

# 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 modeling exercise. Planktonic communities of the open ocean and continental shelf showed threshold GPP values ranging 30-fold, from 0.34 mmol O<sub>2</sub> m<sup>-3</sup> d<sup>-1</sup> to 9.45 mmol O<sub>2</sub> m<sup>-3</sup> d<sup>-1</sup>, with those for estuarine and coastal locations reaching 50.60 mmol O<sub>2</sub> m<sup>-3</sup> d<sup>-1</sup>. Antarctic and ultra-oligotrophic ecosystems showed the lowest threshold GPP values (<2.2 mmol O<sub>2</sub> m<sup>-3</sup> d<sup>-1</sup>), 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 C m<sup>-2</sup> d<sup>-1</sup>, consistent with recent estimates of allochthonous inputs of organic carbon to the ocean.

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<sub>2</sub> and inorganic nutrients and sources of organic matter and O<sub>2</sub>. Conversely, heterotrophic communities (GPP < R, NCP < 0) act as sources of CO<sub>2</sub> and inorganic nutrients and sinks of organic matter and O<sub>2</sub>.

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<sub>2</sub> m<sup>-3</sup> d<sup>-1</sup> 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 meager (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 modeling 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,

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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<sub>2</sub> 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<sup>18</sup>, O<sup>16</sup>, and O<sup>17</sup> 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 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 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 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<sup>3</sup>) 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 1).

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 1). Whereas comparative analyses of planktonic metabolism in coastal and estuarine systems revealed very high thresholds of 50.60 mmol O<sub>2</sub> m<sup>-3</sup> d<sup>-1</sup> (Duarte and Agustí 1998; Table 1; Fig. 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 1) between the lowest threshold (0.45 mmol O<sub>2</sub> m<sup>-3</sup> d<sup>-1</sup>, reported for the subtropical NE Atlantic; Duarte et al. 2001) and the highest thresholds (9.45 mmol O<sub>2</sub> m<sup>-3</sup> d<sup>-1</sup>, 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 ~2.3–2.77 mmol O<sub>2</sub> m<sup>-3</sup> d<sup>-1</sup> (Table 1; Fig. 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. 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 modeling analysis (López-Urrutia et al. 2006) is the lowest of all 35 estimates compiled (Table 1; Fig. 1). The modeling approach used by López-Urrutia et al. (2006) carries considerable uncertainty because it is a semi-empirical approach that calculates organism-specific

Table 1. Estimates of the threshold gross primary production separating heterotrophic from autotrophic planktonic communities derived from cross-comparative synthesis studies, time-series, experimental, and modeling studies. GPP = gross primary production; NCP = net community production; R = community respiration; ns = not statistically significant (see text).

Approach and Region	Y vs. X	Intercept	SE	Slope	SE	R <sup>2</sup> adj	Threshold GPP		Reference
							(mmol O <sub>2</sub> m <sup>-3</sup> d <sup>-1</sup> )		
Comparative analyses									
NW Indian Ocean	NCP vs. GPP	-3.18	0.33	0.76	0.06	0.83	4.2		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	-1.37	0.06	1.14	0.97	0.53	0.49		Duarte et al. (2001)
N. Atlantic	NCP vs. GPP	-2.56	0.27	1.24	0.1	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. (2002b)
Subtropical E Atlantic	NCP vs. GPP	-3.34	0.45	0.94	0.04	0.94	3.56		Robinson et al. (2002a)
Eastern N. Atlantic	NCP vs. GPP	-1.83	0.19	0.87	0.04	0.79	2.1		Serret et al. (2002)
N. Atlantic	NCP vs. GPP	-1.91	0.15	0.98	0.02	0.98	1.94		Aristegui and Harrison (2002)
Subtropical NE Atlantic	NCP vs. GPP	-1.16	0.26	0.8	0.06	0.63	1.45		N. Navarro et al. (unpubl. data)
Subtropical Atlantic	NCP vs. GPP	-3.32	0.32	2.02	0.22	0.21	1.65		S. Agustí (unpubl. data)
Subtropical NE Atlantic	NCP vs. GPP	-0.63	0.04	0.99	0.01	0.99	0.63		A. 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	-1.5	0.8	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	2.2		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		N. 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 <sup>ns,†</sup>	NCP vs. GPP	-0.27	1.09	0.59	0.07	0.67	0.46		Aristegui et al. (1996)
Arctic Ocean	NCP vs. GPP	-7.11	1.06	1.3	0.13	0.38	5.45		A. Regaudie-de-Gioux (unpubl. data)
Subtropical N. Pacific <sup>ns</sup>	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) DSR II
Mediterranean Sea	NCP vs. GPP	-7.8	1.96	0.83	0.13	0.53	9.45		R. Vaquer-Sunyer et al. (unpubl. data)
Mediterranean Sea	NCP vs. GPP	-3.16	0.41	1.59	0.23	0.29	1.99		A. Regaudie-de-Gioux (unpubl. data)
European coast	NCP vs. GPP	-6.24	0.58	1.08	0.04	0.83	5.76		J.P. Gattuso (unpubl. data)
Global coastal	R vs. GPP	0.65	0.04	1.1		0.6	50.6		Duarte and Agustí (1998)
Global	R vs. GPP	0.5	0.04	0.2		0.42	1.09		Duarte & Agustí (1998)
Global‡	R vs. GPP	-1.37	2.09	1.3	0.14	0.46	1.06		Robinson and Williams (2004)
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	0.4	2.12	0.11	0	3.51		Duarte et al. (2004)
Palma Bay (Mediterranean)	NCP vs. GPP	-3.8	0.91	0.96	0.2	0.41	3.97		Navarro et al. (2004)
Experiments									
Mediterranean coast	NCP vs. GPP	-3.81		0.92	0	0.99	4.14		Duarte et al. (2004)
European coast§	R vs. GPP	2.62	0	0.39	0.04	0.82	4.25		Olsen et al. (2006)
Southern Ocean	GPP/R vs. GPP	0.08		0.41		0.75	2.24		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)
Modeling									
Atlantic Ocean	lnR vs. ln GPP	0.79		0.74		0.67	0.34		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 <sup>14</sup>C.

‡ Includes records 1–3,5–9,16–19.

§ Based on inverse modeling.

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

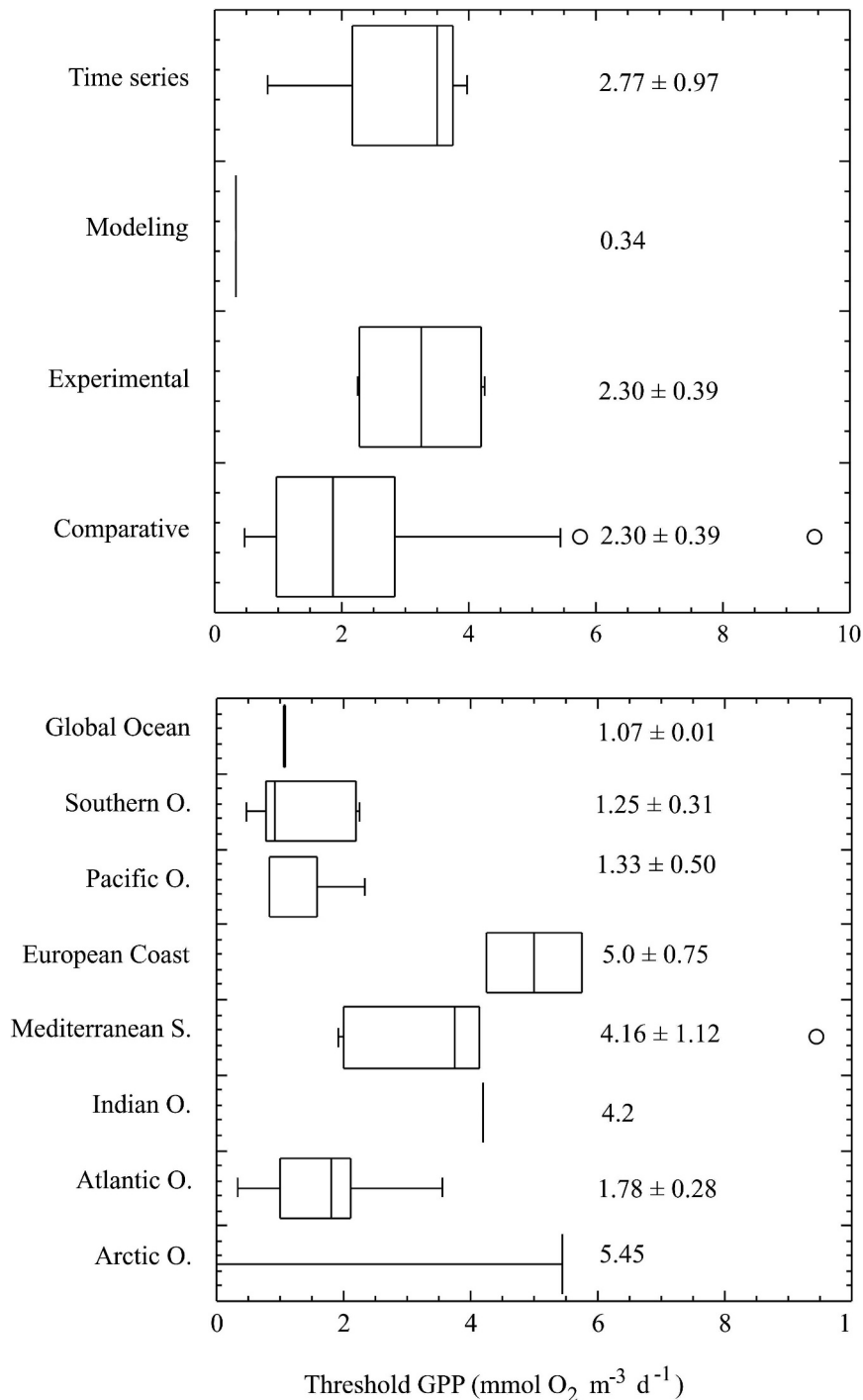


Fig. 1. Box-plots showing the distribution of GPP thresholds for metabolic balance of planktonic communities depending on the method of assessment and the region from where the data were derived. The lines extend to range, the box extends from the 25th to the 75th percentile and the central line represents the median (50th percentile). Open circles identify outliers. When only one observation was available a vertical line is shown to indicate the corresponding value, because boxes could not be drawn. The comparative estimate for coastal waters ( $50.6 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ ; Table 1) has been excluded from the comparison.

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 <sup>14</sup>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 modeled 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 modeled P should underestimate GPP, it is unlikely that this estimate be different from the value of  $1.07 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$  indicated by the global comparative analysis.

There was substantial variability in the threshold GPP for metabolic balance within basins (Table 1; Fig. 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. 1). The Atlantic Ocean, the Southern Ocean, and, particularly, the Pacific Ocean showed the lowest mean GPP threshold values (Fig. 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 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 ( $1.06 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$  and  $1.09 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ , respectively; Table 1; Fig. 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 modeling 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 1).

Two objections were initially raised to the inference of Duarte and Agustí (1998) of a threshold GPP of  $1.09 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$  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.,  $94 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$  for the subtropical NE Atlantic, Duarte et al. 2001;  $500 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$  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  $80.4 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ .

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.,  $R > \text{GPP}$ ) 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  $^{14}\text{C}$  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  $\sim 3\text{--}5 \text{ mmol C m}^{-3} \text{ d}^{-1}$  (Carlson et al. 2004), comparable to the threshold GPP estimates (Table 1; Fig. 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,

conducive 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.,  $\sim 1\text{--}3 \text{ mmol C m}^{-2} \text{ d}^{-1}$ , on average, for open-ocean communities; Table 1; Fig. 1), and the organic carbon export ( $\text{OC}_{\text{export}}$ ,  $\text{mmol C m}^{-2} \text{ d}^{-1}$ ), which in less productive communities reaches  $\sim 4 \text{ mmol C m}^{-2} \text{ d}^{-1}$  considering both particulate and dissolved export (Aristegui et al. 2005), be subsidized by inputs of allochthonous organic carbon ( $\text{AOC}_{\text{input}}$ ,  $\text{mmol C m}^{-2} \text{ d}^{-1}$ ). Hence, the allochthonous organic inputs to the less productive regions of the ocean, approximated as  $\text{AOC}_{\text{input}} = \text{GPP}_{\text{threshold}} + \text{OC}_{\text{export}}$ , must be in the order of  $5\text{--}6 \text{ mmol C m}^{-2} \text{ d}^{-1}$  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  $\sim 3 \text{ Gmol C yr}^{-1}$  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  $1 \text{ mmol C m}^{-2} \text{ d}^{-1}$  and that have been calculated to deliver  $245 \text{ Tg C}$  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  $\sim 25\text{--}31 \text{ mmol C m}^{-2} \text{ d}^{-1}$  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  $5\text{--}6 \text{ mmol C m}^{-2} \text{ d}^{-1}$  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  $\text{O}_2$  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 1), consistent with the high threshold value of  $500 \text{ mmol C m}^{-2} \text{ d}^{-1}$  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 allochthonous 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 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 1).

In addition to allochthonous inputs, climate may also affect threshold GPP. The modeling 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<sub>2</sub> m<sup>-3</sup> d<sup>-1</sup> in cold environments to 4 mmol O<sub>2</sub> m<sup>-3</sup> d<sup>-1</sup> at temperatures of 15°C, 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°C 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<sub>2</sub> m<sup>-3</sup> d<sup>-1</sup> 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.

#### Acknowledgments

We thank S. Agustí, J. P. Gattuso, N. Navarro, and R. Vaquer-Sunyer for access to unpublished data, P. le B. Williams for providing raw data from a published report, and C. A. Robinson for sharing to the global metabolism data set. This research was supported by project “COCA: Flujo de carbono en la región Canaria: acoplamiento entre exportación costera y demanda oceánica,” “RODA: Remolinos oceánicos y deposición atmosférica: efectos biológicos y biogeoquímicos en aguas del Atlántico Este,” “ATOS: Atmospheric inputs of organic carbon and pollutants to the polar ocean: Rates, significance and Outlook,” and the “Malaspina 2010” CONSOLIDER project funded by the Spanish Ministry of Science and Innovation, and the integrated project Thresholds and the EUR-OCEANS network of excellence funded by the European Commission. A. R. d. G was supported by the META-OCEANS Marie Curie Network, of FP 6 of the European Commission.

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Associate editor: Peter A. Jumars

Received: 28 November 2008

Accepted: 12 January 2009

Amended: 09 February 2009