± 0.1	1.5 ± 0.1	1.1 ± 0.3 (57)	1.6 ± 0.1	0.8 ± 0.1
	523	*209*	*27*	*35*	*47*	*150*	*64*
% heterotrophic stations	35 %	42 %	33 %	26 %	40 %	9 %	63 %
Chl a	1.2 ± 0.1	0.9 ± 0.0	0.5 ± 0.1	0.5 ± 0.0	1.4 ± 0.1	2.8 ± 0.3	0.5 ± 0.0
(mg m^{-3})	*1328*	*617*	*43*	*38*	*183*	*243*	*205*
Bacterial Abundance	1.0 ± 0.1	0.9 ± 0.0	n.d.	0.9 ± 0.0	1.7 ± 0.4	0.7 ± 0.1	0.6 ± 0.0
(10^6 cell ml^{-1})	*451*	*142*		*29*	*109*	*94*	*77*
% analysed area	17 %	38.9 %	8.5 %	9.2 %	9.2 %	11.5 %	n.d.

The majority of the chlorophyll a values (71 %) were observed between the range 1.6 mg Chl a m^{-3} to 0.25 mg Chl a m^{-3} and 41 % between 1 and 0.40 mg Chl a m^{-3}, suggesting that data base on metabolic rates in the ocean is biased towards productive communities, since globally most of the chlorophyll a values in ocean surface waters are comprised between 0.08 and 0.6 mg Chl a m^{-3} (Morel *et al*., 2001).

The distribution of observations on metabolic rates across the ocean remains sparse and imbalanced despite the improved geographical coverage of metabolic rate estimates in the present data set (Figs. 3.4.1 and 3.4.2). Indeed, there are no observations of planktonic metabolism rates for at least 83 % of the ocean surface (Figs. 3.4.1 and 3.4.2, Table 3.4.2). When estimates of planktonic metabolism are apportioned among biogeographic provinces, data are available for a total of 25 out of a total of 54 biogeochemical provinces (Longhurst, 1998), with the provinces for which data are available encompassing about 50 % of the ocean area. Whereas coverage is relatively high for the Atlantic Ocean, where metabolic rates have been estimated across 39 % of the area (Table 3.4.2), all other oceans remain grossly undersampled, as the stations where metabolic rates have been evaluated spread over less than 12 % of the surface of these oceanic basins (Figs. 3.4.1 and 3.4.2, Table 3.4.2). Research effort has also been greater over the coastal than over the open ocean (20 vs. 11 % of the area sampled, respectively) and for the Northern Hemisphere compared to the Southern Hemisphere (18 % and 12 % of the surface area sampled, respectively). The most intensively studied area of the ocean is located within the 40º to 50 º N latitudinal band, where 22 % of the ocean surface has been sampled (> 300 stations, Fig. 3.4.4), and the latitudinal band least studied for planktonic metabolism is that between 30º and 40 º S, where less than 7 % of the ocean surface has been sampled (Fig. 3.4.4). The median depth-integrated metabolic rates (GPP and CR) varied greatly along latitudinal bands (Fig. 3.4.5) with the highest GPP rates near the Equator and the Southern Ocean.

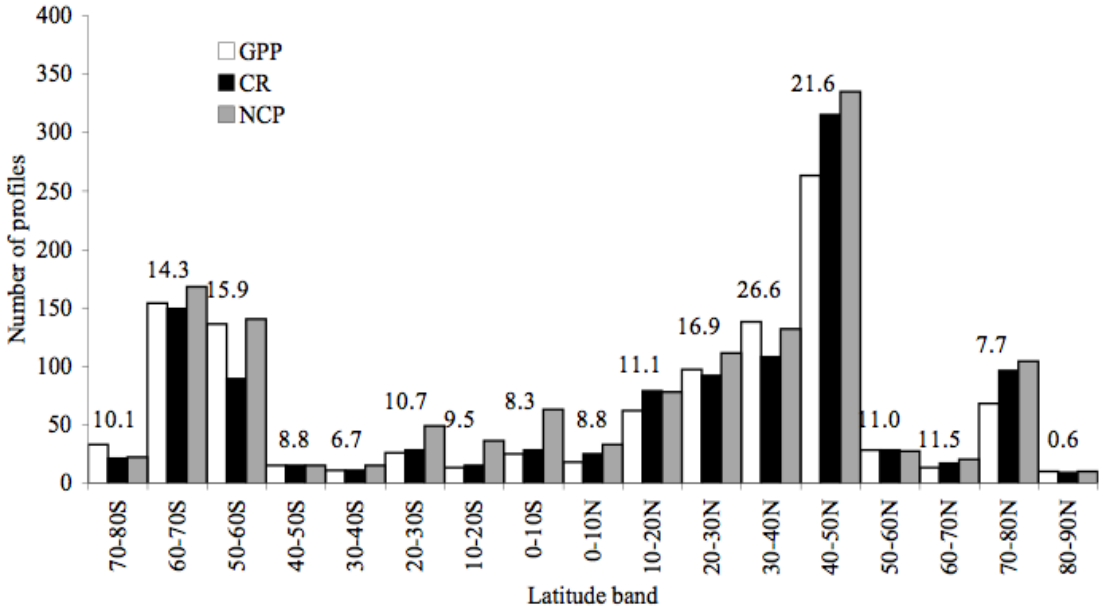

Figure 3.4.4. Latitudinal distribution of the number of observations of volumetric gross primary production (GPP), community respiration (CR) and net community production (NCP). The percentage of coverage of metabolic rates data for each latitude band is shown above each histogram.

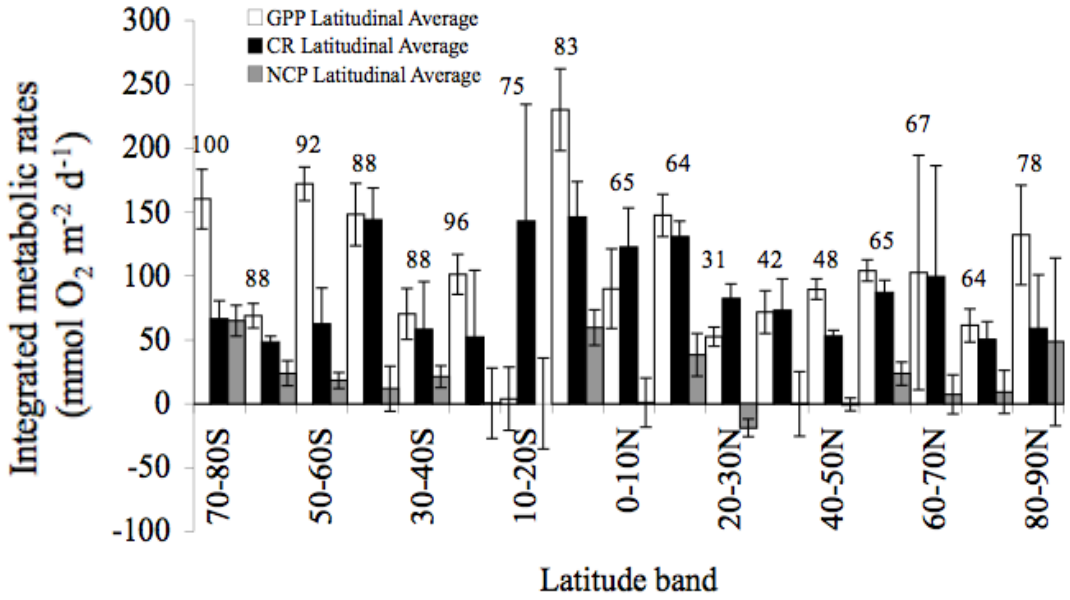

Figure 3.4.5. Comparison of the latitudinal distribution of integrated gross primary production, community respiration and net community production. (a) Medians for 10º latitude bands and (b) the total rates for each latitude band where data exist. The oceanic area for each latitude band proceeds from Robinson and Williams (2005), Fig. 9.12(a).

The highest median depth-integrated CR rates were observed between 20 ºS and 20 ºN (Fig. 3.4.5). These median rates should be considered approximations that may not fully represent the latitudinal bands, provided the poor coverage and bias towards coastal stations of the data available. There were significant differences in NCP and the prevalence of heterotrophic stations among latitudinal bands (ANOVA, $F = 159.11$, $p < 0.05$). Heterotrophic communities were far more prevalent in the Northern Hemisphere (> 50 % of stations), particularly between 30 and 60 ºN, than in the Southern Hemisphere (11.3 % of stations), where autotrophic communities prevailed across all latitudinal bands (Fig. 3.4.5).

There were significant differences in volumetric and integrated GPP and CR rates of stations sampled among ocean basins (ANOVA, $P < 0.001$, Tables 3.4.2, Fig. 3.4.6). The volumetric and integrated GPP were significantly higher in stations sampled in the Southern than in the Northern Hemisphere (ANOVA, $p < 0.05$, Fig. 3.4.7, 3.4.8 and 3.4.9). In contrast, the volumetric CR was significantly lower in stations sampled in the Southern than in the Northern Hemisphere (ANOVA, $p < 0.05$). No significant difference was observed between the integrated CR in stations sampled in the Southern and Northern Hemisphere (ANOVA, $p > 0.05$, Fig. 3.4.7, 3.4.8 and 3.4.9). The volumetric GPP and CR rates differed significantly between coastal stations (stations located in the continental shelf) and open-ocean stations, with the coastal stations supporting higher rates (ANOVA, $p < 0.05$).

There was evidence of seasonality in the metabolic rates of planktonic communities in stations sampled in both the Northern and Southern Hemisphere (Fig. 3.4.10), particularly for communities in latitudes > 30 º and there was no apparent seasonality for communities growing within 10 º from the Equator. In stations sampled in the Northern Hemisphere, metabolic rates (GPP, CR and NCP) were low during winter and fall, and increased during the spring to achieve maximum rates in the summer. Seasonal variations were smaller in stations sampled in the Southern Hemisphere (Fig. 3.4.10).

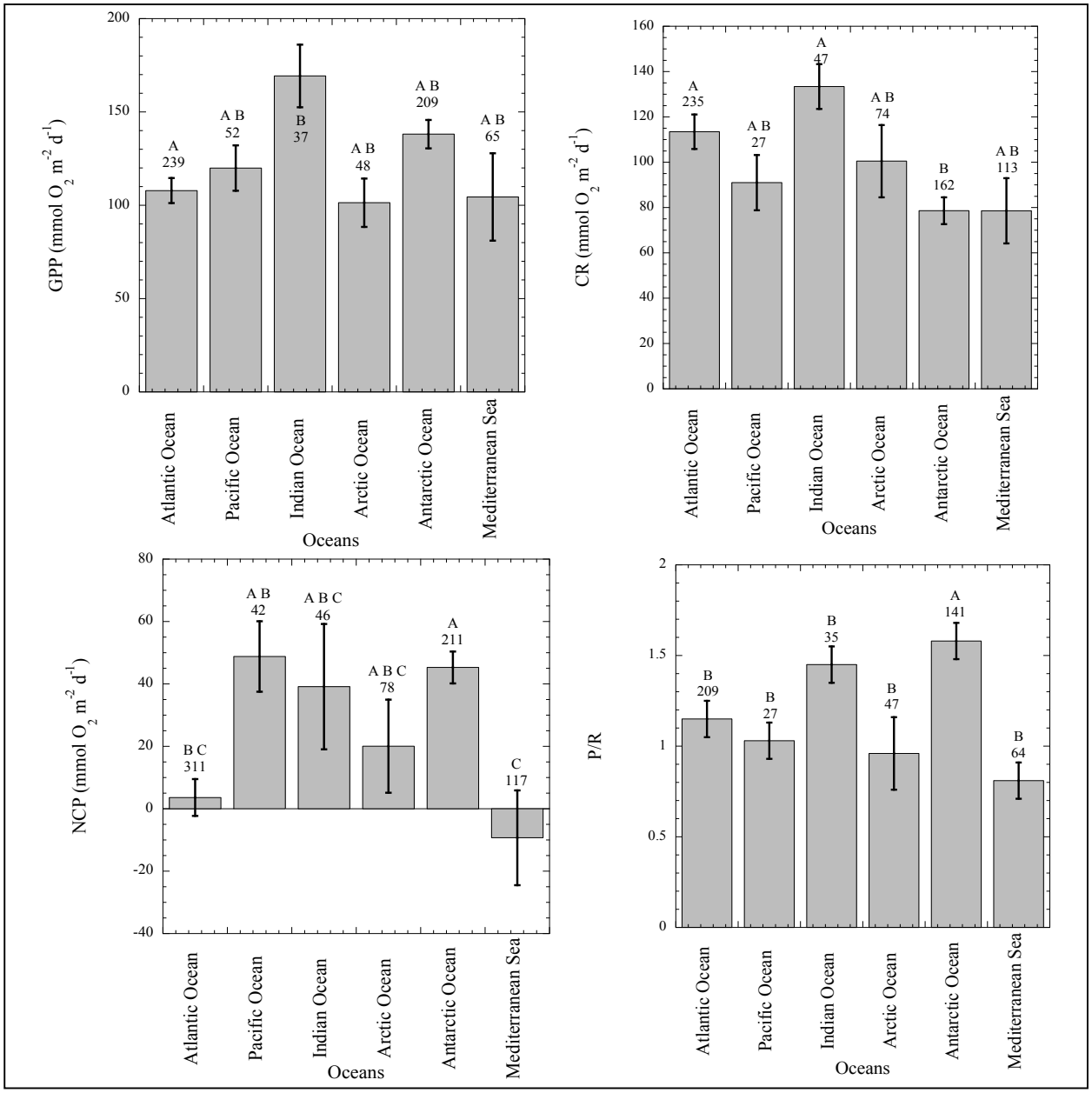

Figure 3.4.6. Mean of integrated metabolism rates (GPP, CR and NCP) and median of integrated P/R ratio in different oceans. The number of data for each ocean is shown above each histogram. Levels not connected by same letter are significantly different (Tukey test).

The median depth-integrated NCP rates were in general low, with negative values in the 20-30 ºN and 60-70 ºN latitudinal bands (Fig. 3.4.5). There were significant differences in volumetric and integrated NCP and P/R ratios among ocean basins (ANOVA, $p < 0.001$, Tables 3.4.2 and 3.4.3, Fig. 3.4.6). Plankton communities were strongly autotrophic in the Antarctic Ocean, which showed the highest median P/R ratio (P/R = 1.6), whereas the lowest median P/R ratio was found in the Mediterranean Sea (P/R = 0.8 Table 3.4.2, Fig. 3.4.6, Tukey HSD test, $p < 0.05$). The communities sampled in the

Mediterranean Sea also showed the lowest integrated NCP (mean -9.3 ± 15.2 mmol O_2 m^{-2} d^{-1}, Tukey HSD test, $p < 0.05$, Table 3.4.2, Fig. 3.4.6)

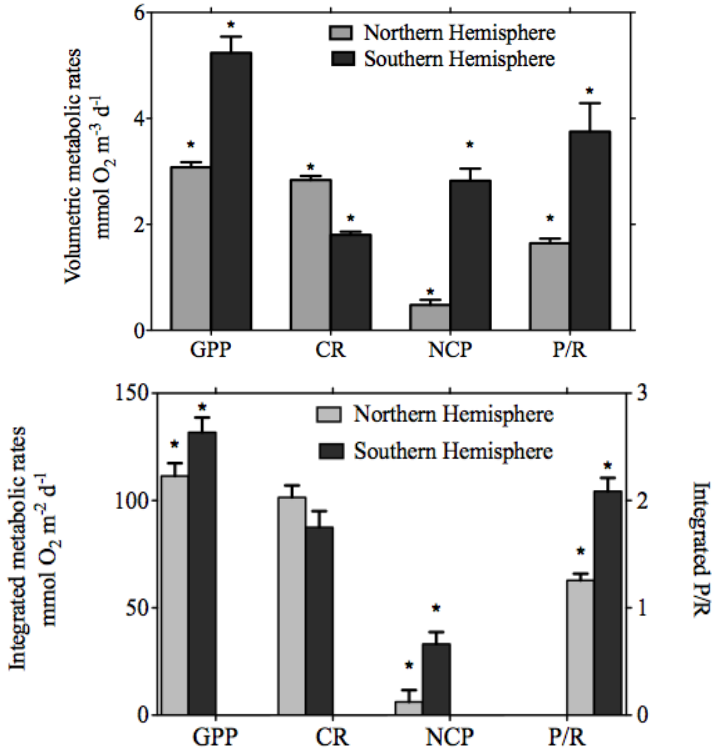

Figure 3.4.7. Mean of volumetric and integrated metabolism rates (GPP, CR, NCP and P/R) for the Northern and Southern Hemisphere. The metabolic levels connected by an asterisk are significantly different between the two hemispheres (Wilcoxon test, $p < 0.05$).

There were significant differences in the distribution of heterotrophic and autotrophic communities in the data set among ocean basins (ANOVA, $F = 69.19$, $p < 0.05$). Autotrophic communities were most prevalent in the Southern Ocean whereas heterotrophic ones were most abundant in the Atlantic Ocean and the Mediterranean Sea (Figs. 3.4.8 and 3.4.9). Approximately half (42 %) of the stations examined in the Atlantic Ocean supported net heterotrophic communities (Fig. 3.4.1 and Fig. 3.4.8, Table 3.4.2). The Arctic Ocean and the Mediterranean Sea also include a high proportion of net heterotrophic communities (47 % and 63 %, respectively, Fig. 3.4.1 and Fig. 3.4.8, Table 3.4.2). In contrast, most (91 %) of the stations investigated in the Southern Ocean supported autotrophic communities. Heterotrophic stations were significantly more prevalent on the continental shelf than in the open ocean (42 % and 39 % of the stations, respectively, ANOVA, $F = 15.48$, $p < 0.05$). Heterotrophic stations were also significantly more prevalent in the Northern Hemisphere than in the

Southern Hemisphere (51 % vs. 22 % of the stations, respectively, ANOVA, $F = 203.37$, $p < 0.05$).

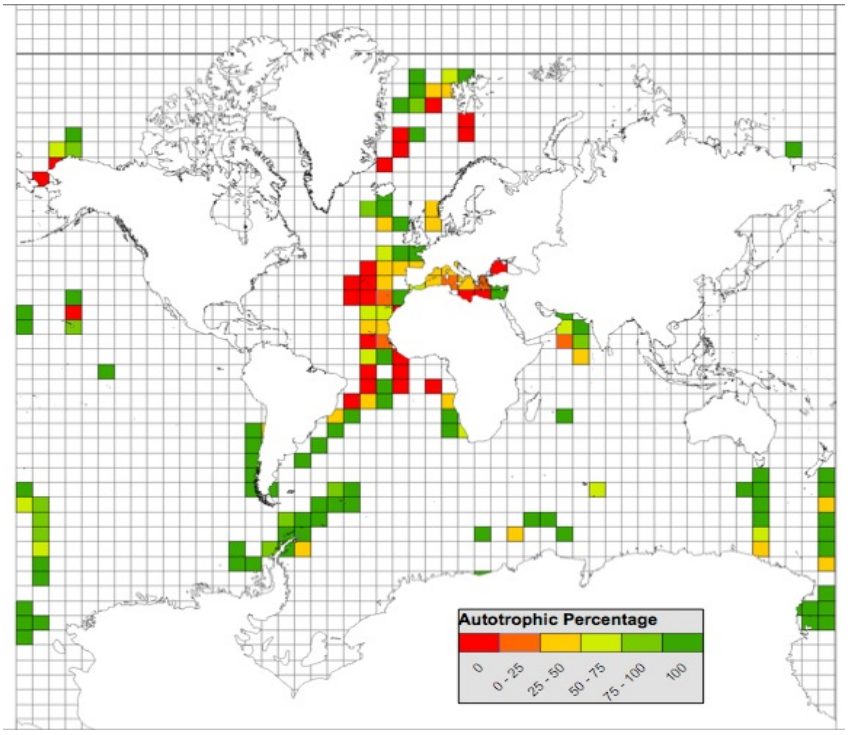

Figure 3.4.8. Geographic distribution of autotrophic percentage (when NCP < 0) for each gridbox where planktonic metabolism have been analysed. Colour gradation indicates the autotrophic percentage per gridbox.

Heterotrophic and autotrophic communities differed significantly in GPP and CR (t-test, $p < 0.05$) with heterotrophic communities supporting averages (± SE) GPP of 1.3 ± 0.1 mmol O_2 m^{-3} d^{-1} and CR of 2.9 ± 0.1 mmol O_2 m^{-3} d^{-1} compared to a mean GPP of 5.5 ± 0.2 mmol O_2 m^{-3} d^{-1} and a mean CR of 2.3 ± 0.1 mmol O_2 m^{-3} d^{-1} for autotrophic communities (Table 3.4.3). Similar differences in GPP between heterotrophic and autotrophic communities were observed for individual oceanic basins and latitudinal bands (t-test, $p < 0.05$, Table 3.4.3). Significant differences in CR among autotrophic and heterotrophic communities were observed for the majority of individual basins and latitudinal bands except for the Southern Ocean (t-test, $p > 0.05$, Table 3.4.3).

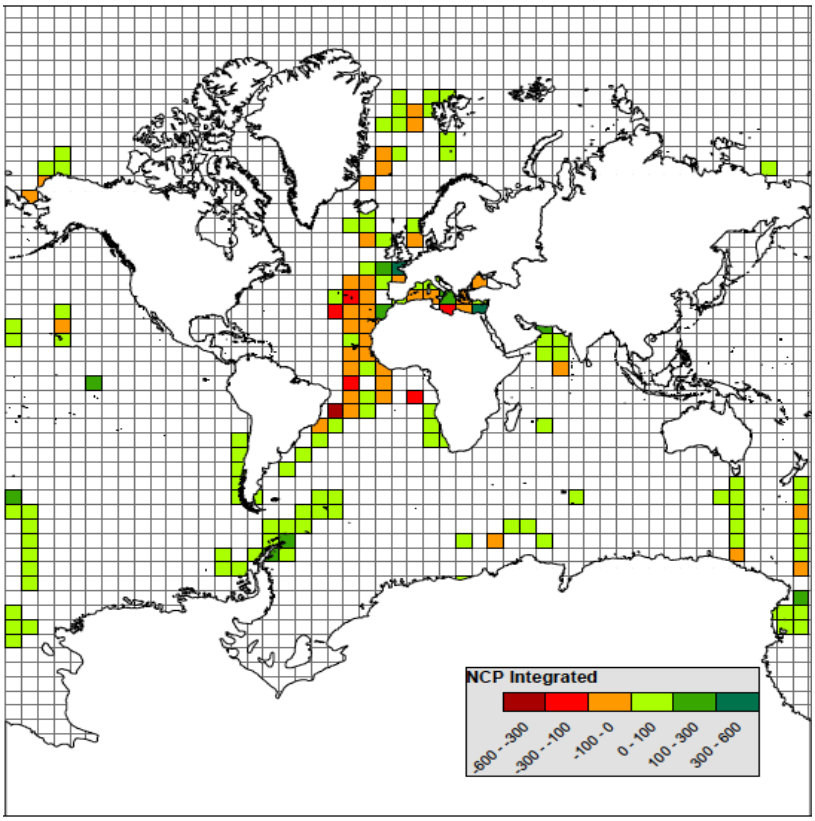

Figure 3.4.9. Geographic distribution of integrated NCP (mmol O_2 m^{-2} d^{-1}) for each gridbox where planktonic metabolism have been analysed. Colour gradation indicates the integrated NCP per gridbox.

GPP rates were significantly higher for autotrophic communities than those for heterotrophic communities (t-test, $p < 0.05$, Table 3.4.3) for the Southern and Northern Hemisphere whereas CR rates were similar for autotrophic and heterotrophic communities in the Southern Hemisphere (t-test, $p > 0.05$, Table 3.4.3). Autotrophic stations supported also greater chlorophyll a concentration than heterotrophic ones did (1.65 ± 0.10 mg Chl a L^{-1} vs. 0.81 ± 0.06 mg Chl a L^{-1}, data not shown here) but bacterial abundance did not differ significantly between heterotrophic and autotrophic stations (t-test, $p > 0.05$). Fitted logistic regression was used to derive the threshold GPP separating autotrophic from heterotrophic communities, which was estimated 1.50 mmol O_2 m^{-3} d^{-1} ($\chi 2$ test, $p < 0.0001$) and the threshold Chl a separating autotrophic from heterotrophic communities was found to be 0.34 mg Chl a L^{-1} ($\chi 2$ test, $p < 0.0001$).

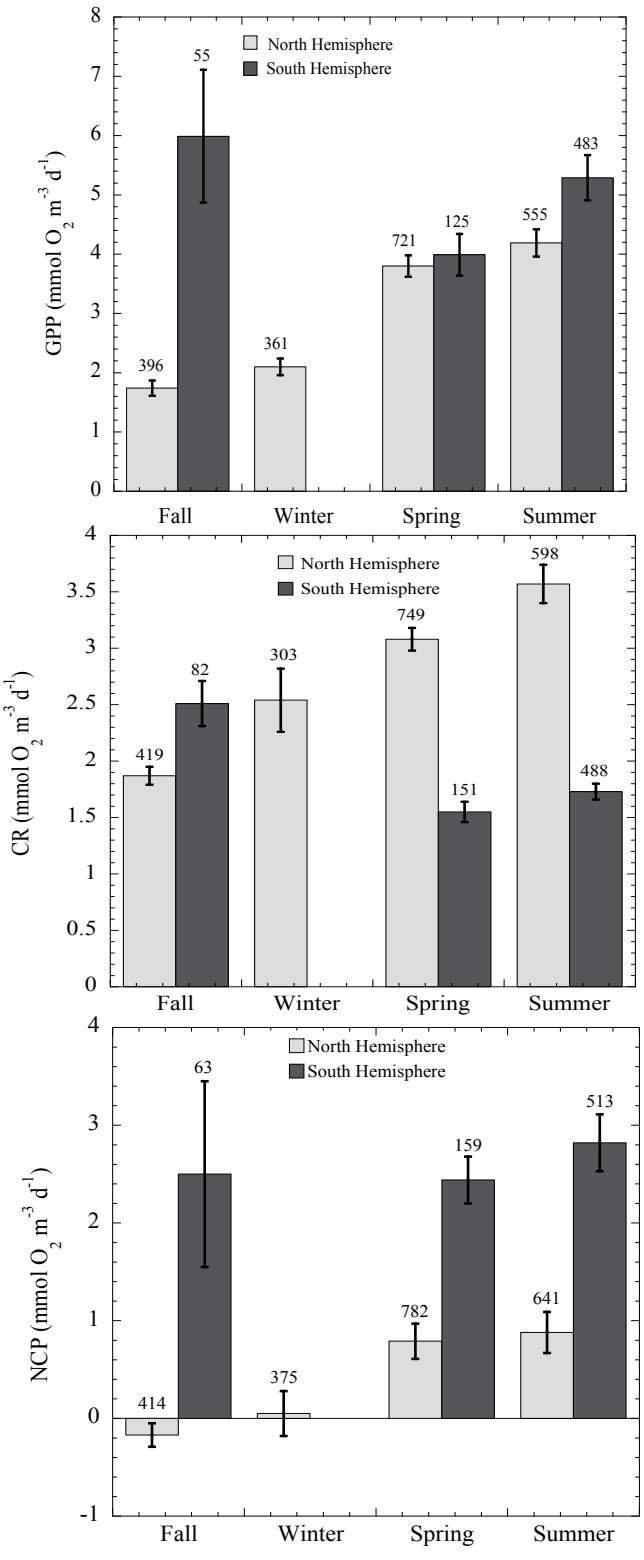

Figure 3.4.10. Mean of volumetric metabolism rates (GPP, CR and NCP) in different seasons across the North and South Hemispheres. The number of data for each ocean is shown above each histogram.

The threshold of GPP for balanced community metabolism, derived using logistic regression, tended to increase with increasing latitude and was highest for the Mediterranean Sea and Indian Oceans and lowest for the Southern Ocean (Table 3.4.4). The threshold GPP for balanced community metabolism did not differ between oceanic basins (Table 3.4.4) expect for polar basins, which showed the lowest threshold of GPP. The threshold of GPP for balanced community metabolism tended to be higher for the Northern Hemisphere and for coastal stations than for the Southern Hemisphere and open-ocean stations, respectively (Table 3.4.4).

Table 3.4.3. Mean of the volumetric metabolic rates (mmol O_2 m^{-3} d^{-1} ± SE) (GPP and CR) for the global ocean, different oceans, oceanic basins and different hemispheres for autotrophic (A) and heterotrophic (H) communities. Autrotophic and heterotrophic stations were statistically compared (t-test): NS, not significantly different ($p > 0.05$), *, $p \leq 0.05$, **, $p < 0.001$.

		GPP (mmol O_2 m^{-3} d^{-1})	SE		CR (mmol O_2 m^{-3} d^{-1})	SE	
Global Ocean	**A**	5.47	0.17	**	2.30	0.07	**
	H	1.34	0.06		2.93	0.10	
Arctic Ocean	**A**	6.10	0.86	**	2.80	0.58	*
	H	2.37	0.38		4.52	0.59	
Atlantic Ocean	**A**	5.21	0.27	**	2.44	0.11	**
	H	0.85	0.05		1.98	0.08	
Indian Ocean	**A**	6.92	0.33	**	3.70	0.17	*
	H	1.42	0.15		3.00	0.18	
Mediterranean Sea	**A**	3.89	0.34	**	2.25	0.16	**
	H	2.02	0.14		4.75	0.26	
Pacific Ocean	**A**	4.10	0.59	**	1.86	0.18	**
	H	0.78	0.11		1.09	0.11	
Southern Ocean	**A**	6.18	0.38	**	1.69	0.07	NS
	H	1.24	0.15		1.71	0.14	
Polar Basins	**A**	6.81	0.42	*	2.23	0.17	*
	H	1.76	0.20		3.01	0.32	
Temperate Basins	**A**	4.76	0.20	**	2.14	0.08	**
	H	1.39	0.07		3.19	0.14	
Subtropical Basins	**A**	5.40	0.35	**	2.95	0.15	**
	H	0.91	0.08		2.06	0.13	
Tropical Basins	**A**	3.91	0.30	**	2.05	0.16	*
	H	1.48	0.24		3.02	0.35	
Northern H.	**A**	5.05	0.18	**	2.62	0.11	*
	H	1.36	0.06		3.06	0.11	
Southern H.	**A**	6.35	0.37	**	1.75	0.07	NS
	H	1.23	0.12		1.97	0.14	

Table 3.4.4. Model II regression parameters (slope, intercept, R^2, P and number of observation, N) of the relation log CR vs. log GPP for the different oceans, Hemispheres, oceanic basins and for coastal and open ocean stations. The threshold of GPP (mmol O_2 m^{-3} d^{-1}) was evaluated when GPP equals CR and corresponding to the mean value of threshold GPP evaluated by logistic regressions.

	Slope (± SE)	Intercept (± SE)	R^2	P	N	Threshold
Arctic Ocean	0.97 (± 0.04)	0.76 (± 1.17)	0.24	< 0.0001	180	1.52
Indian Ocean	0.60 (± 0.04)	1.41 (± 1.09)	0.34	< 0.0001	189	2.72
Pacific Ocean	0.71 (± 0.05)	0.95 (± 1.07)	0.58	< 0.0001	141	0.95
Southern Ocean	0.84 (± 0.03)	0.50 (± 1.05)	0.35	< 0.0001	540	0.47
Atlantic Ocean	0.71 (± 0.01)	1.22 (± 1.05)	0.37	< 0.0001	1010	1.54
Mediterranean Sea	0.96 (± 0.04)	1.55 (± 1.05)	0.23	< 0.0001	575	3.36
Northern Hemisphere	0.78 (± 0.01)	1.29 (± 1.02)	0.34	< 0.0001	1995	2.01
Southern Hemisphere	0.84 (± 0.05)	0.53 (± 1.09)	0.34	< 0.0001	640	0.54
Polar Basins	0.93 (± 0.03)	0.54 (± 1.05)	0.34	< 0.0001	493	0.65
Temperate Basins	0.81 (± 0.02)	1.22 (± 1.02)	0.28	< 0.0001	1513	1.79
Subtropical Basins	0.71 (± 0.02)	1.21 (± 1.05)	0.45	< 0.0001	475	1.69
Tropical Basins	0.76 (± 0.10)	1.15 (± 1.22)	0.09	< 0.0016	108	1.90
Coastal Stations	0.82 (± 0.02)	1.12 (± 1.01)	0.21	< 0.0001	1420	1.13
Open ocean Stations	0.76 (± 0.02)	0.96 (± 1.02)	0.38	< 0.0001	1217	1.88

Volumetric GPP rates increased significantly with increasing chlorophyll a, although the relationship was relatively weak (Fig. 3.4.11), as described by the fitted model II regression equation:

Log GPP (mmol O_2 m^{-3} d^{-1}) = 0.52 (± 0.02) + 1.04 (± 0.03) log Chl a (mg m^{-3}) (Eq. 1)
(R^2 = 0.27, $p < 0.05$)

where the slope is close to 1.0, suggesting that GPP increases proportionally to chlorophyll a. Similarly, NCP and CR rates increased significantly with increasing chlorophyll a (R^2 = 0.18 and R^2 = 0.07, respectively, $p < 0.05$), but these relationships were weak.

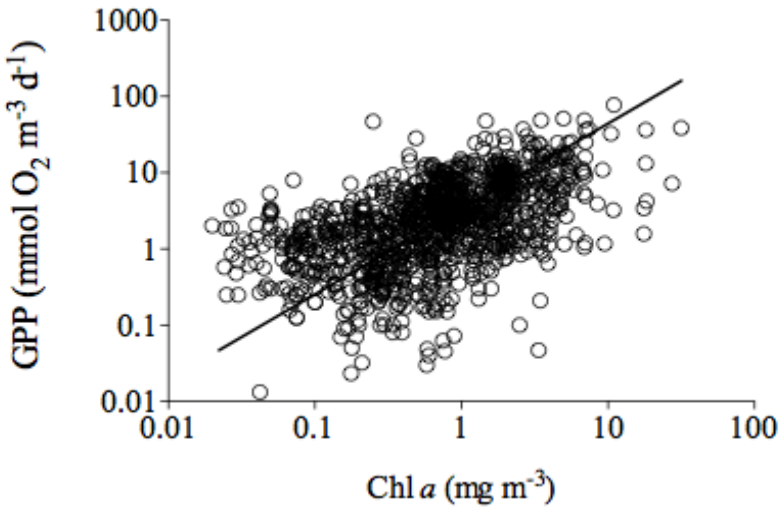

Figure 3.4.11. Log-log plot of GPP (mmol O_2 m^{-3} d^{-1}) and Chl a (mg m^{-3}). The fitted model II regression has the following equation: log GPP = 0.52 (± 0.03) + 1.04 (± 0.06) log Chla, R^2 = 0.27, $p < 0.05$, n = 1120.

Volumetric CR rates tend to increase with increasing bacterial abundance (Fig. 3.4.12), but the relationship was weak (R^2 = 0.04, $p < 0.05$). Significant, but also weak relationship between GPP and NCP rates with bacterial abundance were also observed (R^2 = 0.07 and 0.02, $p < 0.05$).

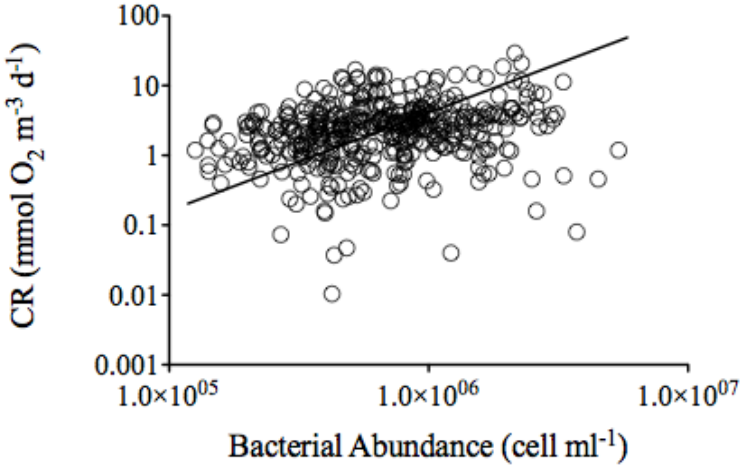

Figure 3.4.12. Log-log plot of CR (mmol O_2 m^{-3} d^{-1}) and bacterial abundance (BA, cell l^{-1}). The fitted model II regression has the following equation: log CR = -8.13 (± 0.40) + 1.45 (± 0.07) log BA, $R^2 = 0.04$, $p < 0.05$, n = 415.

Community respiration rates increased with increasing gross primary production (Fig. 3.4.13) as described by the fitted model II regression equation,

Log CR (mmol O_2 m^{-3} d^{-1}) = 0.02 (± 0.01) + 0.80 (± 0.01) log GPP (mmol O_2 m^{-3} d^{-1}) (Eq. 2)

($R^2 = 0.30$, $p < 0.05$)

where the slope is < 1 indicating that community respiration is highest relative to GPP in communities with low GPP.

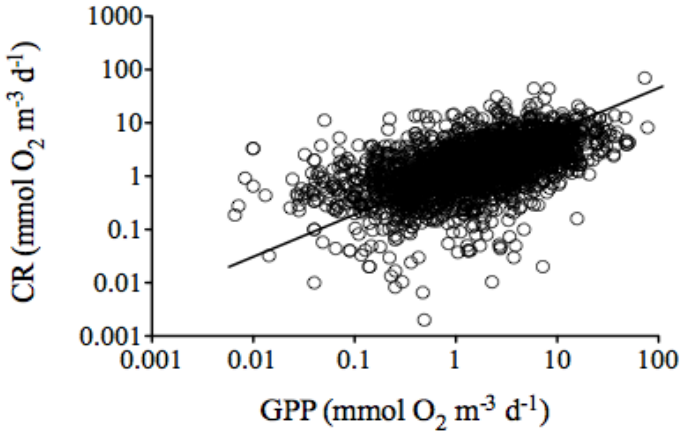

Figure 3.4.13. Relation between log CR (mmol O_2 m^{-3} d^{-1}) and log GPP (mmol O_2 m^{-3} d^{-1}) for the global ocean. The fitted regression has the following equation: log CR = 0.80 (± 0.03) log GPP + 0.02 (± 0.03), $R^2 = 0.3$, $p < 0.05$, n = 2635.

The relationship between CR and GPP did not differ significantly among hemispheres or latitudinal bands (ANCOVA, t-test, $p > 0.05$), however, it was significantly different in the Indian Ocean, compared to other oceans (ANCOVA, t-test, $p > 0.05$, Fig. 3.4.14). The slope of log CR vs. log GPP was highest for the Arctic Ocean and the Mediterranean Sea (slope > 0.90, Table 3.4.4) and lowest for the Indian Ocean (slope = 0.60, Table 3.4.4 and Fig. 3.4.14). Communities in polar oceans had steeper log CR vs. log GPP slopes (slope = 0.93) than those in the subtropical ocean (slope = 0.71). The slope of log CR vs. log GPP tended to be somewhat steeper for the Southern Hemisphere than it was for the Northern Hemisphere (0.84 ± 0.05 vs. 0.78 ± 0.01, ANCOVA, t-test test, $p < 0.05$, Table 3.4.4) and was also somewhat steeper for coastal communities than for open-ocean ones (0.82 ± 0.0 vs. 0.76 ± 0.02, ANCOVA, t-test test, $p < 0.05$, Table 3.4.4).

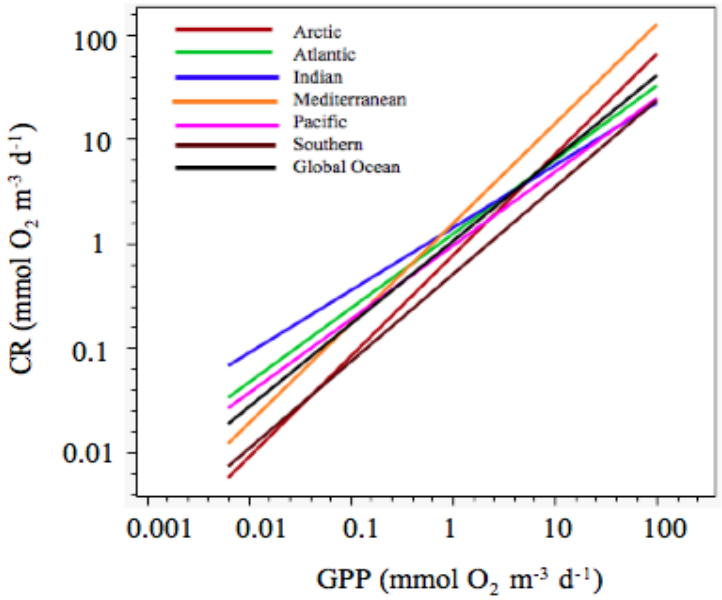

Figure 3.4.14. Relationship between CR (mmol O_2 m^{-3} d^{-1}) and GPP (mmol O_2 m^{-3} d^{-1}) for the different oceanic basins. Regressions parameters are presented in Table 3.4.5.

The mean volumetric and depth-integrated GPP rates in the data set (3.60 ± 0.10 mmol O_2 m^{-3} d^{-1} and 121.3 ± 4.6 mmol O_2 m^{-2} d^{-1}, respectively) were significantly higher (t-test, $p < 0.05$) than the mean volumetric and depth-integrated CR rates (2.6 ± 0.1 mmol O_2 m^{-3} d^{-1} and 97.9 ± 4.5 mmol O_2 m^{-2} d^{-1}, respectively Table 3.4.3). Accordingly, both the mean volumetric and depth-integrated net community production rates in our data set (1.1 ± 0.1 and 18.6 ± 4.0, respectively) were significantly higher than 0 (one sided t-test, $p < 0.05$, Table 3.4.5) and the median P/R ratios were > 1 (Table 3.4.4), indicative

of an overall autotrophic metabolism in the extended data set of ocean metabolism compiled here. Whereas autotrophic communities prevailed in the data set, heterotrophic ones were also abundant, comprising 35 % and 43 % of the depth-integrated and volumetric estimates in the data set, respectively (Table 3.4.3). Scaling of our results to the global ocean using Longhurst's Biogeochemical Provinces (Longhurst *et al*., 1995; Longhurst 1998, see Appendix) indicated that autotrophic communities (depth-integrated NCP < 0) are expected to extend over 176 106 km^2 of the ocean, with a mean depth-integrated GPP mean value of 170.4 ± 19.9 mmol O_2 m^{-2} d^{-1}, while heterotrophic communities are expected to extend over 145 106 km^2 of the ocean, supporting a mean depth-integrated GPP of 97.5 ± 15.6 mmol O_2 m^{-2} d^{-1} (see Appendix). Scaling of global metabolic rates from the mean values for the different biogeochemical provinces and their area extent deliver an estimated global GPP of GPP global = 144.8 Pg C y^{-1}, with CR global = 169.6 Gg C y^{-1} and a negative global NCP at -19.22 Gg C y^{-1}, although these values carry considerable uncertainty, largely due to the sparse coverage of estimates of metabolic rate in the ocean.

Table 3.4.5. Mean (± SE), range (Minimum – Maximum), and number of observations of GPP, CR, NCP and the median (± SE), range (Minimum – Maximum), and number of observations of P/R ratio, integrated (mmol O_2 m^{-2} d^{-1}) and volumetric (mmol O_2 m^{-3} d^{-1}).

	GPP	CR	NCP	P/R	% heterotrophic rates
Integrated (± SE)	121.3 ± 4.6	97.9 ± 4.5	18.6 ± 4.0	1.2 ± 0.1	35 %
Range	0 - 1447.3	0 - 1122.8	-1057 - 1118	0 - 12.7	
N	650	658	805	523	
Volumetric (± SE)	3.6 ± 0.1	2.6 ± 0.1	1.1 ± 0.1	1.2 ± 0.2	43 %
Range	0 - 77.9	0 - 69.7	-38.7 - 70.5	0 - 31.6	
N	2835	2915	3140		
Volumetric surface water (< 10 m) (± SE)	2.3 ± 0.1	2.0 ± 0.1	0.5 ± 0.1	1.1 ± 0.2	48 %
Range	0 - 32.5	0 - 69.7	-21.7 - 70.5	0 - 31.6	
N	1418	1544	1627	1364	

Discussion

The results presented are based on an expanded data set (3597 communities and 1004 individual stations) on metabolic rates by plankton communities in the photic zone of the ocean (Table 3.4.1, Fig. 3.4.1 and Fig. 3.4.2). In addition to the greater sample size, the present database encompasses communities in all oceans and the Mediterranean Sea, for different periods of the year. This represents an improvement relative to previous assessments, such as that of Robinson and Williams (2005), who compiled 957-paired observations of volumetric plankton metabolism and respiration,

dominated by estimates derived from mid latitudes in the Atlantic Ocean, with very few estimates available for the rest of the ocean (cf. Figs. 9.2 and 9.12 in Robinson and Williams, 2005). Despite these improvements, the data set on plankton metabolic rates analysed here encompasses < 17 % of the ocean surface, and is highly imbalance, with a dominance of measurements in chlorophyll-rich, coastal waters and N. Atlantic waters (40 % of all measurements), with a particularly poor representation of the South Pacific and South Indian Oceans. Less than 8.5 % of the Pacific Ocean, the largest ocean basin, has been ever assessed for metabolic rates. In addition, values for the polar oceans are dominated by summer values. Provided these limitations, the average values presented cannot be directly extrapolated to derive global estimates of gross primary production and respiration of planktonic communities nor the metabolic balance of the ocean. We are, thus, still far from achieving a globally-balanced representation of metabolic rates in the global ocean. However, this analysis provides can help direct the research community contributing to this topic into targeting the regions and seasons underrepresented in the data set, thereby helping build a data base allowing global scaling of ocean metabolism. Efforts should concentrate in the Southern Hemisphere, as the ratio of available data in the Southern and Northern Hemispheres is opposite to the land to ocean ratio in the Southern and Northern Hemispheres of about 1 to 4 and 1 to 1.5, respectively.

The mean integrated metabolic rates in the present study do not differ significantly (t-test, $p > 0.05$) from those reported by Robinson and Williams (GPP = 115.8 mmol O_2 m^{-2} d^{-1}, CR = 114 ± 5.1 mmol O_2 m^{-2} d^{-1}, Robinson and Williams 2005). However, the mean integrated NCP derived from this data set is half of that (30.7 mmol O_2 m^{-2} d^{-1}) reported by Robinson and Williams (2005). However, these rates are expected to be overestimates, as there is a particularly low density of observations in the oligotrophic gyres of the ocean (Fig. 3.4.1), which encompass 70 % of the ocean surface and where the lowest metabolic rates are found (Duarte and Agustí, 1998). The depth-integrated GPP rates averaged 112 ± 5 mmol O_2 m^{-2} d^{-1} compared to a mean depth-integrated CR value of 98 ± 5 mmol O_2 m^{-2} d^{-1} in the data set. Metabolic differences were observed among the different oceanic regions, latitudinal bands and hemispheres. Plankton communities supported, as expected, increased metabolic rates in coastal compared to open ocean locations, likely a result of the increased nutrient and organic carbon inputs in the coastal zone. Plankton communities in the Northern Hemisphere supported a higher respiration rate than those in the Southern Hemisphere, but GPP

followed the opposite pattern. Allochthonous carbon inputs due to human activity and river discharge are much greater in the Northern Hemisphere than in the Southern Hemisphere consistent with the differences in community respiration. The high GPP in the Southern Hemisphere is likely a consequence of a bias in cover toward high production areas, such as the Eastern Pacific and Benguela upwelling zones, the most productive regions of the world's oceans, and other productive areas, such as the Antarctic Peninsula and the Patagonian Shelf.

The relationship between GPP and chlorophyll a concentration provided could possibly provide an avenue to scale up GPP at the global scale from chlorophyll a concentration. However, this relationship account for only 20 % of the variance in GPP, indicating that predicting GPP from chlorophyll a concentration involves considerable uncertainty, and that factors other than chlorophyll a concentration, possibly including irradiance (Copeland, 1965; Goldsborough and Kemp, 1988), temperature (Brown *et al*., 2004; López-Urrutial *et al*., 2006) nutrient concentration (Oviatt *et al*., 1993; Taylor *et al*., 1995), among others, must play an important role in regulating planktonic GPP. Moreover, the global inventory of chlorophyll a concentration is available only for surface waters, those accessible to satellite-based instruments, and thus does not allow integration of GPP across the entire photic layer.

Our results confirm that the respiration of planktonic communities increased with increasing gross primary production (Fig. 3.4.13). However, we observed CR to be scaled as the 0.80 ± 0.01 power of GPP, compared to the 0.5 ± 0.03 power derived by Duarte and Agustí (1998) and the 0.62 power derived by Robinson and Williams (2005). That the power slope of the log CR vs. log GPP relationship changes significantly despite the 957 observations used to derive the previous relationship (Robinson and Williams 2005) is evidence of the present bias in the results, as the slope is expected to be robust against changes in the number of observations if these represented a random sample of ocean metabolism. Hence, present biases are affecting our capacity to conclusively establish the mean global respiration and gross primary production of oceanic plankton communities as well as the scaling between these properties. That CR is scaled as a power < 1 than GPP indicates that, as observed in the past, CR increases more slowly with increasing GPP than GPP does, so that unproductive communities tend to have low P/R ratios (Duarte and Agustí, 1998). There were, however, important differences in the scaling of CR to GPP across ocean basins, ranging from a 0.60 ± 0.04 power scaling of GPP to CR in communities sampled in the

Indian Ocean to a 0.97 ± 0.04 scaling of CR to GPP in communities sampled in the Mediterranean Sea (Table 3.4.5). Moreover, CR was scaled as the 0.82 ± 0.02 power of GPP in coastal stations compared to a power scaling of 0.76 ± 0.02 power of GPP in open-ocean stations (Table 3.4.5). These differences point at fundamental differences in the dependence of CR on GPP, where shallow slopes, such as those in open-ocean and, particularly, Indian Ocean communities indicate a relatively high CR relative to GPP in the communities with the lowest GPP. The results presented here shows that the scaling between CR and GPP is not universal across the ocean and that there is a 5 to 10-fold variability in the mean CR expected for any given GPP among ocean basins. Differences in the scaling of GPP to CR may depend on the allochthonous inputs of organic carbon to the communities, which may elevate CR relative to GPP (i.e. higher intercept), particularly so at low GPP (i.e. shallow slopes), as well as water temperature and nutrient availability.

Our results also confirm earlier indications that communities with low GPP and low chlorophyll a concentrations tend to be heterotrophic (Duarte and Agustí, 1998), with logistic regression indicating that the thresholds separating communities likely to be heterotrophic from autotrophic ones being 1.50 mmol O_2 m^{-3} d^{-1} and 0.35 mg Chl a L^{-1} across the ocean, although these thresholds also differed across basins. A total of 43 % of the communities sampled here were net heterotrophic and 34 % of the stations supported net heterotrophic integrated metabolism. Heterotrophic stations were mostly located in the subtropical Atlantic and the Mediterranean Sea in our database. However, the fraction of heterotrophic communities in our analysis is likely underestimated as the least productive regions of the ocean, the southern subtropical gyres were grossly under-represented in the data set. Heterotrophic communities were prevalent in the continental shelf stations and in the Northern Hemisphere, which receives relatively high allochthonous inputs of organic carbon. The best possible approximation to the metabolic balance of the upper ocean, at the global scale, is that derived from the use of biogeochemical provinces (Longhurst, 1998) to upscale rates. Scaling of global metabolic rates from the mean values for the different biogeochemical provinces and their area extent deliver an estimated global GPP of 144.8 Pg C y^{-1}, and a global CR of 169.6 Gg C y^{-1} and a negative global NCP at -19.22 Gg C y^{-1}. These estimates suggest a negative metabolic balance for the upper ocean, a suggestion that must be taken with caution since these values carry considerable uncertainty, largely due to the sparse coverage of estimates of metabolic rate in the ocean. Hence, resolving the metabolic

balance of the ocean remains an elusive goal that awaits an effort to improve the distribution of the empirical basis on metabolic rates in the ocean, particularly for oligotrophic gyres in the southern hemisphere. Likewise, understanding the prevalence of heterotrophic communities in the less productive regions of the ocean requires that allochthonous organic inputs be quantified as a necessary step to reconcile the carbon budget of these important regions of the ocean.

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References

Agustí S, Duarte CM (2005) Threshold of gross primary production for planktonic metabolic balance in the Southern Ocean: An experiment test. Limnol Oceanogr 50 (4): 1334-1339

Agustí S, Satta MP, Mura MP (2004) Summer community respiration and pelagic metabolism in upper surface Antarctic waters. Aquat Microb Ecol 35 (2): 197-205

Arístegui J, Barton ED, Tett P, Montero MF, Garcia-Munoz M, Basterretxea G, Cussatlegras A-S, Ojeda A, de Armas D (2004) Variability in plankton community structure, metabolism, and vertical carbon fluxes along an upwelling filament (Cape Juby, NW Africa). Prog Oceanogr 62 (2-4): 95-113

Arístegui J, Harrison WG (2002) Decoupling of primary production and community respiration in the ocean: Implications for regional carbon studies. Aquat Microb Ecol 29: 199–209

Arístegui J, Montero MF, Ballesteros S, Basterretxea G, Van Lenning K (1996) Planktonic primary production and microbial respiration measured by 14C assimilation and dissolved oxygen changes in coastal waters of the Antarctic Peninsula during the austral summer: Implications for carbon flux studies. Mar Ecol Prog Ser 132: 191–201

Bender ML, Grande K, Johnson K, Marra J, Williams PJLeB, Sieburth J, Pilson M, Langdon C, Hitchcock G, Orchardo J, Hunt C, Donaghay P, Heinemann K (1987) A comparison of four methods for determining planktonic community production. Limnol Oceanogr 32(5): 1085-1098

Bender ML, Orchardo J, Dickson ML, Barber R, Lindley S (1999) In vitro fluxes compared with 14C production and other rate terms during the JGOFS Equatorial Pacific experiment. Deep Sea Res Pt I 46: 637-654

Bender ML, Dickson ML, Orchardo J (2000) Net and gross production in the Ross sea as determined by incubation experiments and dissolved O2 studies. Deep Sea Res Pt II 47: 3141-3158

Blight SP (1996) Microbial metabolism and temperature. Comparative studies in the Southern Ocean and a temperate coastal ecosystem. M.S. thesis, University of Wales, Bangor

Bouquegneau JM, Gieskes WWC, Kraay GW, Larsson AM (1992) Influence of physical and biological processes on the concentration of O2 and CO2 in the ice-covered Weddell Sea in the spring of 1988. Polar Biol. 12: 163-170

Boyd PW, Robinson C, Savidge G, Williams PJLeB (1995) Water column and sea-ice primary production during Austral spring in the Bellingshausen Sea. Deep Sea Res Pt II 42 (4-5): 1177-1200

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. Ecology 85(7): 1771-1789

Carpenter JH (1965) The accuracy of the Winkler method for dissolved oxygen analysis. Limnol Oceanogr 10: 135-140

Carrit DE, Carpenter JH (1966) Comparison and evaluation of currently employed modifications of the Winkler method for determining dissolved oxygen in sea-water. J Mar Res 24: 286-318

Copeland BJ (1965) Evidence for regulation of community metabolism in a marine ecosystem. Ecology 46: 563-564

Cota GF, Pomeroy LR, Harrison WG, Jones EP, Peters F, Sheldon WM, Weingartner JrTR (1996) Nutrients, primary production and microbial heterotrophy in the southeastern Chukchi Sea: Arctic summer nutrient depletion and heterotrophy. Mar Ecol Prog Series 135: 247-258

Cottrell MT, Malmstrom RR, Hill V, Parker AE, Kirchman DL (2006) The metabolic balance between autotrophy and heterotrophy in the western Arctic Ocean. Deep Sea Res Pt I 53: 1831-1844

Dachs J, Calleja MLl, Duarte CM, del Vento S, Turpin B, Polidori A, Herndl G, Agustí S (2005) High Atmosphere-Ocean Exchange of Organic Carbon in the NE Subtropical Atlantic. Geophys Res Lett 32: doi:10.1029/2005GL023799

Davies JM, Williams PJLeB (1984) Verification of 14C and O2 derived primary organic production measurements using an enclosed ecosystem. J Plankt Res 6(3): 457-474

del Giorgio PA, Williams PJLeB (2005) Respiration in aquatic ecosystems. Oxford University Press, 315 pp., New York

del Giorgio PA, Duarte CM (2002) Respiration in the open ocean. Nature 420: 379-384

Dickson MJ, Orchado J (2001a) Oxygen production and respiration in the Antarctic Polar Front region during the austral spring and summer. Deep Sea Re. Pt II 48: 4101-4126

Dickson MJ, Orchado J, Barber RT, Marra J, McCarthy JJ, Sambrotto RN (2001b) Production and respiration rates in the Arabian Sea during the 1995 Northeast and Southwest Monsoons. Deep Sea Res Pt II 48: 1199-1230

Duarte CM, Cebrián J (1996) The fate of marine autotrophic production. Limnology and Oceanography 41: 1758-1766

Duarte CM, Agustí S (1998) The CO2 balance of unproductive aquatic ecosystems. Science 281

Duarte CM, Agustí S, Kalff J (2000) Particulate light absorption and the prediction of phytoplankton biomass and planktonic metabolism in northeastern Spanish aquatic ecosystems. Can J Fish Aquat Sci 57: 25-33

Duarte CM, Agustí S, Aristegui J, González N, Anadon R (2001) Evidence of heterotrophic Subtropical Northeast Atlantic. Limnol Oceanogr 46(2): 425-428

Duarte CM, Agustí S, Vaqué D (2004) Controls on planktonic metabolism in the Bay of Blanes, northwestern Mediterranean littoral. Limnol Oceanogr 49(6): 2162-2170

Duarte CM, Prairie YT (2005) Prevalence of heterotrophy and atmospheric CO_2 emissions from aquatic ecosystems. Ecosystems 8: 862–870

Duarte CM, Regaudie-de-Gioux A (2009) Thresholds of Gross Primary Production for the Metabolic Balance of Marine Planktonic Communities. Limnol. Oceanogr. 54: 1015-1022, 2009

Falkowski PG (1994) The role of phytoplankton photosynthesis in global biogeochemical cycles. Photosynth Res 39: 235-258

Field CB, Behrenfeld MJ, Randerson JT, Falkowski P (1998) Primary production of the biosphere: interacting terrestrial and oceanic components. Science 281(5374): 237-240

Gasol JM, del Giorgio PD, Duarte CM (1997) Biomass distribution in marine planktonic communities. Limnol Oceanogr 42: 1353–1363

Goldsborough WJ, Kemp WM (1988) Light responses of a submersed macrophyte: implications for survival in turbid tidal waters. Ecology 69: 1775-1786

González N, Anadon R, Mourino B, Fernandez E, Sinha B, Escanez J, de Armas D (2001) The metabolic balance of the planktonic community in the north Atlantic Subtropical gyre: the role of mesoscale instabilities. Limnol. Oceanogr. 46(4): 946-952

González N, Anadón R, Marañon E (2002) Large-scale variability of planktonic net community metabolism in the Atlantic Ocean: importance of temporal changes in oligotrophic subtropical waters. Mar Ecol Prog Ser 233, 21-30

González N, Anadón R, Viesca L (2003) Carbon flux through the microbial community in a temperate sea during summer: role of bacterial metabolism. Aquat Microb Ecol 33: 117-126

González N, Gattuso J-P, Middelburg JJ (2008) Oxygen production and carbon fixation in oligotrophic coastal bays and the relationship with gross and net primary production. Aquat Microb Ecol 52: 119-130

Grande KD, Kroopnick P, Burns D, Bender ML (1982) 18O as a tracer for measuring gross primary production in bottle experiments. Eos

Hashimoto S, Horimoto N, Ishimaru T, Saino T (2006) Metabolic balance of gross primary production and community respiration in Sagami Bay, Japan. Mar Ecol Prog Ser 321: 31-40

Hendricks MB, Bender ML, Barnett BA (2004) Net and gross O2 production in the southern ocean from measurements of biological O2 saturation and its triple isotope composition. Deep-Sea Res I 51: 1541–1561

Holligan PM, Williams PJLeB, Purdie D, Harris PR (1984) Photosynthesis, respiration and nitrogen supply of plankton populations in stratified, frontal and tidally mixed shelf waters. Mar Ecol Prog Ser 17: 201-213

Jurado E, Dachs J, Duarte CM, Simó R (2008) Atmospheric deposition of organic and black carbon to the global ocean. Atmospheric Environment 42: 7931–7939

Juranek LW, Quay PD (2005) In vitro and in situ gross primary and net community production in the North Pacific Subtropical Gyre using labeled and natural abundance isotopes of dissolved. Global Biogeochem Cy 19: 1-15

Karl DM, Tien G, Dore J, Winn CD (1993) Total dissolved nitrogen and phosphorous concentrations at U.S.-JGOFS Station ALOHA: Redfield reconcilitaion. Mar Chem 41: 203-208

Kiddon J, Bender ML, Marra J (1995) Production and respiration in the 1989 North Atlantic Spring bloom—an analysis of irradiance dependent changes. Deep-Sea Res I 42: 553–576

Lefèvre D, Minas HJ, Minas M, Robinson C, Williams PJLeB, Woodward EMS (1997) Review of gross community production, primary production, net community production and dark community respiration in the Gulf of Lions. Deep-Sea Res II 44: 801–832

Lefèvre D, Guigue C, Obernosterer I (2008) The metabolic balance at two contrasting sites in the Southern Ocean: The iron-fertilized Kerguelen area and HNLC waters. Deep Sea Res Pt II 55(5-7): 766-776

Longhurst AR (1998) Ecological Geography of the Sea. Academic Press, San Diego, pp. 398

Longhurst AR, Sathyendranath S, Platt T, Caverhill C (1995) An estimate of global primary production in the ocean from satelitte radiometer data. J Plankt Res 17(6): 1245-1271

López-Urrutia A, San Martín E, Harris RP, Irigoyen X (2006) Scaling the metabolic balance of the oceans. Proc Natl Acad Sci USA 103: 8739–8744

Lucea A, Duarte CM, Agustí S, Kennedy H (2005) Nutrient dynamics and ecosystem metabolism in the Bay of Blanes (NW Mediterranean). Biogeochemistry 73: 303-323

Luz B, Barkan E (2000) Assessment of oceanic productivity with the triple-isotope composition of dissolved oxygen. Science 288: 2028–2031

Maixandeau A, Lefèvre D, Fernandez IC, Sempere R, Sohrin R, Ras J, Van Wambeke F, Caniaux G, Queguiner B (2005) Mesoscale and seasonal variability of community production and respiration in the surface waters of the N.E. Atlantic Ocean. Deep Sea Res. 52(9): 1663-1676

McAndrew PM, Björkam KM, Church MJ, Morris PJ, Jachowski N, Willians PJLeB, Karl DM (2007) Metabolic response of oligotrophic plankton communities to deep water nutrient enrichment. Mar Ecol Prog Ser 332: 63–75

Moran XAG, Fernandez E, Perez V (2004) Size-fractionated primary production, bacterial production and net community production in subtropical and tropical domains of the oligotrophic NE Atlantic in autumn. Mar Ecol Prog Ser 274: 17-29

Morel A, Maritorena S (2001) Bio-optical properties of oceanic waters: A reappraisal. J Geophys Res 104(C4): 7163-7180

Navarro N, Agustí S, Duarte CM (2004) Plankton metabolism and dissolved organic carbon use in the Bay of Palma, NW Mediterranean Sea. Aquat Microb Ecol 37: 47-54

Odate T, Furuya K, Fukuchi M (2002) Photosynthetic oxygen production and community respiration in the Indian sector of the Antarctic Ocean during austral summer. Polar Biol 25: 859-864

Oviatt CA, Doering PH, Nowicki BL, Zoppini A (1993) Net system production in coastal waters as a function of eutrophication, seasonality, and benthic macrofaunal abundance. Estuaries 16: 247-253

Regaudie-de-Gioux A, Vaquer-Sunyer R, Duarte CM (2009) Patterns in planktonic metabolism in the Mediterranean Sea. Biogeosciences 6: 3081-3089

Regaudie-de-Gioux A, Duarte CM (2010a) Plankton metabolism in the Greenland Sea during the polar summer of 2007. Polar Biol, in press

Regaudie-de-Gioux A, Duarte CM (2010b) The compensation irradiance for planktonic community metabolism in the ocean. Global Biogeoch Cycles, in press

Reuer MK, Barnett BA, Bender ML, Falkowski PG, Hendricks MB (2007) New estimates of Southern Ocean biological production rates from O2/Ar ratios and the triple isotope composition of O2. Deep Sea Res Pt I 54(6): 951-974

Robinson C, Williams PJLeB (1993) Temperature and Antarctic plankton community respiration. J Plankton Res 15(9): 1035-1051

Robinson C, Williams PJLeB (1999) Plankton net community production and dark respiration in the Arabian Sea during September 1994. Deep-Sea Res II 46: 745–766

Robinson C (2000) Plankton gross production and respiration in the shallow water hydrothermal systems of Miles, Aegean Sea. J Plankton Res 22(5): 887-906

Robinson C, Serret P, Tilstone G, Teira E, Zubkov MV, Rees AP, Woodward EMS (2002) Plankton respiration in the Eastern Atlantic Ocean. Deep-Sea Res I 49: 787–813

Robinson C, Williams PJLeB (2005) Respiration and its measurement in surface waters. In del Giorgio PA, Williams PJLeB (ed), Respiration in aquatic ecosystems. Oxford Univ Press. pp 147–180

Satta MP, Agustí S, Mura MP, Vaqué D, Duarte CM (1996) Microplankton respiration and net community metabolism in a bay on the NW Mediterranean coast. Aquat Microb Ecol 10: 165-172

Serret P, Fernández E, Sostres JA, Anadon R (1999) Seasonal compensation of microbial production and respiration in a temperate sea. Mar Ecol Prog Ser 187: 43-57

Serret P, Fernández E, Anadon R, Varela M (2001a) Trophic control of biogenic carbon export in Bransfield and Gerlache Straits, Antarctica. J Plankton Res 23(12): 1345-1360

Serret P, Robinson C, Fernández E, Teira E, Tilstone G (2001b) Latitudinal variation of the balance between plankton photosynthesis and respiration in the eastern Atlantic Ocean. Limnol Oceanogr 46(7): 1642-1652

Serret P, Fernández E, Robinson C, Woodward EMS, Pérez V (2006) Local production does not control the balance between plankton photosynthesis and respiration in the open Atlantic Ocean. Deep Sea Res Pt II 53: 1611-1628

Steeman Nielsen E (1952) The use of radioactive carbon (14C) for measuring production in the sea. J Cons Perm Int Explor Mer 18: 117-140

Taylor D, Nixon S, Granger S, Buckley B (1995) Nutrient limitation and the eutrophication of coastal lagoons. Mar Ecol Prog Ser 127: 235-244

Teira E, Serret P, Fernández E (2001) Phytoplankton size-structure, particulate and dissolved organic carbon production and oxygen fluxes through microbial communities in the NW Iberian coastal transition zone. Mar Ecol Prog Ser 219: 65-83

Van Wambeke F, Lefèvre D, Prieur L, Sempéré R, Bianchi M, Oubelkheir K, Bruyant F (2004) Distribution of microbial biomass, production, respiration dissolved organic carbon and factors controlling bacterial production across a geostrophic front (Almeria-Oran, SW Mediterranean Sea). Mar Ecol Prog Ser 269: 1-15

Williams PJLeB, Raine RCT, Bryan JR (1979) Agreement between the 14C and oxygen methods of measuring phytoplankton production: reassessment of the photosynthetic quotient. Oceanol Acta 2: 441-416

Williams PJLeB, Purdie PA (1991) In vitro and in situ derived rates of gross production, net community production and respiration of oxygen in the oligotrophic subtropical gyre of the North Pacific Ocean. Deep-Sea Res I 38: 891–910

Williams PJLeB (1998) The balance of plankton respiration and photosynthesis in the open ocean. Nature 394: 55–57

Williams PJLeB, Bower DG (1999) Determination of organic carbon balance in the oceans from field observations—A reevaluation. Science 284: 1735a

Williams PJLeB (2000) Net production, gross production and respiration: what are the interconnections and what controls what? In: Hanson RB, Ducklow HW, Fields JG (Ed.), The changing ocean carbon cycle: A midterm synthesis of the joint global ocean flux study. Cambridge University Press, Oxford, p. 514

Williams PJLeB, Morris PJ, Karl DM (2004) Net community production and metabolic balance at the oligotrophic ocean site, station ALOHA. Deep-Sea Res I 51: 1563–1578

APPENDIX

Average of the integrated metabolic rates (GPP, CR and NCP) for the distinct marine provinces determined by Longhurst (1998). When data in our database was not available for a given province, the metabolic rates in our database from the most similar province (PP and oceanographic characteristics) as defined by Longhurst (1998) were assigned.

Code	Longhurst Provinces Description	Area (10^6 km^2)	GPP (mmol O_2 m^{-2} d^{-1})	CR (mmol O_2 m^{-2} d^{-1})	NCP (mmol O_2 m^{-2} d^{-1})	Assigned with
ALSK	Coastal - Alaska Downwelling Coastal Province	0.6	115.60	112.69	27.48	*BPLR
ANTA	Polar - Antarctic Province	8.9	89.86	77.53	18.06	
APLR	Polar - Austral Polar Province	1.9	116.78	59.35	71.87	
ARAB	Coastal - NW Arabian Upwelling Province	2.9	165.41	144.67	8.20	
ARCH	Trades - Archipelagic Deep Basins Province	8.8	19.00	119.83	-119.79	*NSAW
ARCT	Polar - Atlantic Arctic Province	2.1	73.67	78.35	0.81	
AUSE	Coastal - East Australian Coastal Province	1.1	168.26	114.43	50.95	*NADR
AUSW	Coastal - Australia-Indonesia Coastal Province	2.9	115.19	142.84	-16.42	*MEDI
BENG	Coastal - Benguela Current Coastal Province	1.1	160.03	198.02	77.40	
BERS	Polar - N. Pacific Epicontinental Province	3.9	240.78	218.82	-33.68	*CNRY
BPLR	Polar - Boreal Polar Province (POLR)	1.7	115.60	112.69	27.48	
BRAZ	Coastal - Brazil Current Coastal Province	1.2	240.78	218.82	-33.68	*CNRY
CAMR	Coastal - Central American Coastal Province	1.3	160.03	198.02	77.40	*BENG
CARB	Trades - Caribbean Province	4.5	9.71	93.00	-51.61	*ETRA
CCAL	Coastal - California Upwelling Coastal Province	3.4	160.03	198.02	77.40	*BENG
CHIN	Coastal - Chile-Peru Current Coastal Province	1.0	120.43	112.69	27.48	
CNRY	Coastal - China Sea Coastal Province	0.8	240.78	218.82	-33.68	
EAFR	Coastal - Canary Coastal Province (EACB)	3.7	440.70	82.57	358.13	*NECS
ETRA	Coastal - E. Africa Coastal Province	5.3	9.71	93.00	-51.61	
FKLD	Trades - Eastern Tropical Atlantic Province	1.4	165.41	144.67	8.20	*ARAB
GFST	Coastal - SW Atlantic Shelves Province	1.1	115.19	142.84	-16.42	*MEDI
GUIA	Westerlies - Gulf Stream Province	1.2	440.70	82.57	358.13	*NECS
GUIN	Coastal - Guianas Coastal Province	1.4	440.70	82.57	358.13	*NECS
HUMB	Coastal - Guinea Current Coastal Province	2.6	78.16	59.49	18.67	
INDE	Coastal - E. India Coastal Province	1.0	160.03	198.02	77.40	*BENG
INDW	Coastal - W. India Coastal Province	0.8	160.03	198.02	77.40	*BENG
ISSG	Trades - Indian S. Subtropical Gyre Province	19.3	90.72	44.91	45.81	
KURO	Westerlies - Kuroshio Current Province	3.7	115.19	142.84	-16.42	*MEDI
MEDI	Westerlies - Mediterranean Sea, Black Sea Province	3.1	115.19	142.84	-16.42	
MONS	Trades - Indian Monsoon Gyres Province	14.2	177.65	158.05	44.22	
NADR	Westerlies - N. Atlantic Drift Province (WWDR)	3.5	168.26	114.43	50.95	
NAST (E)	Westerlies - N. Atlantic Subtropical Gyral Province (East) (STGE)	4.4	81.71	95.15	-7.44	
NAST (W)	Westerlies - N. Atlantic Subtropical Gyral Province (West) (STGW)	5.8	19.00	119.83	-119.79	
NATR	Trades - N. Atlantic Tropical Gyral Province (TRPG)	8.3	108.66	183.45	-20.38	
NECS	Coastal - NE Atlantic Shelves Province	1.4	440.70	82.57	358.13	
NEWZ	Coastal - New Zealand Coastal Province	1.0	160.03	198.02	77.40	*BENG
NPPF	Westerlies - N. Pacific Polar Front Province	3.0	23.16	13.95	10.54	
NPSW	Trades - N. Pacific Subtropical Gyre Province (West)	3.9	108.66	183.45	-20.38	*NATR
NPTG	Trades - N. Pacific Tropical Gyre Province	21.1	56.27	60.82	-18.03	
NWCS	Coastal - NW Atlantic Shelves Province	2.0	165.41	144.67	8.20	*ARAB
PEQD	Trades - Pacific Equatorial Divergence Province	10.3	279.13	159.13	119.72	
PNEC	Trades - N. Pacific Equatorial Countercurrent Province	8.2	177.65	158.05	44.22	
PSAE	Westerlies - Pacific Subarctic Gyres Province (East)	3.2	115.19	142.84	-16.42	*MEDI
PSAW	Westerlies - Pacific Subarctic Gyres Province (West)	2.9	78.16	59.49	18.67	*HUMB
REDS	Coastal - Red Sea, Persian Gulf Province	0.6	0.00	112.69	27.48	*CHIN
SANT	Westerlies - Subantarctic Province	30.3	192.98	112.27	54.49	
SARC	Polar - Atlantic Subarctic Province	2.3	88.45	78.98	13.55	
SATL	Trades - South Atlantic Gyral Province (SATG)	17.8	59.05	142.36	-79.89	
SPSG	Trades - S. Pacific Subtropical Gyre Province	37.3	19.00	119.83	-119.79	*NSAW
SSTC	Westerlies - S. Subtropical Convergence Province	16.8	99.52	203.15	-85.71	*WTRA
SUND	Coastal - Sunda-Arafura Shelves Province	6.3	160.03	198.02	77.40	*BENG
TASM	Westerlies - Tasman Sea Province	1.7	89.86	77.53	18.06	*MEDI
WARM	Trades - W. Pacific Warm Pool Province	16.8	59.05	142.36	-79.89	*SATL
WTRA	Trades - Western Tropical Atlantic Province	5.4	99.52	203.15	-85.71	

Chapter 4

The compensation irradiance for planktonic community metabolism in the ocean

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Global Biogeochemical Cycles, in press

Abstract

The light compensation irradiance for planktonic metabolic balance, defined as the irradiance where gross planktonic primary production equals community respiration is an important property describing ecosystem dynamics. Planktonic communities receiving irradiances above the compensation irradiance or compensation depth (i.e. the depth at which the compensation irradiance is received) are autotrophic and act as CO_2 sinks, whereas those at lower irradiances or located deeper in the water column act as CO_2 sources. However, this property is undefined for heterotrophic communities which metabolic balance is not set by light availability. The compensation irradiance for planktonic metabolism in the ocean was quantified experimentally and calculated using data available in the literature to assess its variability and possible controls. Gross primary production by the oceanic planktonic communities examined here meet their respiratory requirements at irradiances of about 1.1 ± 0.4 mol quanta m^{-2} d^{-1} and tend to be autotrophic above a depth of 36 ± 9 m, on average. The depth of nitracline is closely correlated with the compensation depth for community metabolism across the studied areas but the compensation depth tends to be located above the depth of the nitracline. This is expected from the facts that the underlying, net heterotrophic, communities should act as sources of inorganic nutrients and that the nitracline cannot develop within the mixed layer where the compensation depth is often located. These results imply that the planktonic communities examined extending from 36 m depth, on average, to the bottom of the euphotic layer tend to be heterotrophic, acting as CO_2 and inorganic nutrient sources.

Introduction

The community metabolic balance, referring to the balance between the photosynthetic production of organic matter and its respiratory destruction, is a key trait of ecosystems affecting the carbon and nutrient budgets and the role of ecosystems on carbon sequestration and the CO_2 balance of the atmosphere (Duarte and Agustí, 1998). Heterotrophic communities are those where primary production falls short of meeting the respiratory demands and autotrophic communities are those where organic matter is produced in excess of respiratory demands, being available to be accumulated or exported from the ecosystem. Communities in productive aquatic ecosystems tend to be autotrophic whereas those in unproductive aquatic ecosystems are often heterotrophic (Duarte and Agustí, 1998; Duarte and Prairie, 2005). Hence, limitation of primary

production by the supply of key resources, such as nutrients and irradiance, may drive aquatic ecosystems to net heterotrophy.

Light limitation is arguably the factor most often conducive to heterotrophic community metabolism in the ocean (Sverdrup, 1953), responsible for the heterotrophic nature over most of the 95 % of the ocean volume corresponding to the dark ocean. The euphotic layer of the ocean is defined as the layer receiving sufficient photosynthetically active radiation (PAR) for net photosynthesis to occur. It is conventionally defined as the layer receiving more than 1 % of the PAR incident below the ocean surface (Ryther, 1956). This conventional definition, however, may not necessarily refer to the irradiance required for the planktonic community to be autotrophic, as its definition only considers the respiration by the autotrophs, which typically comprises a modest fraction of the community respiration (del Giorgio *et al*., 1997).

The compensation irradiance for community metabolism (E_{com}, units mol quanta m^{-2} d^{-1}) is defined as the irradiance at which gross community primary production (GPP) balances respiratory carbon losses (R) for the entire community (Gattuso *et al.,* 2006). The compensation irradiance is an important property for planktonic metabolism as it helps determine the depth below which planktonic metabolism becomes heterotrophic as well as the impact of changes in light penetration on the planktonic metabolic balance. Sverdrup (1953) defined this depth as the critical depth and derived equations to calculate this. However, Sverdrup's calculations assumed that the only loss of photosynthetic carbon in the community was through phytoplankton respiration (Nelson, 1991), which would grossly underestimate the irradiance necessary for photosynthesis to balance whole-community respiration. Hence, instead of using the equations developed by Sverdrup (1953), daily E_{com} is typically inferred from the relationship between daily net community production (NCP) at different depths and concurrent measurements of daily irradiance (Gattuso *et al*., 2006).

Gacía *et al.* (2005) experimentally determined the compensation irradiance for metabolic balance of a Philippine seagrass meadow to be close to 80 % of the incident light. Gattuso *et al*. (2006) reviewed the compensation irradiance for metabolic balance of benthic communities (macroalgae, seagrass and microphytobentos) to range between 0.24 to 4.4 mol quanta m^{-2} d^{-1}. To date, few estimates of the compensation irradiance for planktonic metabolism are available and basic properties such as its regional variability and patterns of variation have not yet been established.

The goal of this paper is to quantify the compensation irradiance for planktonic metabolism in the ocean, and assess its variability and possible controls. We do so by experimentally estimating E_{com} during three different cruises (Subtropical Atlantic Ocean, Eastern Arctic Ocean, and Southern Ocean) and searching the literature and databases for data on planktonic metabolism at various irradiances suitable to derive E_{com} estimates. We then combined the two data sets (experimental and reported) to derive estimates of E_{com} for different regions of the ocean and search for patterns in its distribution across the ocean.

Methods

The experimental studies were conducted in the RODA II cruise in the Subtropical Atlantic Ocean (-30ºE to -15ºE; 28ºN to 18ºN) in February 2007, in the ATOS-Arctic cruise in the Eastern Arctic Ocean (-30ºE to 12ºE; 78ºN to 81ºN) in July 2007, and finally in the ATOS-Antarctic cruise in the Antarctic Ocean (-75ºE to -51ºE; -69ºN to -61ºN) in January-February 2009. For the first cruise, the compensation irradiance was determined at 7 different stations. Seawater was sampled at 5 m depth, and then incubated at different irradiances, using neutral screen material, over 24 hrs in an on-deck incubator at in situ temperature, continuously flushed with surface seawater (5 m depth). For the second and third cruise, the compensation irradiance was determined at 8 and 15 different stations respectively. Seawater was sampled at three different depths (surface layer, Deep Chlorophyll Maximum depth and an intermediate depth), and incubated as described above. Net community production (NCP) was measured at those different depths at each station. Seven replicates were used to determine the initial oxygen concentration, and seven replicated transparent Winkler bottles were incubated in the light. The bottles were suspended in seawater and incubated on the deck for 24 h at the in situ temperature at 5 m depth, under natural sunlight with neutral density screening set as to mimic the incident irradiance at the sampled depths. During these two cruises, the thermocline was located deeper than the sampled depths, which showed a uniform temperature distribution, thereby avoiding temperature effects on metabolism rates during the incubation time. The use of neutral screens is expected to reproduce the total irradiance reaching at different sampled depths, but cannot reproduce its spectral quality. For instance, the borosilicate glass material of the Winkler bottles excludes UVB irradiance, which may affect primary production in surface waters, and the light field would be progressively deprived at

depth of the red and green fields (Kirk, 1994) relative to that in the incubation system. However, experimental evaluations of the action spectra of phytoplankton photosynthesis have shown that the differences in total photosynthetic rates associated with differences in the spectral composition of irradiance are generally modest (Kirk, 1994). In addition to potential artefacts of bottle incubations on photosynthetic rates, community respiration may also be underestimated, as the larger components of the heterotrophic community as typically omitted from incubation bottles, although this generally involves a modest error (Robinson and Williams, 2005). Whereas confinement-free techniques would potentially be free of these sources of error, the techniques available yield estimates for the mixed layer (triple O_2 isotope techniques or others, Luz *et al*., 2000; Grande *et al*., 1982; Bender *et al*., 1987), and are thus far unable to resolve the NCP at depth, required to estimate the compensation irradiance.

NCP was measured by monitoring oxygen concentration changes in light bottle incubations (Carpenter, 1965; Carritt and Carpenter, 1966). Oxygen concentrations were analysed by high-precision Winkler titration using a potentiometric electrode and automated endpoint detection (Mettler Toledo, DL28 titrator). NCP was calculated from the changes in dissolved oxygen concentration after incubation of samples in the light.

The light extinction coefficient was calculated, at each station sampled, from the vertical profile of irradiance derived by deploying a Satlantic OCP-100FF irradiance profiler, fitted with a PAR sensor, down to 100 m depth. The compensation irradiance was estimated as the irradiance at which NCP = 0, calculated from the relationship between NCP and PAR irradiance (Fig. 4.1), derived by fitting the regression equation:

$$NCP = a + b\log(E) \qquad \text{(Eq. 1)}$$

Where NCP is the net community production (mmol O_2 m^{-3} d^{-1}), E is the corresponding PAR irradiance (mol quanta m^{-2} d^{-1}), and a and b are the fitted intercept and slope, respectively. The compensation irradiance, E_{com} (mol quanta m^{-2} d^{-1}) was calculated by solving the equation for NCP = 0 (GPP = R) as:

$$E_{com} = \exp^{(-a/b)} \qquad \text{(Eq. 2)}$$

The compensation depth (Z_{com}) for metabolic balance can be estimated from E_{com} and the light extinction coefficient, *k*, using the equation (Sverdrup, 1953):

$$E_{com} = E_0 \times \exp^{(-k_{PAR} \times Z_{com})} \qquad \text{(Eq. 3)}$$

$$Z_{com} = \ln\left(E_{com}/E_0\right)\Big/-k_{PAR}$$

Where E_0 is the surface PAR irradiance (mol quanta m^{-2} d^{-1}), k_{PAR}, the extinction coefficient for the downwelling PAR (m^{-1}) and Z_{com}, the compensation depth for metabolic balance (m).

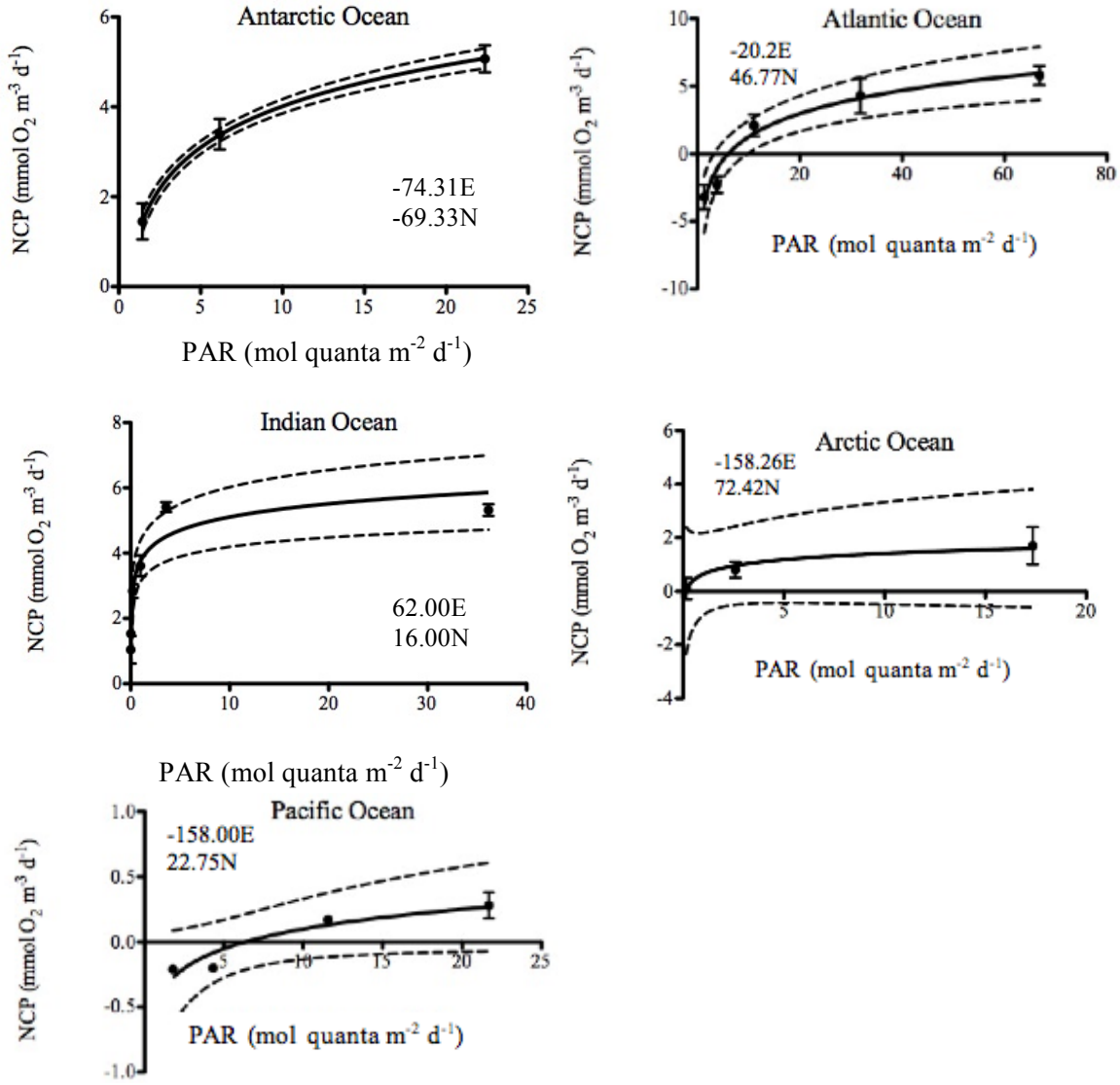

Figure 4.1. Examples of the exponential relationships between net community production (NCP, mmol O_2 m^{-3} d^{-1}) and *in situ* irradiance (mol PAR quanta m^{-2} d^{-1}) for stations in the Atlantic Ocean (Kiddon *et al*., 2005), Pacific Ocean (Williams *et al*., 2004), Indian Ocean (Dickson *et al*., 2001), Arctic Ocean (Cottrell *et al*., 2006) and Antarctic Ocean (this study) (Table 4.1). The compensation irradiance for metabolic balance (E_{com}) of the communities is determined as the intercept on the Y axis (i.e. irradiance at NCP = 0) of the fitted regression line. Error bars show the SE of the mean NCP values and the dashed lines show the 95 % confidence intervals for the fitted regression line.

The compensation irradiance is undefined for heterotrophic communities, where the net community metabolism remains negative even at the highest incident irradiance, as there is no irradiance at which NCP equals 0. Hence, estimates of the compensation irradiance and depth for community metabolism can only be derived for stations supporting autotrophic communities within the euphotic layer.

In addition to the estimates of the compensation irradiance and depth for community metabolism derived here, we searched the published literature and public data sources for data allowing calculation of additional estimates. The majority of the reports used the same method to derive net community metabolism as used here, but most failed to report the light extinction coefficient, precluding calculation of the compensation depth. Only five different published reports (Kiddon *et al.*, 1995; Bender *et al.*, 1999; Dickson *et al.*, 2001; Williams *et al.*, 2004; Cottrell *et al.*, 2006; Table 4.1) provided sufficient data to derive the compensation irradiance for planktonic community metabolism.

The error involved in calculations of individual estimates of the compensation irradiance was estimated using bootstrapping techniques to propagate the error across the various components of the estimates, namely, the error about the irradiance just below the surface and the error about the light extinction coefficient yielding the error in the irradiance at depth, and the error about individual net community production estimates and the error in fitting the regression equation. Values for each of these components were derived by sampling random values from normal distributions with the observed mean and standard deviation for each component, and an E_{com} estimate derived by fitting regression analysis as described above. This procedure was derived multiple times to retrieve a frequency distribution for E_{com} estimates. We could only complete this exercise for our own data, for which we had all necessary components. This exercise was conducted for all stations for which sufficient information was provided (24 out of 61 stations). The mean E_{com} value and it error standard for data of which this exercise was done, was 0.77 ± 0.07 mol quanta m^{-2} d^{-1}, which provides an indication of the magnitude of the uncertainty associated with individual E_{com} estimates. To evaluate the accuracy of the estimate, the mean deviation of the E_{com} was calculated. The mean absolute deviation between the bootstrapped average E_{com} and the experimental one was 0.183 mol quanta m^{-2} d^{-1}. No significant difference was observed

between the bootstrapped and the experimental average E_{com}, indicating that the experimental values were unbiased (Wilcoxon test, $p > 0.05$).

Table 4.1. Average (± SE) of the compensation irradiance for metabolic balance (E_{com}) and its depth uncertainties (Min – Max), the corresponding percentage of incident irradiance for metabolic balance (% I_0), the compensation depth for metabolic balance (Z_{com}), the incident irradiance at the surface (E_0), the light extinction coefficient (k_{PAR}), the depth-integrated chlorophyll a concentration (Chl a) and its range (Min – Max, the upper depth nitracline (Z_{nit}), the nitrate gradient within the upper layer of the nitracline, and the mixed layer depth (Z_{MLD}) across sampling stations (number of sampling stations shown) for oceanic planktonic communities examined experimentally here (this study) and calculated from data reported in published reports derived from different regions of the ocean. The E_{com} means and theirs errors were calculated as the mean and standard errors calculated from the series of individual E_{com} values derived or reported in each study cited. n. d. not determined. [a] number of data was insufficient to calculate the standard error. Cruise 1 : RODA II cruise ; Cruise 2 : ATOS-Arctic cruise ; Cruise 3 : ATOS-Antarctic cruise.

Location	References	Studied Location	Number of stations	E_{com} (mol quanta m^{-2} d^{-1})	% I_0	Z_{com} (m)	E_0 (mol quanta m^{-2} d^{-1})	k_{PAR} (m^{-1})	Chl a (mg m^{-2})	Z_{nit} (m)	ΔNO^{3-} (mmol m^{-4})	Z_{MLD} (m)
Atlantic Ocean	Kiddon et al. (1995)	North Eastern Atlantic	10	1.8 ± 0.2	3%	36 ± 2	60.2 ± 8.0	0.10 ± 0.01	33.2 ± 2.2 (23.6 - 42.3)	n. d.	n. d.	n. d.
	This study (1)	North Subtropical Atlantic	2	1.2 ± 0.3	2%	32[a]	94.4[a]	0.12[a]	32.5 ± 4.3 (11.7 - 44.2)	110 ± 19	0.06 ± 0.03	115 ± 11
		Mean		***1.5 ± 0.2***	***3%***	***36 ± 9***	***66.4 ± 8.0***	***0.10 ± 0.01***	***32.9 ± 2.1***	***110 ± 19***	***0.06 ± 0.03***	115 ± 11
Pacific Ocean	Bender et al. (1999)	Equatorial Pacific	1	0.1 a	0.2%	95[a]	28.9[a]	0.06[a]	n. d.	n. d.	n. d.	n. d.
	Williams et al. (2004)	North Subtropical Pacific	3	3.3 ± 1.1 (71m - 77m)	4%	85 ± 10	88.7 ± 0.7	0.04 ± 0.01	n. d.	n. d.	n. d.	n. d.
	Duarte et al. (unpublished)	South Eastern Pacific	2	0.8 a	3%	27[a]	33.4[a]	0.13[a]	18.7[a]	n. d.	n. d.	n. d.
		Mean		***1.9 ± 0.9***	***3%***	***67 ± 15***	***60.3 ± 14.6***	***0.08 ± 0.02***	***n. d.***	***n. d.***	***n. d.***	***n. d.***
Indian Ocean	Dickson et al. (2001)	Arabian Sea	11	0.4 ± 0.2 (23 m - 35 m)	3%	29 ± 3	39.9 ± 2.2	0.31 ± 0.06	n. d.	n. d.	n. d.	n. d.
Arctic Ocean	Cottrell et al. (2006)	Western Arctic	4	1.0 ± 0.8	4%	37 ± 18	20.5 ± 4.2	0.56 ± 0.52	n. d.	n. d.	n. d.	n. d.
	This study (2)	Eastern Arctic	8	1.3 ± 0.4 (20 m - 24 m)	4%	22 ± 2	50.5 ± 16.9	0.19 ± 0.04	54.1 ± 9.8 (34.0 - 89.8)	38 ± 7	0.22 ± 0.04	16 ± 3
		Mean		***1.2 ± 0.4***	***4%***	***27 ± 6***	***40.5 ± 11.7***	***0.31 ± 0.16***	***54.1 ± 9.8***	***38 ± 7***	***0.22 ± 0.04***	***16 ± 3***
Antarctic Ocean	This study (3)	Antarctic Peninsula	15	0.3 ± 0.1 (21 m - 22 m)	2%	21 ± 3	30.2 ± 5.9	0.30 ± 0.05	91.0 ± 47.3 (7.9 - 560.9)	24 ± 9	0.84 ± 0.58	27 ± 7
Overall Means			**56**	**1.1 ± 0.4**	**3%**	**36 ± 9**	**47.5 ± 7.6**	**0.22 ± 0.05**	**56.0 ± 16.5**	**66 ± 12**	**0.23 ± 0.08**	**61 ± 13**

The upper depth of the nitracline was determined from vertical profiles of nitrate concentration at the stations, when available, as the mean depth where nitrate concentration start to present a sharp gradient (Table 4.1). The uncertainty about the nitracline depth depends on the vertical resolution of the profiles, and was represented as half the vertical distance, in m, between the two shallower depths within which nitrate concentrations first increased sharply. The mixed layer depth was determined using the criteria proposed by de Boyer Montégut *et al*. (2004) for the global ocean of Kara *et al*. (2000),

$\Delta T = 0.5$ ºC and $\Delta\rho_0 = \rho_0 (T + \Delta T, S) - \rho_0 (T, S)$ with $\Delta T = 0.8$ ºC (Eq. 4)

Where T is the temperature, ρ_0 the potential density, S, the salinity, ΔT and $\Delta\rho_0$, the variation of temperature and potential density relative to the surface at a reference depth (Z_{ref}, here 10 m).

All of the estimates derived from our own studies, RODA II, ATOS-Arctic and ATOS-Antarctic cruises. Samples for nutrient (nitrate + nitrite, silicate and phosphate) analyses were collected at each depth and kept frozen until analyzed in a Bran Luebe AA3 autoanalyzer using standard methods (Hansen and Koroleff, 1999).

Results

The data set compiled (Table 4.1, Fig. 4.2) included our own experimental assessment and the literature reports for different areas of the ocean. The compensation irradiance of the pelagic planktonic communities examined here averaged 1.1 ± 0.4 mol quanta m^{-2} d^{-1} and ranged four fold from 0. 1 to 3.3 mol quanta m^{-2} d^{-1}. E_{com} was lower in the communities examined in the Antarctic Ocean than that in communities studied elsewhere, significantly different of E_{com} from the Atlantic, Pacific and Antarctic oceans (t-test, $p < 0.05$), and the highest E_{com} was observed in the Pacific Ocean, significantly different of E_{com} from the Indian and Antarctic oceans (t-test, $p < 0.05$) (Table 4.1). There was no significant relationship between E_{com} and the rates of respiration ($p > 0.05$), but there was a significant negative ($p < 0.05$) correlation between E_{com} and NCP and GPP (Fig. 4.3), indicating that productive planktonic communities tend to have lower E_{com} than unproductive ones. No significant relationship was observed between E_{com} and chlorophyll *a* or nutrient concentration for the cruises where we determined E_{com} experimentally, where data on chlorophyll a and nutrient concentration were available.

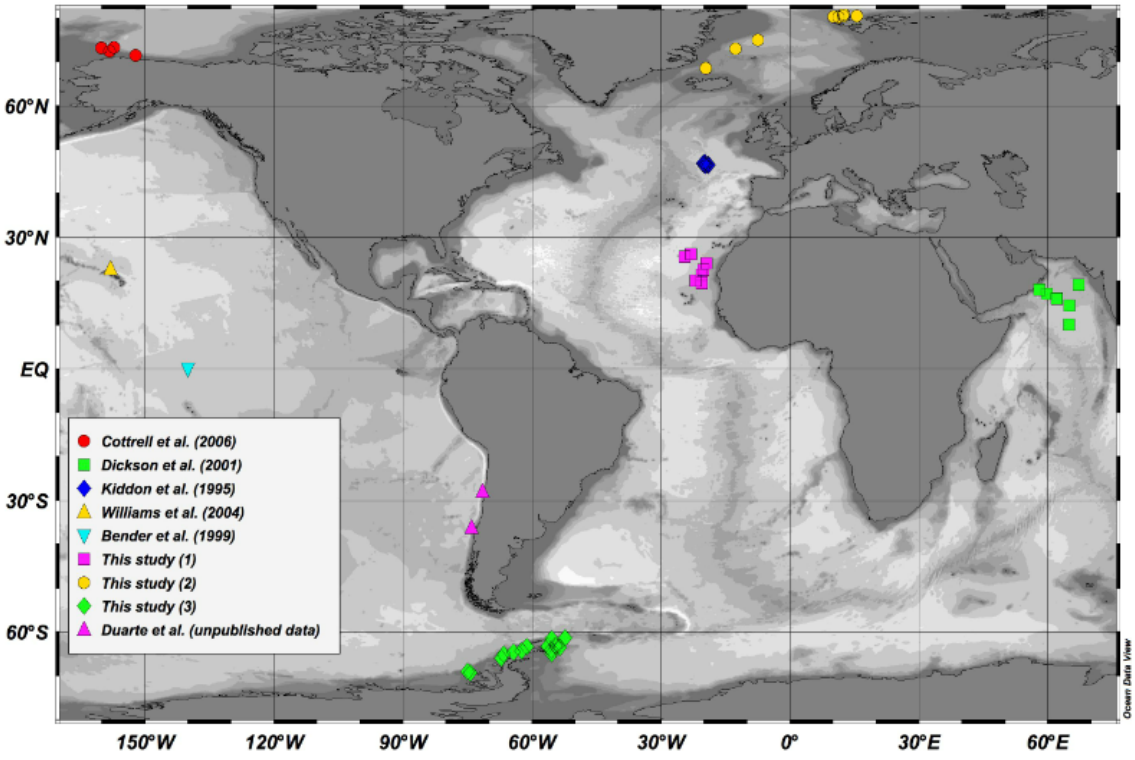

Figure 4.2. Geographic distribution of the stations included in the analysis of the compensation irradiance of plankton communities.

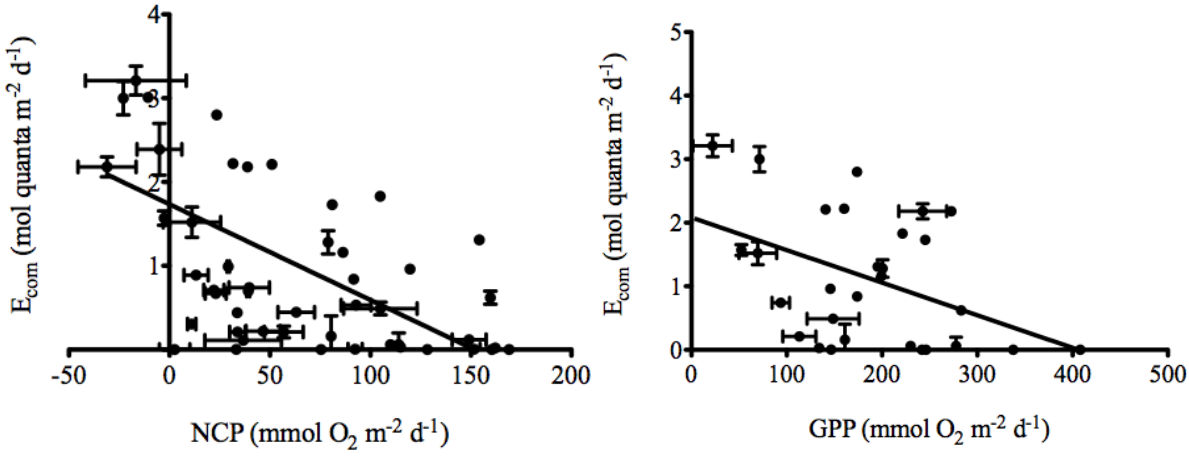

Figure 4.3. The relationship between the compensation irradiance for metabolic balance, E_{com} (mol quanta m^{-2} d^{-1}), and the integrated net community production (NCP, mmol O_2 m^{-2} d^{-1}) and gross primary production (GPP, mmol O_2 m^{-2} d^{-1}). The solid lines represent the model II regression equations: E_{com} = 1.74 (± 0.20) – 0.01 (± 0.002) NCP, R^2 = 0.32, p < 0.0001 and E_{com} = 2.08 (± 0.38) – 0.01 (± 0.002) GPP, R^2 = 0.21, p = 0.011, respectively. Bars show the standard error for E_{com}, calculated by bootstrapping.

The compensation depth for pelagic metabolism (Z_{com}, m) averaged 36 ± 9 m and ranged from 21 m to 95 m for the communities investigated, with the deeper and shallower Z_{com} observed in the Pacific Ocean and the Arctic Ocean, respectively. A strong correlation was observed, as expected, between the compensation depth (Z_{com}) and the extinction coefficient (Fig. 4.4). The nitracline depth was closely correlated (R^2= 0.47, $p < 0.05$) with Z_{com} for the stations where Z_{com} has been resolved. However, Z_{com} tended to be shallower than the nitracline depth (Wilcoxon sign, paired test, $p < 0.05$, Fig. 4.5).

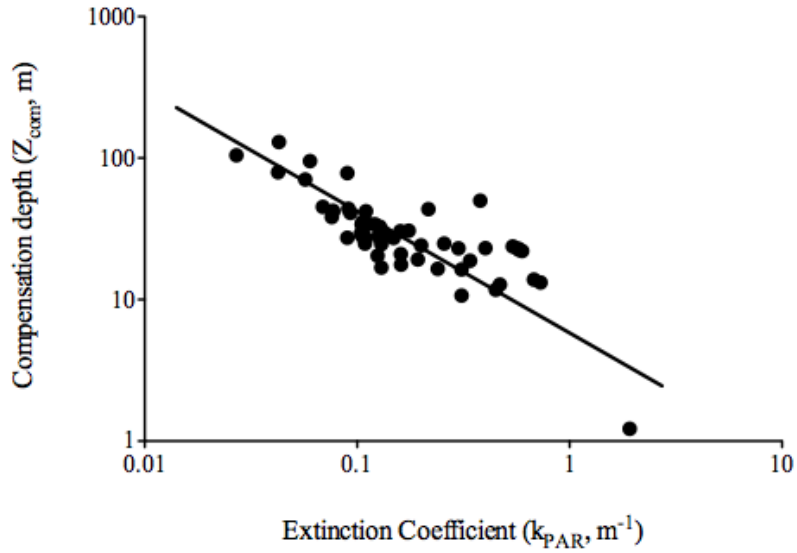

Figure 4.4. The relationship between the compensation depth (Z_{com}, m) and the extinction coefficient for PAR (k_{PAR}, m^{-1}). The solid line represents the model II regression: Log (Z_{com}) = 0.79 (± 0.06) – 0.84 (± 0.07) Log (k_{PAR}), r^2 = 0.63, $p < 0.0001$.

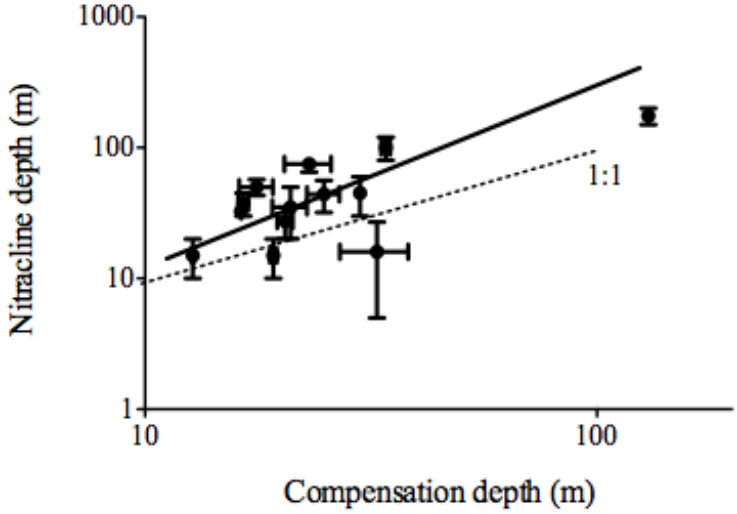

Figure 4.5. The relationship between the upper depth of the nitracline (m) and the compensation depth for net community metabolism (Z_{com}, m). The solid line represents the model II regression equation: Log (Nitracline depth) = -0.18 (± 0.40) + 1.27 (± 0.28) Z_{com}, r^2 = 0.47, p = 0.0092. The dashed line represents the 1:1 line. The errors bars for the nitracline depth represent half the vertical distance, in m, between the two depths within which nitrate concentrations increased sharply.

Discussion

The values provided here provide, however, useful indications of the compensation irradiance for plankton communities, which help assess irradiance-derived constraints to net community production in oceanic plankton communities. The results observed here of compensation irradiance and depth of the planktonic communities are derived from a limited set of communities, which provide an insufficient basis to represent the global ocean or any one of its basins (Fig. 4.2). Indeed, the communities examined here do not represent a random sample of the global ocean or any of its basins, so that direct extrapolation of the results derived here to other areas involves uncertainties.

The results presented here demonstrate that net autotrophic planktonic communities in the studied oceanic regions meet their respiratory requirements at irradiances at about 1.1 ± 0.4 mol quanta m^{-2} d^{-1} and tend to be autotrophic above an average depth of 36 ± 9 m (Table 4.1). These properties varied by an order of magnitude across communities and two-fold across communities studied in different ocean basins (Table 4.1). The communities studied in the Pacific Ocean had the highest compensation irradiance for metabolic balance, whereas the communities studied in the Arctic and Antarctic Ocean had respectively the lowest Z_{com} and E_{com}. The balance between photosynthesis and respiration for the planktonic communities studied in the Pacific Ocean seemed to occur deeper into the water column than that for the communities studied in Polar Oceans. Whereas our data set is too limited to be representative of ocean basins these observations suggests that the light requirements for metabolic balance may vary with latitude. Indeed, the compensation irradiance for studied pelagic metabolism tends to be lower for strongly autotrophic communities (Fig. 4.3), which shows that productive communities in this study are more tolerant to a light reduction in the water column. As planktonic respiration rate increases relative to photosynthesis in oceanic communities the compensation irradiance increases and the depth for metabolic compensation of the communities approaches the surface. In heterotrophic communities, where respiration exceeds production, the compensation irradiance and the compensation depth for pelagic metabolism are undefined. These heterotrophic communities have been typically found in the most oligotrophic areas of the ocean (Duarte and Agustí, 1998; Duarte and Prairie, 2005), those with the highest light requirements for metabolic balance. The E_{com} values derived here (Table 4.1) are much higher than the values derived, on the basis of phytoplankton respiration losses

alone by Sverdrup (1953), of 0.25 to 0.5 mol quanta m^{-2} d^{-1} (Sverdrup, 1953; Nelson and Smith, 1991). As a consequence the compensation depths derived here are much shallower than the critical depth values Sverdrup calculated for (Sverdrup, 1953; Nelson and Smith, 1991).

As observed Sverdrup (1953), a strong relationship was observed between the Z_{com} and k_{PAR} (Fig. 4.4). This relationship could be used to predict Z_{com} from estimates of light extinction coefficient of PAR, available at the global level (e.g. Morel and Maritorena, 2001) and approach possibly allowing inference of Z_{com} for ocean waters not included in our study. In addition, the E_{com} values derived here are independent of chlorophyll a concentration (R^2 = 0.08, p = 0.204), so that the mean value of E_{com} presented here (Table 4.1) can be used, together with estimated of the light extinction coefficient for PAR to approximate Z_{com} for ocean waters not included in this analysis, before direct estimates become available.

The estimates reported here are, to the best of our knowledge, the first estimates of the compensation irradiance and compensation depth of autotrophic planktonic phytoplankton communities reported to date. The compensation irradiance for planktonic photosynthesis has been experimentally determined for individual species (Falkowski and Owen, 1978; Langdon, 1987), or communities (Sverdrup, 1953; Riley, 1957; Siegel, 2002; Marra, 2004; Gattuso *et al*., 2006), with values ranging from 0.3 to 3.5 mol quanta m^{-2} d^{-1}. These values are within the same range than the compensation irradiance for metabolic balance of planktonic communities determined here, which range from 0.1 to 3.3 mol quanta m^{-2} d^{-1} in the open ocean (Tables 4.1 and 4.2). Similarly, the compensation irradiance for photosynthesis is used to determine the depth of the euphotic layer of the ocean, with a convention that this corresponds to the irradiance receiving about 1 % of the incident irradiance at the surface (Banse, 2004). The compensation irradiance for planktonic metabolic balance is slightly higher, and corresponds, on average, to 3 % of the incident irradiance (range 0.2 % to 4 %).

The E_{com} determined here tends to be somewhat higher than that reported for microphytobenthos, and comparable to that for macroalgal beds (Table 4.2). Hence, the metabolic balance of the planktonic communities studied is more sensitive to changes in irradiance or water transparency than that of microphytobenthic communities. Indeed, our results support the earlier suggestion that the high respiration rates of planktonic heterotrophs should lead to a higher E_{com} for the metabolic balance of pelagic communities compared to that of benthic communities (Gattuso *et al.,* 2006). In

addition, benthic primary production live at fixed depths, offering better opportunities for photoadaptation than pelagic phytoplankton, which is mixing vertically in the water column.

Table 4.2. Average compensation irradiance (E_{com}, mol quanta PAR m^{-2} d^{-1}) for the metabolic balance of different autotrophic marine communities.

References	Community type	E_{com} mol quanta m^{-2} d^{-1}
This study	Oceanic plankton	1.1
Gattuso et al. [2006]	Microphytobenthos	0.2
	Macroalgal beds	1.6
	Seagrass beds	2.4
	Coral reefs	4.4

Whereas the compensation irradiance for photosynthesis is a key property for the dynamics of phytoplankton communities, the E_{com} for metabolic balance is a key property determining the role of planktonic communities in oceanic carbon budgets, biogeochemical cycles and ecosystem dynamics. Communities receiving irradiances above the compensation irradiance or compensation depth are autotrophic and act as CO_2 sinks, whereas those at lower irradiances or located deeper in the water column act as CO_2 sources. Moreover, communities located above the compensation depth for community metabolism act as sinks for inorganic nutrients, whereas those below act as sources for inorganic nutrients, as illustrated by the relationship between the depth of the upper nitracline and the compensation depth for community metabolism shown here. The observation that the compensation depth tends to be shallower than the nitracline depth is explained by the fact that the compensation depth is often encountered within the mixed layer, where a nitracline cannot develop. Hence, the nitracline depth is constrained by the mixed layer depth, but the compensation depth is not. Hence, the studied plankton communities become heterotrophic and act as nutrient sources toward the bottom of the mixed layer, but this can only be reflected in a nitracline below the mixed layer. The determination here that the studied pelagic oceanic communities tend to be autotrophic at depths above 36 m, indicates that the studied communities extending from this depth to the bottom of the euphotic layer, roughly down to 100 m, tend to be heterotrophic, acting as CO_2 sources despite supporting measureable photosynthetic rates. The finding that the compensation

irradiance for metabolic balance for the studied pelagic oceanic communities tend to be higher than that for microphytobenthos communities is indicative of the high rates of respiration in planktonic communities, associated with the high biomass (Gasol *et al.,* 1997) and metabolic activity (del Giorgio and Duarte, 2002) of the heterotrophic components of planktonic communities. As a result, autotrophic plankton communities tend to occupy a thin layer encompassing about 36 m of the studied ocean, and yet affect, through their uptake of CO_2, the gaseous composition and climate of the planet.

Increased ocean temperature is expected to have a greater impact in enhancing respiration rates than it does for photosynthetic rates (López-Urrutia *et al*., 2006). Accordingly ocean warming should lead to an increase in the prevalence of heterotrophic plankton communities. Furthermore, increased inputs of organic carbon, from, for instance, enhanced deposition of dust and volatile organic carbon emitted to the atmosphere (Dachs *et al*., 2005), would lead to even shallower layers of autotrophy in the ocean. Both these processes should weaken the capacity of plankton communities to regulate atmospheric CO_2 and, therefore, climate. Detecting such changes in the E_{com} and Z_{com} of plankton communities requires, however, extensive observational sets that are not yet available. The results presented here should prompt efforts to improve these estimates and assess the variability and controls of compensation irradiance for plankton metabolism in the ocean. While these data become available, the results and relationships presented here may help address this important property of the functioning of plankton communities in ocean ecosystem models.

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References

Banse K (2004) Should we continue to use the 1% light depth convention for estimating the compensation depth of phytoplankton for another 70 years? Limnol Oceanogr 13: 49-52

Bender ML, Grande K, Johnson K, Marra J, Williams PJLeB, Sieburth J, Pilson M, Langdon C, Hitchcock G, Orchardo J, Hunt C, Donaghay P, Heinemann K (1987) A comparison of four methods for determining planktonic community production. Limnol Oceanogr 32(5): 1085-1098

Bender ML, Orchardo J, Dickson ML, Barber R, Lindley S (1999) In vitro fluxes compared with 14C production and other rate terms during the JGOFS Equatorial Pacific experiment. Deep-Sea Res (1. Oceanogr Res Pap) 46**:** 637-654

Carpenter JH (1965) The accuracy of the Winkler method for dissolved oxygen analysis Limnol Oceanogr 10**:** 135-140

Carrit DE, Carpenter JH (1966) Comparison and evaluation of currently employed modifications of the Winkler method for determining dissolved oxygen in sea-water. J Mar Res 24: 286-318

Cottrell M. T., R. R. Malmstrom, V. Hill, A. E. Parker, and D. L. Kirchman (2006), The metabolic balance between autotrophy and heterotrophy in the western Arctic Ocean. Deep-Sea Res (1. Oceanogr Res Pap) 53: 1831-1844

Dachs J, Calleja MLl, Duarte CM, Del Vento S, Turpin B, Polidori A, Herndl G, Agustí S (2005) High atmosphere-ocean exchange of organic carbon in the NE Subtropical Atlantic. Geophys Res Lett 32 doi:10.1029/2005GL023799

de Boyer Montégut C, Madec G, Fischer AS, Lazar A, Iudicone D (2004) Mixed layer depth over the global ocean: An examination of profile data and a profile-based climatology. J Geophys Res 109 doi:10.1029/2004JC002378

del Giorgio PA, Cole JJ, Cimbleris A (1997) Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic systems. Nature 385: 148-151

del Giorgio PA, Duarte CM (2002) Respiration in the open ocean. Nature 420: 379-384

Dickson MJ, Orchado J, Barber RT, Marra J, McCarthy JJ, Sambrotto RN (2001) Production and respiration rates in the Arabian Sea during the 1995 Northeast and Southwest Monsoons. Deep-Sea Res (2. Oceanogr Res Pap) 48: 1199-1230

Duarte CM, Agustí S (1998) The CO_2 balance of unproductive aquatic ecosystems. Science 281: 234-236

Duarte CM, Prairie YM (2005) Prevalence of heterotrophy and atmospheric CO2 emissions from aquatic ecosystems. Ecosystems 8: 862-870

Falkowski PG, Owens TG (1978) Effects of light intensity on photosynthesis and dark respiration in six species of marine phytoplankton. Mar Biol 45: 289-295

Gacía E, Kennedy H, Duarte CM, Terrados J, Marba N, Papadimitriou S, Fortes M (2005) Light-dependence of the metabolic balance of a highly productive Philippine seagrass community. J Exp Mar Biol Ecol 316: 55-67

Gasol JM, del Giorgio PA, Duarte CM (1997) Biomass distribution in marine planktonic communities. Limnol Oceanogr 42: 1353-1363

Gattuso J-P, Gentili B, Duarte CM, Kleypas JA, Middelburg JJ, Antoine D (2006) Light availability in the coastal ocean: impact on the distribution of benthic photosynthetic organisms and their contribution to primary production. Biogeosciences 3: 489-513

Grande KD, Kroopnick P, Burns D, Bender ML (1982) ^{18}O as a tracer for measuring gross primary production in bottle experiments. Eos 63: 107

Hansen K, Koroleff FF (1999) Determination of nutrients, in Methods of seawater analysis edited by Grasshoff K et al., pp. 159-228, Wiley-VCH, Germany

Kara AB, Rochford PA, Hurlburt HE (2000) An optimal definition for ocean mixed layer depth. J Geophys Res 105: 803-821

Kiddon J, Bender ML, Marra J (1995) Production and respiration in the 1989 north-Atlantic spring bloom - An analysis of irradiance-dependent changes. Deep-Sea Res (1. Oceanogr Res Pap) 42: 553-576

Kirk JTO (1994) Light and photosynthesis in aquatic ecosystems. 2nd ed., Cambridge Univ. Press

Langdon C (1987) On the causes of interspecific differences in the growth-irradiance relationship for phytoplankton. Part 1. A comparative study of the growth-irradiance relationship of three marine phytoplankton species: Skeletonema costatum, Olisthodiscus luteus and Gonyaulax tamarensis. J Plankton Res 9: 459-482

López-Urrutia Á, San Martin E, Harris RP, Irigoyen W (2006) Scaling the metabolic balance of the oceans. Proc Natl Acad Sci 103: 8739-8744

Luz B, Barkan E (2000) Assessment of oceanic productivity with the triple-isotope composition of dissolved oxygen. Science 288: 2028-2031

Marra J (2004) The compensation irradiance for phytoplankton in nature. Geophys Res Lett 31

Morel A, Maritorena S (2001) Bio-optical properties of oceanic waters: A reappraisal. J Geophys Res 104: 7163-7180

Nelson DM, Smith WOJr (1991) Sverdrup revised: Critical depths, maximum chlorophyll levels, and the control of Southern Ocean productivity by the irradiance-mixing regime. Limnol Oceanogr 36: 1650-1661

Riley GA (1957) Phytoplankton of the North Central Sargasso Sea. Limnol Oceanogr 2: 252

Robinson C, Williams PJLeB (2005) Respiration and its measurement in surface marine waters, in Respiration in aquatic ecosystems edited by del Giorgio PA and Williams PJLeB (Eds.), pp. 148-181, Oxford Univ. Press

Ryther JH (1956) Photosynthesis in the ocean as a function of light intensity. Limnol Oceanogr 1: 61-70

Siegel DA, Doney SC, Yoder JA (2002) The North Atlantic spring phytoplankton bloom and Sverdrup's critical depth hypothesis. Science 296: 730-733

Sverdrup HU (1953) On conditions for the vernal blooming of phytoplankton. J Mar Sci 287-295

Williams PJLeB, Morris PJ, Karl DM (2004) Net community production and metabolic balance at the oligotrophic ocean site, station ALOHA. Deep-Sea Res (1. Oceanogr Res Pap) 51: 1563-1578

Chapter 5

Temperature dependence of planktonic metabolism in the ocean

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Abstract

Standard metabolic theory predicts that both respiration and photosynthesis should increase with increasing temperature, albeit at different rates. However, test of this prediction for ocean planktonic communities is limited, despite the broad consequences of this prediction in the present context of global ocean warming. We compiled a large data set on planktonic metabolism in the open ocean and tested the relationship between standardised metabolic rates and water temperature. The relationships derived are consistent with predictions derived from metabolic theory of ecology, yielding activation energy for planktonic metabolism consistent with predictions from the metabolic theory. These relationships can be used to predict the effect of warming on ocean metabolism and, thus, the role of planktonic communities in the flow of carbon in the global ocean.

Introduction

Ocean biota play through their metabolic processes a major role in controlling the CO_2 partial pressure and hence, the air-sea exchange, which depends, therefore, on the metabolic balance of planktonic communities (Calleja *et al*., 2005). The metabolic balance of planktonic communities refers to the balance between gross primary production (GPP) and community respiration (CR), defining whether plankton communities act as net CO_2 sources (CR > GPP) or sinks (CR < GPP) in the ecosystem. Although the metabolism of oceanic planktonic communities appears to be in approximate balance across large scales (GPP ≈ CR) (Duarte and Agustí, 1998; Williams, 1998; Duarte *et al.*, 2001; del Giorgio and Duarte, 2002), regional disequilibria may be brought about by allochthonous inputs of organic matter, which generates a potential for CR to exceed GPP (Smith and Hollibaugh, 1993; del Giorgio and Duarte, 2002; Duarte and Prairie, 2005) or upwelling of deep, nutrient-rich waters, which enhances GPP (Marra *et al*., 1990; Falkowski *et al*., 1998). Metabolic processes are also greatly affected by temperature, as described by the Arhenius equation, which represents the foundation of the metabolic theory of ecology (Brown *et al*., 2004). The metabolic theory of ecology introduced by Gillooly *et al.* (2001) and Brown *et al*. (2004) uses first principles to predict the role of temperature in regulating the metabolism of an ecosystem and how metabolic rate controls ecological processes at all levels of organization. Metabolic theory predicts that both respiration and

photosynthesis should increase with increasing temperature, albeit at different rates (Brown *et al*., 2004; Harris *et al*., 2006; López-Urrutia *et al*., 2006).

The predicted role of temperature in modulating metabolic rates is of fundamental importance as a framework to predict the response of the metabolic balance of plankton communities in the ocean to global warming and, therefore, possible feedbacks between warming and the global carbon cycle. The Intergovernmental Panel on Climate Change (IPCC) predicts that increased greenhouse gases in the atmosphere are expected to raise air temperatures by about 3-4 ºC with an increase of sea surface temperature between 1-3 ºC (Houghton, 2001; *IPCC*, 2007). In particular, metabolic theory predicts that heterotrophic respiration should increase faster in response to warming than production rate does (Harris *et al*., 2006), thereby weakening CO_2 uptake by ocean biota (López-Urrutia *et al*., 2006). Metabolic theory predicts the activation energy for photosynthesis, describing its functional response to temperature, to be 0.32 eV, whereas that for respiration is expected to be 0.65 eV (López-Urrutia *et al*., 2006). However, test of this prediction for ocean planktonic communities is limited, despite the broad consequences of this prediction in the present context of global ocean warming, because the temperature dependence of plankton metabolism in the ocean has not yet been examined at the global scale.

We examine here the temperature-dependence of planktonic metabolism in the oceans. We do so on the basis of a dataset including 1517 volumetric estimates of oceanic planktonic metabolism and temperature in the photic layer of the ocean. We test here the predicted rate of increase in photosynthesis and respiration with increasing temperature and use the relationships derived here to formulate predictions on the role of ocean biota in CO_2 budgets in a warmer ocean.

Methods

We compiled a database containing volumetric estimates of GPP (Gross Primary Production) and CR (Community Respiration) across the photic zone of the ocean and the corresponding water temperature by compounding the data set compiled by Robinson and Williams (2005), with recently published data and our own unpublished data. The data was extracted from 36 individual reports collected between 1996 and 2010, from stations in the Open Ocean and the Mediterranean Sea (Table 5.1).

Table 5.1. Sources of data on plankton metabolic rates, water temperature and chlorophyll a concentration for different oceans and the number of observations derived from each of them (n data).

Oceans	Reference	n data	Oceans	Reference	n data
Arctic Ocean			**Mediterranean Ocean**		
	Cota, G.F., et al. (1996)	37		Lucea, A., et al. (2005)	23
	Cottrell, M.T., et al. (2006)	112		Navarro, N., et al. (2004)	15
	Regaudie-de-Gioux, A. and C. M. Duarte (2010a)	66		Regaudie-de-Gioux, A. et al., 2009	69
	Robinson, C., et al. (2002) (1)	35		Lefevre, D. Unpublished data held at Robinson, C. Database (2005)	41
	Vaquer-Sunyer, R. Unpublished data	59		Satta, M. P., et al. (1996)	24
Atlantic Ocean			**Antarctic Ocean**		
	Gonzalez, N., et al. (2002)	22		Agustí et al., (2004)	8
	Gonzalez, N., et al. (2003)	12		Bender, M.L., et al. (2000)	59
	Moran, X.A.G., et al. (2004)	36		Blight, S. Unpublished data PhD thesis University of Wales; Bangor	17
	Regaudie-de-Gioux, A. and C. M. Duarte (2010b)	71		Dickson, M.L and J. Orchado (2001a)	39
	Robinson, C. Unpublished (1)	7		Hendricks, M.B., et al. (2004)	50
	Robinson, C. Unpublished data held at Robinson, C. Database (2005)	4		Lefevre, D., et al. (2008)	42
	Serret, P., et al. (1999)	45		Navarro, et al., unpublished data (2005)	33
	Serret, P., et al. (2001b)	20		Odate, T., et al. (2002)	12
	Serret, P., et al. (2001b); Robinson, C., et al. (2002)(1)	111		Regaudie-de-Gioux, A. Unpublished data	77
	Serret, P., et al. (2006)	87		Robinson, C. and P. J. Le B. Williams (1993)	11
	Teira, E., et al. (2001)	31		Robinson, C. Unpublished data held at Robinson, C. Database (2005)	11
				Serret, P. (2001a) (2)	20
Pacific Ocean					
	Karl, D., M. Church et al. unpublished data (2007-2009)	15	**Indian Ocean**		
	Williams, P.J.LeB., et al. (2004)	55		Dickson, M.L., et al. (2001b)	117
				Robinson, C. and P. J. Le B. Williams (1999)(1)	35
Total	**1517**				
(1)	Data also held at the British Oceanographic Data Centre (www.bodc.ac.uk)				
(2)	Data held at PANGEA data collection				
(3)	Data held at CMORE data collection				

The resulting database contained 1517 estimates of volumetric metabolic rates and the corresponding water temperature (Table 5.1 and Fig. 5.1). For each report, the chlorophyll a concentration and bacterial abundance were recorded when reported.

The relationship between metabolic rates and temperature was examined on the basis of metabolic rates normalised to chlorophyll a concentration, to remove variability in metabolic rates associated with changes in biomass. No significant relationship ($P > 0.05$) was found between metabolic rates and bacterial abundance, so that normalising by bacterial abundance was not necessary. The normalised metabolic rates were subsequently binned by one º C interval before analyses. The relationship between metabolic rates and water temperature was examining by fitting a model II regression equation describing the relationship between the (chlorophyll *a*) normalised metabolic rates (specific GPP and CR) and the reciprocal of temperature in º Kelvin (Gillooly *et al*., 2001; Brown, 2004). The regression slope, a, equals:

$$a = -Ea / k \quad \text{(Eq. 1)}$$

Where *Ea* represents the average activation energy and *k* is the Boltzmann's constant ($8.617734\ 10^{-5}$ eV K^{-1}). Thus, the activation energy can be calculated from the regression slope as:

$$Ea = -a\ k \quad \text{(Eq. 2)}$$

The Q_{10} describing the temperature-dependence of the metabolic rate (GPP or CR) was determined following Dixon and Web (1964) as:

$$Q_{10} = exp\ (10\ Ea / k.T^2) \quad \text{(Eq. 3)}$$

Where T is the mean temperature (ºK) in the database.

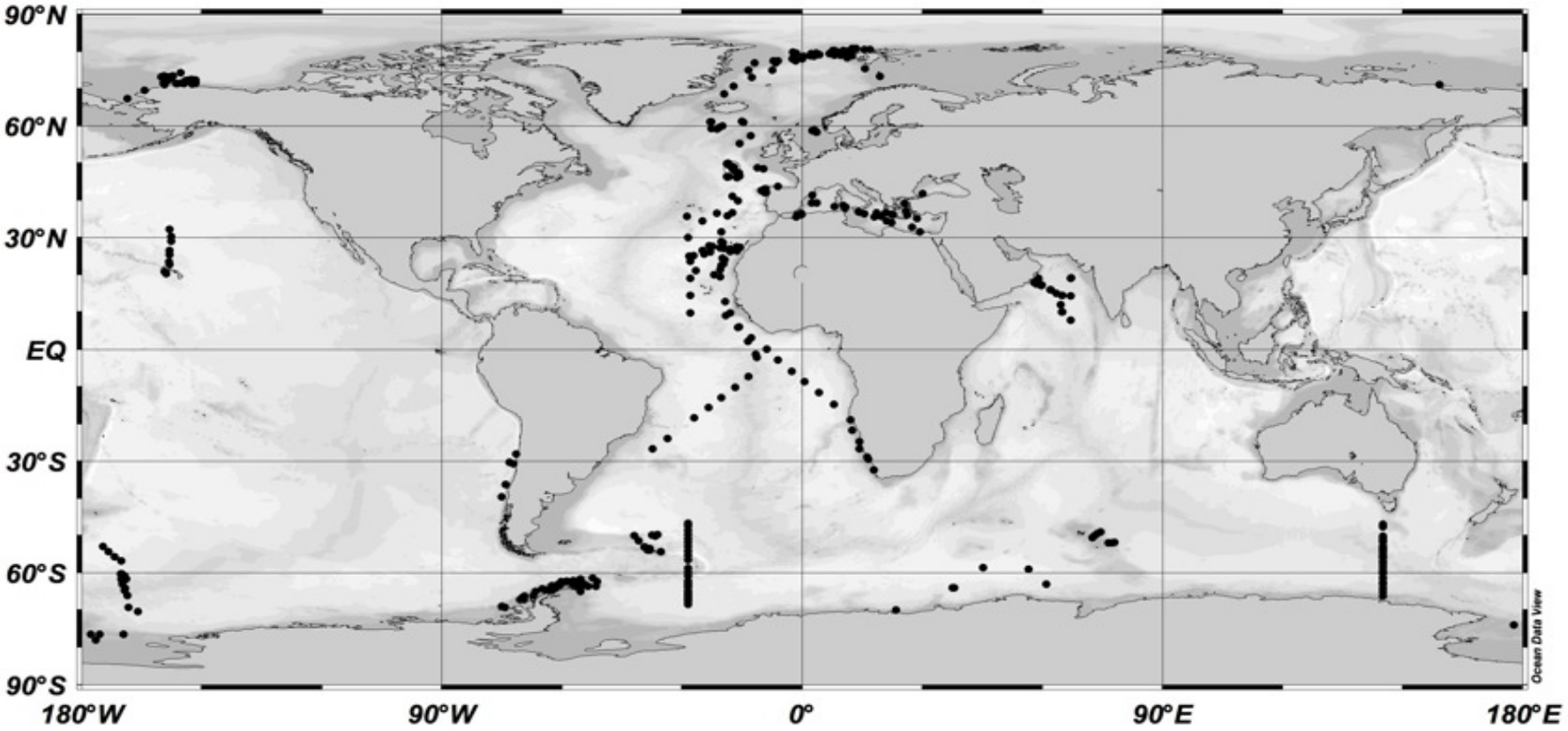

Figure 5.1. Map showing the locations in the data set (Table 5.1) containing records of plankton metabolic rates, water temperature and chlorophyll a concentration (Table 5.1).

Results

The specific GPP and CR rates increased significantly with increasing water temperature (Fig. 5.2), although the relationship between the specific CR and temperature was much stronger than that for GPP (R^2 = 0.85 and 0.55, respectively, both $p < 0.0001$). The corresponding activation energy describing the temperature-dependence of specific GPP and CR rates of planktonic communities in the ocean averaged (± SE) 0.43 ± 0.07 eV for GPP_{Chla} and 0.71 ± 0.06 eV for CR_{Chla}, corresponding to average Q_{10} values of 1.82 for GPP and 2.72 for CR rates. As a consequence of the steeper response to temperature of CR than that of GPP, the P/R ratio decreased with increasing water temperature ($R^2 = 0.52$, $p < 0.0001$, Fig. 5.3), with a calculated Q_{10} value of 0.45.

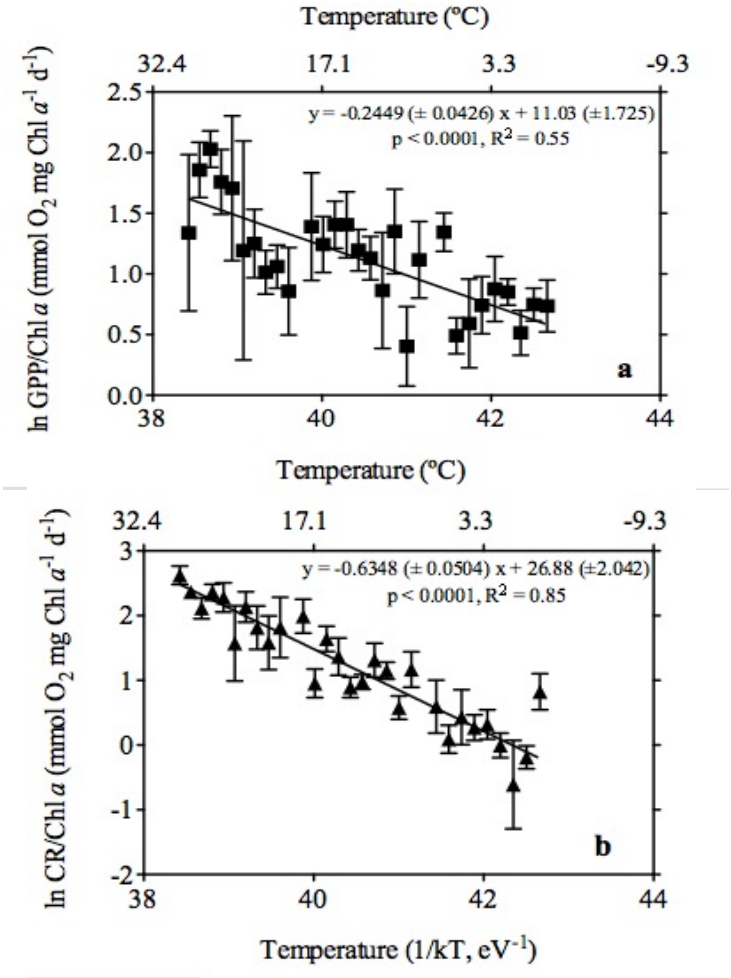

Figure 5.2. The relationship between the average ± SE volumetric metabolic rates within 1 ºC bins (GPP, a, and CR, b) normalised by Chl a concentration and the water temperature (Bottom axis: 1/kT with k, the Boltzmann's constant ($8.617734\ 10^{-5}$ eV K^{-1}) and with T, the water temperature (ºK); Top axis: T, water temperature in ºC). The solid lines shows the regression equation fitted using model II regression.

The regression equation between the P/R ratio and the reciprocal of temperature (Fig. 5.3) allows to calculate, by rearranging the equation, the threshold temperature for P/R to equal 1 (i.e. GPP = CR). We calculated that P/R equals 1 at a temperature of, on average, 23.5 ºC, with the communities tending to be heterotrophic (GPP < CR) at warmer temperatures. Indeed, 59 % of the communities in our data set growing in waters warmer than 23.5 º C were heterotrophic compared to 38 % in colder waters.

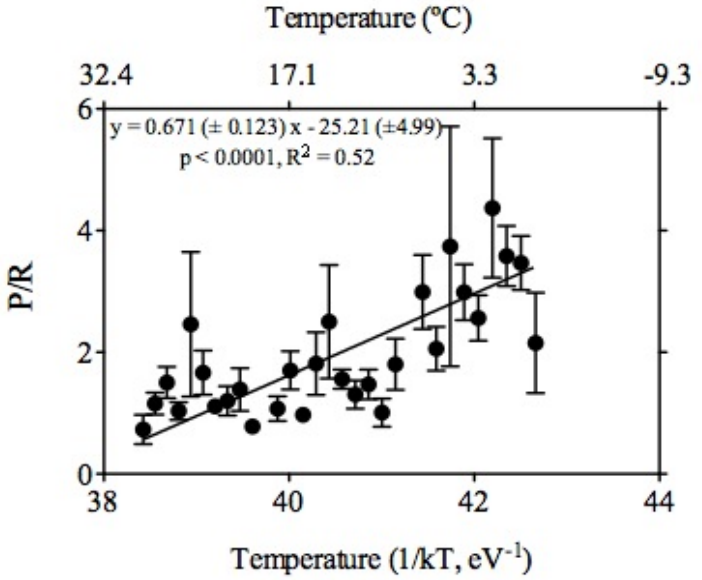

Figure 5.3. The relationship between the average ± SE volumetric P/R ratio within 1 ºC bins and water temperature (Bottom axis: 1/kT with k, the Boltzmann's constant (8.617734 10^{-5} eV K^{-1}) and with T, the water temperature (ºK); Top axis: T, water temperature in º)). The solid line shows the regression equation fitted using model II regression.

Discussion

The results derived showed a strong temperature-dependence of the *chl a*-specific metabolic rates of oceanic plankton communities across the ocean, consistent with the dependence of mass-normalised metabolic rates on temperature expected from metabolic theory (West *et al*., 1997; Gillooly *et al*., 2001; Brown *et al*., 2004; Harris *et al*., 2006; López-Urrutia *et al*., 2006). Moreover, as predicted from metabolic theory (Harris *et al*., 2006; López-Urrutia *et al*., 2006), the temperature dependence of community respiration was stronger, as reflected in a higher activation energy, Ea = 0.71 ± 0.06 eV, for community respiration than for gross primary production, Ea = 0.43 ± 0.07 eV. This results, in turn, in a decline in the P/R ratio for planktonic communities

with increasing temperature, also in agreement with predictions from metabolic theory (Harris *et al*., 2006; López-Urrutia *et al*., 2006).

However, the activation energy derived here for community respiration and gross primary production are both steeper than expected by metabolic theory (Harris *et al*., 2006) and those derived for Atlantic communities by López-Urrutia *et al*. (2006). López-Urrutia *et al*. (2006) derived the Ea for plankton production on the basis of particulate primary production derived with the ^{14}C method (Steeman Nielsen, 1952), which underestimates gross primary production due to remineralisation and release as dissolved organic carbon (DOC) of some of the organic carbon produced during the incubation period [(Bender *et al*., 1987). Peterson *et al.* (1980) reported that the ^{14}C method underestimated the GPP rates by a factor of 2 to 100. Moreover, these effects maybe temperature-dependent as plankton communities in warm oceanic waters often release a higher percent of the fixed carbon as DOC (Zlotnik and Dubrinsky, 1989) and remineralisation rates are likely to be higher in warmer waters, which support higher specific respiration rates, thereby introducing bias in the estimates of gross primary production that maybe derived from the ^{14}C method. The Ea observed here for primary production was similar to that observed by Yvon-Durocher *et al*. (2010) for freshwater GPP (Ea = 0.45 eV). However, the Ea for community respiration observed here was higher than that observed by Yvon-Durocher *et al*. (2010) (Ea = 0.62 eV). Yvon-Durocher *et al*. (2010) examined the temperature dependence on the metabolic balance of freshwater planktonic communities using mesocosms controlling environmental conditions, such as temperature and nutrient concentration. The difference observed between the Ea for CR can be explained by limitations of mesocosms, such as the absence of allochthonous organic matter inputs, that subsidise community respiration in natural ecosystems (e.g. del Giorgio and Duarte, 2002; Duarte and Prairie, 2005), as well as the effect of temperature on community structure.

In contrast, the Q_{10} for CR (Q_{10} = 2.72) in this study is much lower than the Q_{10} for CR reported in the past, including Arctic planktonic communities (Mean Q_{10} = 8.54 ± 2.88, Vaquer-Sunyer *et al*. (2010)), Antarctic planktonic communities (Mean Q_{10} = 4.93 ± 1.10, Robinson and Williams (1993)) or temperate planktonic communities (Mean Q_{10} = 5.53 ± 0.60, Lefèvre *et al*. (1994)). However, the Q_{10} for primary production (Q_{10} = 1.82) found in this study is comparable to published Q_{10} estimates for primary production evaluated for Antarctic planktonic communities (Mean Q_{10} = 1.62 ± 0.41, Neori and Holm-Hansen (1982)), Arctic planktonic communities (Mean Q_{10} =

1.19 ± 0.10, Michel *et al*. (1989)) and temperate planktonic communities (Mean Q_{10} = 1.81 ± 0.28, Lefèvre *et al*. (1994)). Published estimates of Q_{10} values for community metabolism have all been derived experimentally, through short-term experiments across temperature gradients. These experiments do no allow the plankton community structure to change in response to temperature, whereas the Q_{10} values reported here derive from a large number of natural communities growing across a range of ambient temperatures. Q_{10} values derived from comparative analyses across natural communities, such as those reported here, can reflect effects derived from responses in community structure and relevant processes other than the direct physiological effect of temperature on metabolism that co-vary with temperature. Indeed, the primary production contributed by picoplankton increases strongly with increasing temperature in oceanic communities, from < 10 % in polar waters to > 50 % in warm tropical waters (Agawin *et al*., 2001). A dominance of picoplankton has been associated with low P/R ratio (Serret *et al*., 2001a), and the percent extracellular release by primary producers tends to be greater in warmer waters (Zlotnik and Dubinsky, 1989) which also should enhance respiration rates. Accordingly, a greater fraction of primary production is channelled through the microbial food web in warm, picoplankton-dominated waters. Metabolic theory predicts that specific metabolic rates should increase with decreasing size (Peters, 1993; West *et al*., 1997; Gillooly *et al*., 2001; Brown *et al*., 2004). The tendency for autotroph cell size to decrease with increasing temperature, with an associated increase in specific metabolic rates, compounds with the direct effect of temperature on metabolism to yield the higher activation energy and Q_{10} values derived here compared to those expected on the basis of the effect of temperature on specific metabolism alone.

Our results show that the P/R ratio tends to decline with increasing temperature, as a result of the steeper temperature-dependence of community respiration compared to gross primary production. Moreover, our results show that the P/R ratio of 1, indicative of metabolic balance, is observed at an average threshold temperature of 23.5 º C, with warmer waters presenting a tendency to support heterotrophic communities. This is consistent with the observation that communities in the tropical and subtropical ocean are often been reported to be heterotrophic (Duarte and Agustí, 1998; Duarte *et al*., 2001; Williams *et al*., 2004) with these regions often acting as CO_2 sources to the atmosphere (Prairie and Duarte, 2005). This observation also suggests that autotrophic communities should prevail in high-latitude oceans, consistent with observations

(Hoppe *et al*., 2002) and the role of these regions as strong CO_2 sinks (Takahashi *et al*., 2002). Moreover, the threshold temperature for metabolic balance also implies that plankton communities in temperate oceans should oscillate from strongly autotrophic in winter to heterotrophic when the water temperature exceeds 23.5 º C in the summer, also consistent with observations from seasonal shifts in plankton metabolism (e.g. Duarte *et al*., 2005; Navarro *et al*. 2004; Williams *et al*., 2004). Hence, the temperature-dependence of planktonic metabolism reported here helps explain both spatial and seasonal patterns in planktonic metabolism in the ocean.

Most important, the derivation of the activation energy for metabolism of plankton communities across the ocean provided here helps predict the response of plankton metabolism to the forecasted ocean warming. Ocean warming is expected to lead to increased metabolic rates. Indeed, Duarte *et al*. (2004) report a 2.5-fold increase in warming for a 10 years data set of weekly measurements of plankton metabolism data in the Bay of Blanes, NW. Mediterranean. Harris *et al*. (2006) predicted, on the basis of general metabolic theory, that a four degree increase in summer water temperatures, a likely scenario for the end of this century (Meehl *et al*., 2007), will result in a 20 % increase in net primary production and a 43 % increase in heterotrophic metabolism, resulting in a 16 % decrease of the P/R ratios and an increasing likelihood of system heterotrophy. Our results validate this prediction, as the activation energy for planktonic metabolism derived empirically here predict that GPP and CR would increase by 15 % and 42 % with a 4 ºC temperature increase, remarkably close to predictions based on first principles of metabolic theory (Harris *et al*., 2006). However, our results predict a steeper decline, by 31 %, in P/R ratios with a 4 ºC warming than that predicted by Harris *et al*. (2006).

The predictions formulated here hold for metabolic rates per unit chlorophyll, and the absolute change in metabolic rates will depend, therefore, on parallel changes in chlorophyll across the ocean, although the predicted decline of P/R ratios by 31 % with a 4 ºC warming is independent of biomass changes. Because the P/R ratio of planktonic communities in the ocean is very close to 1 (Duarte an Agustí, 1998; Williams, 1998; Robinson and Williams, 2005), a 31% decline in P/R ratios, on average, across the ocean, will greatly increase the prevalence of heterotrophic plankton communities and revert many ocean regions from supporting plankton communities acting as a sink for CO_2 to support communities acting as a source of CO_2 to the atmosphere. This prediction is consistent with evidence of a recent weakening of the ocean carbon sink

(Cox *et al*., 2000). Further weakening, possibly reverting the role of ocean plankton in the global budget, may be expected as result of the decline P/R ratio predicted from ocean warming forecasted for the 21st Century.

The steep response of plankton respiration rates to warming are largely responsible for the predicted weakening of the role of ocean plankton as CO_2 sinks with warming. The key role of respiration in the metabolic balance of the ocean ecosystem is parallel to that in forests (Valentini *et al*., 2000). Indeed, soil respiration has also been predicted to increase in response to increased warming (Bond-Lamberty and Thomson, 2010). However, whereas the response of soil respiration to warming is expected to be a transient response, buffered by soil moisture (Melillo *et al*., 2002), our results predict a steep and sustained increase in plankton respiration with warming. A shift towards a prevalence of heterotrophy in ocean plankton communities in a warmer ocean maybe constrained by the availability and supply of organic carbon to support excess respiration over production. However, the ocean receives significant inputs of organic carbon, in dry and wet deposition (Jurado *et al*., 2008), as well as volatile organic carbon (Dachs *et al*., 2005; Ruiz-Halpern *et al*., 2010) to support heterotrophy, which may also proceed by using further the large stock of dissolved organic carbon in the ocean.

Whereas many properties of the ocean are presently monitored at the global scale, including chlorophyll a concentration, temperature and CO_2, our current observational effort on plankton metabolism is scattered and discontinuous, resulting in an inability to detect changes in plankton metabolic rates, shall these occur. New developments in profiling instruments, such as ARGO floats or gliders fitted with oxygen optodes (Martz *et al*., 2008; Johnson *et al*., 2009) will prove instrumental in helping infer changes in the oxygen budget of the ocean with warming. Provided the predictions derived here and the major role of ocean plankton in the carbon budget, improving our observational basis on plankton metabolism is a matter of urgency.

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References

Agawin NSR, Duarte CM, Agustí S (2000) Nutrient and temperature control of the contribution of picoplankton to phytoplankton biomass and production. Limn Oceanogr 45(3): 591-600

Agustí S, Satta MP, Mura MP (2004) Summer community respiration and pelagic metabolism in upper surface Antarctic waters. Aquat Mircob Ecol 35: 197-205

Bender ML, Grande K, Johnson K, Marra J, Williams PJLeB, Sieburth J, Pilson M, Langdon C, Hitchcock G, Orchardo J, Hunt C, Donaghay P, Heinemann K (1987) A comparison of four methods for determining planktonic community production. Limnol Oceanogr 32(5): 1085-1098

Bender ML, Dickson ML, Orchardo J (2000) Net and gross production in the Ross sea as determined by incubation experiments and dissolved O_2 studies. Deep Sea Res Pt II 47: 3141-3158

Blight SP (1996) Microbial metabolism and temperature. Comparative studies in the Southern Ocean and a temperate coastal ecosystem. M.S. thesis, University of Wales, Bangor

Bond-Lamberty B, Thomson A (2010) Temperature-associated increases in the global soil respiration record. Nature 464: doi:10.1038/nature08930

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. Ecology 85(7): 1771-1789

Calleja MLl, Duarte CM, Navarro N, Agustí S (2005) Control of air-sea CO_2 disequilibria in the subtropical NE Atlantic by planktonic metabolism under the ocean skin. Geophys Res Lett 32: doi:10.1029/2004GL022120

Cota GF, Pomeroy LR, Harrison WG, Jones EP, Peters F, Sheldon WM, Weingartner JrTR (1996) Nutrients, primary production and microbial heterotrophy in the southeastern Chukchi Sea: Arctic summer nutrient depletion and heterotrophy. Mar Ecol Prog Series 135: 247-258

Cottrell MT, Malmstrom RR, Hill V, Parker AE, Kirchman DL (2006) The metabolic balance between autotrophy and heterotrophy in the western Arctic Ocean. Deep Sea Res Pt I 53: 1831-1844

Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408: 184-187

Dachs J, Calleja MLl, Duarte CM, del Vento S, Turpin B, Polidori A, Herndl G, Agustí S (2005) High Atmosphere-Ocean Exchange of Organic Carbon in the NE Subtropical Atlantic. Geophys Res Lett 32: doi:10.1029/2005GL023799

del Giorgio PA, Duarte CM (2002) Respiration in the open ocean. Nature 420: 379-384

Dickson MJ, Orchado J (2001a) Oxygen production and respiration in the Antarctic Polar Front region during the austral spring and summer. Deep Sea Re. Pt II 48: 4101-4126

Dickson MJ, Orchado J, Barber RT, Marra J, McCarthy JJ, Sambrotto RN (2001b) Production and respiration rates in the Arabian Sea during the 1995 Northeast and Southwest Monsoons. Deep Sea Res Pt II 48: 1199-1230

Dixon M, Webb EC (1964) Enzymes. 2nd Ed. Longmans, London

Duarte CM, Agustí S (1998) The CO_2 balance of unproductive aquatic ecosystems. Science 281

Duarte CM, Agustí S, Aristegui J, González N, Anadon R (2001) Evidence of heterotrophic Subtropical Northeast Atlantic. Limnol Oceanogr 46(2): 425-428

Duarte CM, Agustí S, Vaqué D (2004) Controls on planktonic metabolism in the Bay of Blanes, northwestern Mediterranean littoral. Limnol Oceanogr 49(6): 2162-2170

Duarte CM, Prairie YT (2005) Prevalence of heterotrophy and atmospheric CO_2 emissions from aquatic ecosystems. Ecosystems 8: 862–870

Falkowski PG, Barber RT, Smetacek V (1998) Biogeochemical controls and feedbacks on ocean primary production. Science 281: doi:10.1126/science.281.5374.200

Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL (2001) Effects on size and temperature on metabolic rate. Science 293: 2248-2251

González N, Anadón R, Marañon E (2002) Large-scale variability of planktonic net community metabolism in the Atlantic Ocean: importance of temporal changes in oligotrophic subtropical waters. Mar Ecol Prog Ser 233, 21-30

González N, Anadón R, Viesca L (2003) Carbon flux through the microbial community in a temperate sea during summer: role of bacterial metabolism. Aquat Microb Ecol 33: 117-126

Harris LA, Duarte CM, Nixon SW (2006) Allometric laws and prediction in estuarine and coastal ecology. Estuar Coast 29(2): 340-344

Hendricks MB, Bender ML, Barnett BA (2004) Net and gross O_2 production in the southern ocean from measurements of biological O_2 saturation and its triple isotope composition. Deep Sea Res Pt I 51(11): 1541-1561

Hoppe H-G, Gocke K, Koppe R, Belger C (2002) Bacterial growth and primary production along a north-south transect of the Atlantic. Nature 416: 168-171

Houghton J (2001) The science of global warming. Interdisciplinary Sci Rev 26: 247-257

IPCC (2007) Climate change 2007: the physical sciences basis. In a Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. (eds Parry ML, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE), pp. 7-22. Cambridge, UK: Cambridge University Press

Johnson KS, Berelson WM, Boss ES, Chase Z, Claustre H, Emerson SR, Gruber N, Körtzinger A, Perry MJ, Riser SC (2009) Observing biogeochemical cycles at global scale with profiling floats and gliders – Prospects for a global array. Oceanogr 22(3): 216-225

Jurado E, Dachs J, Duarte CM, Simó R (2008) Atmospheric deposition of organic and black carbon to the global ocean. Atmos Env 42: 7931-7939

Lefèvre D, Bentley TL, Robinson C, Blight SP, Williams PJLeB (1994) The temperature response of gross and net community production and respiration in time-varying assemblages of temperate marine micro-plankton. J Exp Mar Biol Ecol 184: 201-215

Lefèvre D, Guigue C, Obernosterer I (2008) The metabolic balance at two contrasting sites in the Southern Ocean: The iron-fertilized Kerguelen area and HNLC waters. Deep Sea Re. Pt II 55(5-7): 766-776

López-Urrutia Á, San Martin E, Harris RP, Irigoyen X (2006) Scaling the metabolic balance of the oceans. Proc Nat Acad Sci USA 103: 8739-8744

Lucea A, Duarte CM, Agustí S, Kennedy H (2005) Nutrient dynamics and ecosystem metabolism in the Bay of Blanes (NW Mediterranean). Biogeochemistry 73: 303-323

Marra J, Bidigare RR, Dickey TD (1990) Nutrients and mixing, chlorophyll and phytoplankton growth. Deep-Sea Res 37(1): 127-143

Martz TR, Jonson KS, Riser SC (2008) Ocean metabolism observed with oxygen sensors on profiling flotas in the South Pacific. Limnol Oceanog 53(5, part 2): 2094-2111

Meehl GA, Stocker TF, Collins WD, Friedlingstein P, Gaye AT, Gregory JM, Kitoh A, Knutti R, Murphy JM, Noda A, Raper SCB, Watterson IG, Weaver AJ, Zhao Z-C (2007) Global Climate Projections. In: Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Millar HL (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA

Melillo JM, Steudler PA, Aber JD, Newkirk K, Lux H, Bowles FP, Catricala C, Magill A, Ahrens T, Morrisseau S (2002) Soil warming and carbon-cycle feedbacks to the climate system. Science 298(5601): 2173-2176

Michel C, Legendre L, Therriault J-C, Demers S (1989) Photosynthetic responses of Arctic Sea-Ice microalgae to short-term temperature acclimation. Polar Biol 9: 437-442

Moran XAG, Fernandez E, Perez V (2004) Size-fractionated primary production, bacterial production and net community production in subtropical and tropical domains of the oligotrophic NE Atlantic in autumn. Mar Ecol Prog Ser 274: 17-29

Navarro N, Agustí S, Duarte CM (2004) Plankton metabolism and dissolved organic carbon use in the Bay of Palma, NW Mediterranean Sea. Aquat Microb Ecol 37: 47-54

Neori A, Holm-Hansen O (1982) Effect of temperature on rate of photosynthesis in Antarctic phytoplankton. Polar Biol 1: 33-38

Odate T, Furuya K, Fukuchi M (2002) Photosynthetic oxygen production and community respiration in the Indian sector of the Antarctic Ocean during austral summer. Polar Biol 25: 859-864

Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge, UK

Peterson BJ (1980) Aquatic primary production and the ^{14}C-CO_2 method: a history of the productivity problem. Annu Rev Ecol Syst 11: 359-385

Regaudie-de-Gioux A, Vaquer-Sunyer R, Duarte CM (2009) Patterns in planktonic metabolism in the Mediterranean Sea. Biogeosciences 6: 3081-3089

Regaudie-de-Gioux A, Duarte CM (2010a) Plankton metabolism in the Greenland Sea during the polar summer of 2007. Polar Biol, in press

Regaudie-de-Gioux A, Duarte CM (2010b) The compensation irradiance for planktonic community metabolism in the ocean. Global Biogeoch Cycles, in press

Robinson C, Williams PJLeB (1993) Temperature and Antarctic plankton community respiration J Plankton Res 15(9): 1035-1051

Robinson C, Archer SD, Williams PJLeB (1999) Microbial dynamics in coastal waters of East Antarctica: plankton production and respiration. Mar Ecol Prog Ser 180: 23-36

Robinson C, Serret P, Tilstone G, Teira E, Zubkov MV, Rees AP, Woodward EMS (2002) Plankton respiration in the Eastern Atlantic Ocean. Deep Sea Res Pt I 49(5): 787-813

Robinson C, Williams PJLeB (2005) Respiration and its measurement in surface marine waters, in Respiration in aquatic ecosystems edited by del Giorgio P, Williams PJLeB (Eds.), pp. 148-181, Oxford Univ. Press

Ruiz-Halpern S, Sejr MK, Duarte CM, Krause-Jensen D, Dalsgaard T, Dachs J, Rysgaard S (2010) Air-water exchange and vertical profiles of organic carbon in a subarctic fjord. Limnol Oceanogr, in press

Satta MP, Agustí S, Mura MP, Vaqué D, Duarte CM (1996) Microplankton respiration and net community metabolism in a bay on the NW Mediterranean coast. Aquat Microb Ecol 10: 165-172

Serret P, Fernández E, Sostres JA, Anadon R (1999) Seasonal compensation of microbial production and respiration in a temperate sea. Mar Ecol Prog Ser 187: 43-57

Serret P, Fernández E, Anadon R, Varela M (2001a) Trophic control of biogenic carbon export in Bransfield and Gerlache Straits, Antarctica. J Plankton Res 23(12): 1345-1360

Serret P, Robinson C, Fernández E, Teira E, Tilstone G (2001b) Latitudinal variation of the balance between plankton photosynthesis and respiration in the eastern Atlantic Ocean. Limnol Oceanogr 46(7): 1642-1652

Serret P, Fernández E, Robinson C, Woodward EMS, Pérez V (2006) Local production does not control the balance between plankton photosynthesis and respiration in the open Atlantic Ocean. Deep Sea Res Pt II 53: 1611-1628

Smith SV, Hollibaugh JT (1993) Coastal metabolism and the oceanic organic carbon balance. Rev Geophys 31(1): 75-89

Steeman Nielsen E (1952) The use of radioactive carbon (^{14}C) for measuring production in the sea. J Cons Perm Int Explor Mer 18: 117-140

Takahashi T, Sutherland SC, Sweeney C, Poisson A, Metzl N, Tilbrook B, Bates N, Wanninkhof R, Feely RA, Sabine C, Olafsson J, Nojiri Y (2002) Global sea-air CO_2 flux base don climatological surface ocean pCO_2 and seasonal biological and temperatura effects. Deep-Sea Res Pt II 49: 1601-1622

Teira E, Serret P, Fernández E (2001) Phytoplankton size-structure, particulate and dissolved organic carbon production and oxygen fluxes through microbial communities in the NW Iberian coastal transition zone. Mar Ecol Prog Ser 219: 65-83

Valentini R, Matteucci G, Dolman AJ, Schulze E-D, Rebmann C, Moors EJ, Granier A, Gross P, Jensen NO, Pilegaard K, Lindroth A, Grelle A, Bernhofer C, Grünwald T, Aubinet M, Ceulemans R,. Kowalski AS, Vesala T, Rannik Ü, Berbigier P, Loustau D, Guðmundsson J, *Thorgeirsson H, Ibrom A, Morgenstern K, Clement R, Moncrieff J, Montagnani L, Minerbi S, Jarvis PG (2000) Respiration as the main determinant of carbon balance in European forests. Nature 404: 861-865*

Vaquer-Sunyer R, Duarte CM, Santiago R, Wassmann P, Reigstad M (2010) Experimental evaluation of planktonic respiration response to warming in the European Arctic Sector. Polar Biol, in press

West GB, Brown JH, Enquist BJ (1997) A general model for the origin of allometric scaling laws in biology. Science 276: 122-126

Williams PJLeB (1998) The balance of plankton respiration and photosynthesis in the open oceans. Nature 394: 55-57

Williams PJLeB, Morris PJ, Karl DM (2004) Net community production and metabolic balance at the oligotrophic ocean site, station ALOHA. Deep Sea Res Pt I 51(11): 1563-1578

Yvon-Durocher G, Jones JI, Trimmer M, Woodward G, Montoya JM (2010) Warming alters the metabolic balance of ecosystems. Philos T R Soc 365, 2117-2126

Zlotnik I, Dubinsky Z (1989) The effect of light and temperatura on DOC excretion by phytoplankton. Limnol Oceanogr 34(5): 831-839

General Discussion

Ocean biota plays through their metabolic processes a major role in controlling CO_2 partial pressure in seawater and hence, air-sea exchange, which depends on the metabolic balance of planktonic communities (Calleja *et al*., 2005). The metabolic status of oceanic ecosystems is defined by the gross primary production (GPP) and the community respiration (CR) of the planktonic community. Resolving and understanding patterns in CR and GPP is important to elucidate whether the biota of aquatic ecosystems acts as net CO_2 sources (P < R) or sinks (R < P). The balance between GPP and CR in oceanic ecosystems has been the subject of much discussion and controversy in the scientific community. The suggestion that heterotrophic communities (CR > GPP) may prevail in oligotrophic ocean ecosystems (del Giorgio *et al*., 1997; Duarte and Agustí, 1998) proved controversial (cf. Williams and Bower, 1999; Duarte *et al*., 2000; del Giorgio and Duarte, 2002; Karl *et al*., 2003). However, this controversy was positive, as it stimulated much-needed research to expand the meager empirical basis (Williams and del Giorgio, 2005) upon which these debates were originally based (Duarte and Agustí, 1998; Williams 1998; Williams and Bower, 1999; del Giorgio and Duarte, 2002). The research presented here synthesized these observations and added a significant amount of new data (342 stations sampled in the Arctic, Antarctic and Atlantic Ocean and the Mediterranean Sea) on metabolic rates of oceanic plankton.

The expanded observational basis resulting from these debates provided an opportunity to elucidate patterns in the metabolic balance in the Ocean, including examination of the magnitude of the differences in rates derived by different methods and describe the scaling among different metrics of plankton metabolic rates, evaluate regional and global variability in plankton metabolism and determine the threshold gross primary production separating heterotrophic from autotrophic communities and the threshold irradiance required to balance primary production and respiration. Environmental parameters such as irradiance or water temperature play have an important role in controlling the metabolic balance of planktonic communities. Evaluating the irradiance at which the gross primary production balances the respiration of the community and determining the temperature-dependence of planktonic metabolism are fundamental to improve our knowledge on the various drivers of the metabolic balance of plankton communities.

The measurement of plankton primary production is a fundamental property of the ocean ecosystem, receiving considerable effort that has resulted in several million estimates available to-date, mostly derived from measurements of ^{14}C incorporation into particulate organic matter (del Giorgio and Williams, 2005). In this work, we examined the magnitude of the differences in rates derived by different methods and described the scaling among different metrics of planktonic primary production, providing equations that allow conversion of estimates among different methods. A new critical view of GPP measurements has been provided here (chapter 1). The results obtained here (chapter 1) indicate that, on average, ^{14}C-TOC significantly underestimate GPP by 2 (bulk oxygen) to 2.60 (^{18}O) fold, in contrast to the conclusion by Williams *et al*. (1983), Bender *et al*. (1987) and González *et al*. (2008), derived from much smaller data sets than that compiled here, that the estimates of primary production derived by ^{14}C-TOC were not significantly different from those derived using the O_2 method. Moreover, the difference between gross primary production and ^{14}C-POC are even highest (3-fold), demonstrating that ^{14}C-POC estimates grossly underestimate gross primary production. Our results confirm that the highest primary production estimates are derived using the ^{18}O method, which best approaches gross primary production The ratios between different metrics of primary production derived here can be used to derive rules of thumb to convert estimates derived with different methods, thereby providing a basis for comparison. The conversion factors, scaled to ^{14}C-POC as the most commonly used metric of primary production, are 6.1 GPP-^{18}O : 3.27 GPP-O_2 : 2.3 ^{14}C-TOC : 1 ^{14}C-POC. The results presented here shows broad differences between estimates of primary production derived using different methods and provide conversion factors and regression equations to interconvert and compare results derived using different methods. The fact that estimates of the role of primary producers on carbon flow in the ocean are derived using ^{14}C-POC-calibrated estimates indicates that the gross flux of carbon through oceanic plankton is severely underestimated in assessments of the global ocean carbon budget, thereby explaining difficulties to reconcile the metabolic budget of the plankton community.

Previous published reports (Williams *et al*., 1998; del Giorgio and Duarte, 2002; Duarte and Prairie, 2005; Robinson and Williams, 2005) attempted to elucidate the metabolic balance along the ocean, compiling and analysing metabolism databases of planktonic communities in the ocean. The limited coverage of available data precluded a robust evaluation of global and regional patterns in planktonic metabolism, which

were nevertheless attempted. Both are necessary, because much of the variance in global patterns in planktonic metabolism may derive from regional differences. A much-expanded database of oceanic planktonic metabolism within the euphotic zone (3-fold larger than the Robinson and Williams one) was collected and analysed here (chapter 2, 3, 4 and 5), from five different oceans and the Mediterranean Sea. Despite efforts to increase our coverage of ocean metabolism, the global database compiled here encompasses about 17 % of the surface of the global ocean and the estimates derive represent, therefore, coarse approximation to global ocean metabolic rates.

The scaling between GPP and CR was not universal across the ocean with a 5 to 10-fold variability in the mean CR expected for any given GPP among oceanic basins. A great variability in metabolic rates and balances was observed across the ocean with heterotrophic planktonic communities prevailing in the continental shelf. Indeed, our estimates suggest a negative metabolic balance for the upper ocean, a suggestion that must be taken with caution due to the sparse coverage of estimates of metabolic rate in the ocean. Thresholds of GPP were also calculated by different approaches (comparative analysis, time-series analysis, experiments and modeling exercises) for different ocean basins, hemispheres and coastal and open ocean stations (chapter 2 and 3) to test the notion that less productive marine planktonic communities tend to be heterotrophic. No difference was observed between the thresholds of GPP derived from different approaches while a great variability was observed between the thresholds of GPP for different oceanic regions. The existence of a threshold of GPP provides evidence that less productive planktonic communities tend to be net heterotrophic, consistent with the tendency for oligotrophic communities to support higher heterotrophic biomass per unit autotrophic biomass than more productive ones (Gasol *et al.*, 1997). This observation is paradoxical considering that less productive planktonic communities possibly net heterotrophic, still export organic matter. The consideration of allochthonous organic carbon inputs, through lateral inputs from land and coastal regions and atmospheric deposition (Dachs *et al*., 2005; Duarte *et al*., 2006) may suffice to explain how net heterotrophic planktonic communities still export organic carbon in less productive regions. Indeed, high GPP thresholds's were observed in oceanic regions receiving high allochthonous inputs, such as the Arctic Ocean the Mediterranean Sea (chapter 2 and 3), and coastal communities (chapter 3), (Guerzoni *et. al*., 1999; Opsahl *et al*., 1999; Benner *et al*., 2005; Dachs *et al*., 2005; Jurado *et al*.,

2008). In comparison, low GPP thresholds were observed in regions receiving low allochthonous inputs (i.e. Southern Ocean, chapter 2 and 3).

Light limitation is considered as the factor most often conducive to heterotrophic community metabolism in the ocean and affects the metabolic balance of planktonic communities. The compensation irradiance for community metabolism is defined as the irradiance at which gross community primary production (GPP) balances respiratory carbon losses (R) for the entire community (Gattuso *et al.,* 2006). The compensation irradiance helps determine the depth below which planktonic metabolism becomes heterotrophic as well as the impact of changes in light penetration on the planktonic metabolic balance. In this work (chapter 4), the communities receiving irradiances above the compensation irradiance (1.1 mol quanta m^{-2} d^{-1}) or compensation depth (36 m depth) were autotrophic and acted as CO_2 sinks, whereas those at lower irradiances or located deeper in the water column act as CO_2 sources. The compensation irradiance for studied pelagic metabolism here tends to be lower for strongly autotrophic communities, which shows that productive communities tend to be more tolerant to light reduction in the water column. The autotrophic planktonic communities occupy a thin layer encompassing about 36 m of the studied ocean, and yet affect, through their uptake of CO_2, the gaseous composition and climate of the planet. The increase of temperature, affecting the respiration rates (chapter 5) and the increase of atmospheric organic carbon inputs would lead to even shallower layers of autotrophy in the ocean, affecting the metabolic balance of the planktonic communities. Moreover, the compensation depth for heterotrophic communities, which extend across a significant fraction of the ocean surface, is undefined as even the surface communities receiving the highest irradiance are heterotrophic in these communities.

The effect of temperature on plankton metabolic rates can be inferred from the metabolic theory of ecology, introduced by Gillooly *et al*. (2001) and Brown *et al*. (2004), which predicts the role of temperature in regulating the metabolism of an ecosystem and how metabolic rate controls ecological processes at all levels of organization. Metabolic theory predicts that both respiration and photosynthesis should increase with increasing temperature, albeit at different rates (Brown *et al*., 2004; Harris *et al*., 2006; López-Urrutia *et al*., 2006). A strong temperature-dependence of chlorophyll-*a* normalised metabolic rates of oceanic plankton communities across the ocean was observed here (chapter 5), consistent with the dependence of mass-normalised metabolic rates on temperature expected from the metabolic theory (West *et*

al., 1997; Gillooly *et al*., 2001; Brown *et al*., 2004; Harris *et al*. 2006; López-Urrutia *et al*., 2006). Moreover, our results show that the P/R ratio of 1, indicative of metabolic balance, is observed at an average threshold temperature of 23.5 ºC, with warmer waters presenting a tendency to support heterotrophic communities. This is consistent with the observation that communities in the tropical and subtropical ocean have often been reported to be heterotrophic (Duarte and Agustí, 1998; Duarte *et al*., 2001; Williams *et al*., 2004) with these regions often acting as CO_2 sources to the atmosphere (Duarte and Prairie, 2005). A shift towards a prevalence of heterotrophy in ocean plankton communities in a warmer ocean may be constrained by the availability and supply of organic carbon to support excess respiration over production (chapter 2 and 3). However, the ocean receives significant inputs of organic carbon, in dry and wet deposition (Jurado *et al.,* 2008), as well as volatile organic carbon (Dachs *et al*., 2005; Ruiz-Halpern *et al*., 2010) to support heterotrophy, which may also proceed by using further the large stock of dissolved organic carbon encountered in the ocean. The response of plankton respiration rates to warming demonstrated here predicts that the role of ocean plankton as a CO_2 sink should decline with increased warming.

Whereas many properties of the ocean are presently monitored at a global scale, including chlorophyll-a concentration, temperature and CO_2, our current observational effort on plankton metabolism is scattered and discontinuous, resulting in an inability to detect changes in plankton metabolic rates, shall these occur. Provided the predictions derived here and the major role of ocean plankton in the carbon budget, improving our observational basis on plankton metabolism is a matter of urgency.

The results presented in this dissertation reveal, in summary, important patterns of metabolic balance for planktonic communities across the ocean, their rates and controls. Continuing to explore the oceans and evaluating the metabolic balance of their planktonic communities is fundamental considering the major role planktonic community play in the global carbon cycle.

References

Bender ML, Grande K, Johnson K, Marra J, Williams PJLeB, Sieburth J, Pilson M, Langdon C, Hitchcock G, Orchardo J, Hunt C, Donaghay P, Heinemann K (1987) A comparison of four methods for determining planktonic community production. Limnol Oceanogr 32(5): 1085-1098

Benner R, Louchouarn P, Amon RMW (2005) Terrigenous dissolved organic matter in the Arctic Ocean and its transport to surface and deep waters of the North Atlantic. Glob Biogeochem Cycles 19 doi: 10.1029/2004GB002398

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. Ecology 85(7): 1771-1789

Calleja MLl, Duarte CM, Navarro N, Agustí (2005) Control of air-sea CO_2 disequilibria in the subtropical NE Atlantic by planktonic metabolism under the ocean skin. Geophys Res Lett 32: doi:10.1029/2004GL022120

Dachs J, Calleja MLl, Duarte CM, del Vento S, Turpin B, Polidori A, Herndl G, Agustí S (2005) High Atmosphere-Ocean Exchange of Organic Carbon in the NE Subtropical Atlantic. Geophys Res Lett 32: doi:10.1029/2005GL023799

del Giorgio PA, Duarte CM (2002) Respiration in the open ocean. Nature 420: 379-384

del Giorgio PA, Williams PJLeB (2005) Respiration in aquatic ecosystems. Oxford University Press, 315 pp., New York

Duarte CM, Agustí S (1998) The CO_2 balance of unproductive aquatic ecosystems. Science 281

Duarte CM, Agustí S, Kennedy H, Vaqué D (1999) The Mediterranean climate as a template for Mediterranean marine ecosystems: the example of the northeast Spanish littoral. Prog Oceanogr 44: 245-270

Duarte CM, Agustí S, Kalff J (2000) Particulate light absorption and the prediction of phytoplankton biomass and planktonic metabolism in northeastern Spanish aquatic ecosystems. Can J Fish Aquat Sci 57: 25-33

Duarte CM, Agustí S, Aristegui J, González N, Anadon R (2001) Evidence of heterotrophic Subtropical Northeast Atlantic. Limnol Oceanogr 46(2): 425-428

Duarte CM, Prairie YT (2005) Prevalence of heterotrophy and atmospheric CO_2 emissions from aquatic ecosystems. Ecosystems 8: 862–870

Duarte CM, Dachs J, Llabrés M, Alonso-Laita P, Gasol JM, Tovar-Sánchez A, Sañudo-Wilhemy S, Agustí S (2006) Aerosol inputs enhance new production in the subtropical northeast Atlantic. J Geophys Res 111: doi:10.1029/2005JG000140

Gasol JM, del Giorgio PD, Duarte CM (1997) Biomass distribution in marine planktonic communities. Limnol Oceanogr 42: 1353–1363

Gattuso J-P, Gentili B, Duarte CM, Kleypas JA, Middelburg JJ, Antoine D (2006) Light availability in the coastal ocean: impact on the distribution of benthic

photosynthetic organisms and their contribution to primary production. Biogeosciences 3: 489-513

Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL (2001) Effects on size and temperature on metabolic rate. Science 293: 2248-2251

González N, Gattuso J-P, Middelburg JJ (2008) Oxygen production and carbon fixation in oligotrophic coastal bays and the relationship with gross and net primary production. Aquat Microb Ecol 52: 119-130

Guerzoni S, Chester R, Dulac F, Herut B, Loÿe-Pilot M-D, Measures C, Migon C, Molinaroli E, Moulin C, Rossini P, Saydam C, Soudine A, Ziveri P (1999) The role of atmospheric deposition in the biogeochemistry of the Mediterranean Sea. Prog Oceanogr 44: 147-190

Harris LA, Duarte CM, Nixon SW (2006) Allometric laws and prediction in estuarine and coastal ecology. Estuar Coasts 29(2): 340-344

Jurado E, Dachs J, Duarte CM, Simó R (2008) Atmospheric deposition of organic and black carbon to the global ocean. Atmospheric Environment 42: 7931–7939

Karl DM, Tien G, Dore J, Winn CD (1993) Total dissolved nitrogen and phosphorous concentrations at U.S.-JGOFS Station ALOHA: Redfield reconcilitaion. Mar Chem 41: 203-208

López-Urrutia A, San Martín E, Harris RP, Irigoyen X (2006) Scaling the metabolic balance of the oceans. Proc Natl Acad Sci USA 103: 8739–8744

Opsahl S, Benner R, Amon RMW (1999) Major flux of terrigenous dissolved organic matter through the Arctic Ocean. Limnol Oceanogr 44(8): 2017-2023

Robinson C, Williams PJLeB (2005) Respiration and its measurement in surface marine waters. In: del Giorgio PA, Williams PJLeB (Ed.), Respiration in aquatic ecosystems. Oxford University Press, p. 328

Ruiz-Halpern S, Sejr MK, Duarte CM, Krause-Jensen D, Dalsgaard T, Dachs J, Rysgaard S (2010) Air-water exchange and vertical profiles of organic carbon in a subarctic fjord. Limnol Oceanogr, in press

West GB, Brown JH, Enquist BJ (1997) A general model for the origin of allometric scaling laws in biology. Science 276: 122-126

Williams PJLeB, Heinemann KR, Marra J, Purdie DA (1983) Comparision of ^{14}C and O_2 measurements of phytoplankton production in oligotrophic waters. Nature 305: 49-50

Williams PJLeB (1998) The balance of plankton respiration and photosynthesis in the open ocean. Nature 394: 55–57

Williams PJLeB, Bower DG (1999) Determination of organic carbon balance in the oceans from field observations—A reevaluation. Science 284: 1735a

Williams PJLeB, Morris PJ, Karl DM (2004) Net community production and metabolic balance at the oligotrophic ocean site, station ALOHA. Deep-Sea Res I 51: 1563–1578

Williams PJLeB, del Giorgio P (2005) Respiration in aquatic ecosystems: history and background. In: del Giorgio PA, Williams PJLeB (Ed.), Respiration in aquatic ecosystems. Oxford University Press, p. 328

Conclusions

1. The metabolism of plankton communities varies greatly across different oceanic regions, with the lowest rates reported for the Mediterranean Sea and the Northern Hemisphere and the highest rates reported for the Southern Ocean and the Southern Hemisphere.

2. Heterotrophic plankton communities are prevalent in the continental shelf consistent with high allochthonous inputs to the coastal ocean.

3. The existence of a threshold of GPP of, on average 1.1 mmol O_2 m^{-3} d^{-1}, separating less productive, heterotrophic communities, from more productive, autotrophic communities, provides evidence that less productive planktonic communities tend to be net heterotrophic.

4. The compensation depth for plankton community metabolism averages 36 ± 9 m irradiance for plankton metabolism ages 1.1 mol quanta m^{-2} d^{-1} and tends to be lower for strongly autotrophic communities.

5. The gross primary production and the respiration of plankton communities increase with temperature, for any given chlorophyll a concentration, with activation energies of 0.43 and 0.71.

6. A 4 ºC increase in ocean temperature is predicted to lead to a 15 % and 42 % increase in gross primary production and respiration, respectively, increasing the prevalence of heterotrophy in the ocean and weakening the role of ocean plankton as a CO_2 sink with increased warming.

7. A P/R ratio of 1, indicative of metabolic balance, is observed at an average threshold temperature of 23.5 ºC, with warmer waters presenting a tendency to support heterotrophic communities.

8. More than 80 % of the area ocean remains unexplored for plankton metabolism.

9. Global GPP and R of plankton communities are calculated to be 145 Gt C $year^{-1}$ and 170 Gt C $year^{-1}$, respectively, although the uncertainty about these estimates precludes their use to derive the net community metabolism of the ocean.

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