

# The Role of Marine Biota in the Functioning of the Biosphere

Carlos M. Duarte (Ed.)

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Offprint of the Chapter

## CHAPTER 2 THE ROLE OF MARINE BIOTA IN THE METABOLISM OF THE BIOSPHERE

by

**Carlos M. Duarte, Susana Agustí and Aurore Regaudie-de-Gioux**

Department of Global Change Research

Mediterranean Institute for Advanced Studies (IMEDEA)

Spanish National Research Council (CSIC)-University of Balearic Islands (UIB)

Esporles, Mallorca, Spain

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## CHAPTER 2

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**CARLOS M. DUARTE, SUSANA AGUSTÍ AND AURORE REGAUDIE-DE-GIOUX**

Department of Global Change Research

Mediterranean Institute for Advanced Studies (IMEDEA)

Spanish National Research Council (CSIC)-University of Balearic Islands (UIB)

Esporles, Mallorca, Spain

**THE TERM METABOLISM REFERS** to the transformations of materials, involving the use or release of energy, necessary to maintain organisms alive. At the ecosystem level, metabolism refers to the transformations of elements from inorganic to organic form and vice versa, through the aggregated metabolic processes of the individual components of the ecosystem. More specifically, ecosystem metabolism refers to the production and destruction of organic matter and the associated fluxes of materials and energy.

Occupying most of the Earth's surface, the oceans are an active component of the Biosphere, with marine biota supporting a significant fraction of the production and destruction of organic matter. Marine biota has therefore served an important role in the metabolism of the Biosphere, although this has not been sufficiently recognised.

Here we examine the role of marine biota in supporting the metabolism of the Biosphere. We first discuss the major processes involved in ocean metabolism, photosynthesis and respiration, and introduce the concept of net

◀ **Photo 2.1: Cyanobacterium *Scytonema*.** Colorized scanning electron micrograph of growing filament tips.

ecosystem production. We then examine the balance between photosynthesis and respiration and the causes and consequences for the functioning of the biosphere of imbalances in these two key properties.

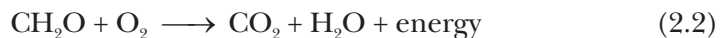
## 2.1. ECOSYSTEM METABOLISM: DEFINITION AND SIGNIFICANCE

Howard T. Odum, arguably the father of ecosystem science, advanced that the metabolism of ecosystems can be defined and studied, not through the sum of the metabolic rates of their individual components, but as a higher-order property (Odum 1958). He proposed that the metabolism of ecosystems can be represented by the production and destruction of organic matter, and the associated fluxes of nutrients, through the gross photosynthetic and respiratory activity of ecosystems (Odum 1958). Photosynthesis is the main pathway for the production of organic matter in the ecosystem proceeding according to the simplified equation:



The organisms able to conduct photosynthesis all have Chlorophyll a, and other accessory pigments, and are known as primary producers. Microorganisms can also use chemical energy to produce organic matter, through a process called chemosynthesis, but although it is significant in some ecosystems such as deep ocean hydrothermal vents, chemosynthesis plays a minor role in the formation of organic matter at the biosphere scale. Photosynthesis is the process responsible for supplying the organic matter required for the ecosystem to function, as all organisms in the food web are consumers of organic matter, which they transform and destroy, to extract energy to support their life processes.

Respiration is the process responsible for the destruction of organic matter to extract energy, in the form of adenosyl triphosphate (ATP), which supports all organismal processes. Respiration can be defined by the simplified equation,



Respiration is the dominant mode of destruction of organic matter, although organic matter can also be destroyed by photochemical oxidation in the presence of strong solar irradiance and high UV levels, but again, this process



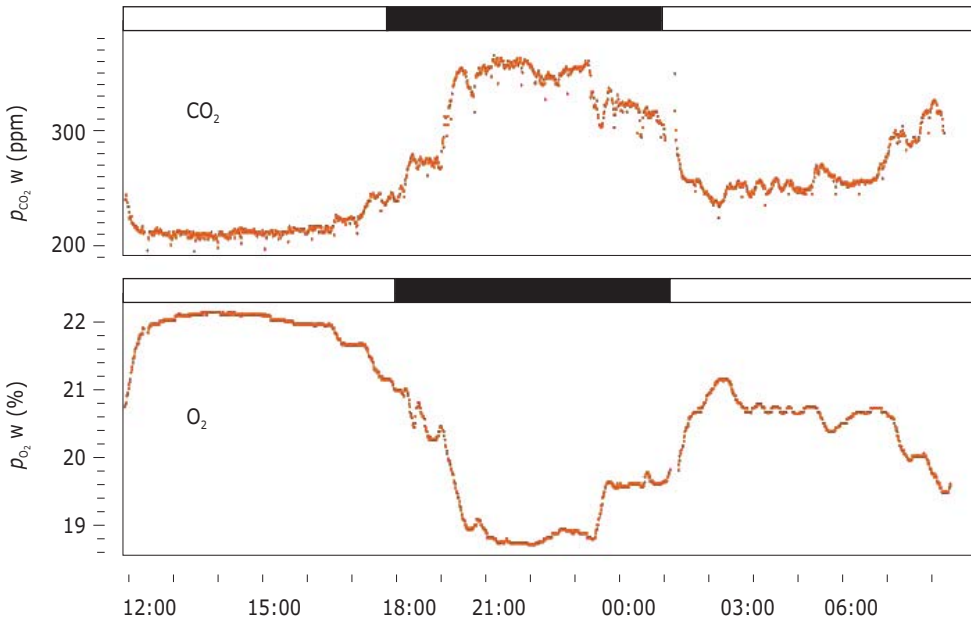
**Photo 2.2:** Giant moon jellyfish (*Aurita aurita*), from Jellyfish Lake in Pelau Island (Micronesia)

although locally important, contributes a negligible fraction of the organic matter destroyed or remineralised every year in the biosphere (photo 2.2).

Inspection of equations 2.1 and 2.2 readily shows that respiration is the opposite process to photosynthesis. Whereas photosynthesis consumes  $\text{CO}_2$  and releases  $\text{O}_2$  (equation 2.1), respiration consumes  $\text{O}_2$  and releases  $\text{CO}_2$  (equation 2.2). These processes link the  $\text{O}_2$  and  $\text{CO}_2$  fluxes in the biosphere on a stoichiometric ratio of approximately 1 mol  $\text{O}_2$ : 1 by mol  $\text{CO}_2$ . Along with the fluxes of  $\text{O}_2$  and  $\text{CO}_2$ , photosynthesis and respiration also support opposite fluxes of nutrients, such as nitrogen phosphorus and iron, among others, which are required to support biological processes, as they are incorporated into organic matter after this is formed through photosynthesis and they are remineralised into inorganic forms, such as ammonia and phosphate, when organic matter is destroyed by respiration. Hence, photosynthetic organisms consume inorganic nutrients and all organisms remineralise nutrients into inorganic forms, thereby linking the fluxes of  $\text{O}_2$  and  $\text{CO}_2$  in the ecosystem to those of nutrient elements.

Photosynthesis and respiration are not only opposite, but also complementary. A much higher rate of photosynthesis over respiration would lead to a depletion of  $\text{CO}_2$  and inorganic nutrients that will eventually compromise, and reduce photosynthetic activity. Likewise, a much higher respiration than photosynthetic rate

**Figure 2.1: Diel variation in the partial pressure of O<sub>2</sub> and CO<sub>2</sub> in surface waters of the Weddell Sea, recorded during the ICEPOS cruise on board *R/V Hespérides*.** Open and closed bars over the graph denote the daytime and nighttime periods, respectively.



would, if sustained over time, deplete O<sub>2</sub> and organic matter, thereby reducing and compromising further respiratory activity. Hence, ecosystems typically show a close balance between photosynthesis and respiration, particularly when examined over large spatial and temporal scales. For instance, figure 2.1 shows diel changes in O<sub>2</sub> and CO<sub>2</sub> in the surface waters of the Weddell Sea, Antarctica, recorded during the ICEPOS cruise on board *R/V Hespérides*. This is characteristic of the mirror image of changes in O<sub>2</sub> and CO<sub>2</sub> in seawater derived from plankton metabolism, with a decline in  $p_{\text{O}_2}$  and an increase in  $p_{\text{CO}_2}$  during the night with the opposite changes occurring during daylight (figure 2.1). Although production and respiration are complementary processes, there has been a historical emphasis in measuring production compared to respiration. Indeed, the numbers of estimates of photosynthetic rates in the open ocean exceed 1 million, compared to a few thousand estimates of respiration rates of plankton communities, resulting in about 20,000 estimates of oceanic production for each estimate of respiration rate (Williams and del Giorgio 2005).

The balance between photosynthesis and respiration is characterised by the net ecosystem production,  $NEP$  ( $NEP = GPP - R$ ) as well as the  $P/R$  ratio



( $P/R$  ratio =  $GPP/R$ ). Ecosystems with  $NEP > 0$  and  $P/R > 1$  are termed autotrophic and act as sinks for  $CO_2$  and inorganic nutrients and sources  $O_2$  and organic matter, which they accumulate or export. In contrast, ecosystems  $NEP < 0$  and  $P/R < 1$  are termed heterotrophic, and act as sinks for  $O_2$  and organic matter, and sources of  $CO_2$  inorganic nutrients. Heterotrophic ecosystems import organic matter from other ecosystems or loss of organic matter. Small miss-matches in ecosystem metabolism at the global scale, where  $NEP$  and  $P/R$  ratios deviate significantly from 0 and 1 respectively, are also possible and when sustained over time are responsible, for instance, for the depletion of  $CO_2$  in the atmosphere down to 180 ppm during interglacial periods (Sigman and Boyle 2000). The formation of many coal, oil and gas deposits is a consequence of the Biosphere sustaining autotrophic status ( $NEP > 0$ ,  $P/R > 1$ ) over very extended geological periods. Likewise the current increase in atmospheric  $CO_2$  can be interpreted as a result of greatly increased respiration, due to the proliferation of animal biomass, including humans, brought about by population growth and life stock production (Prairie and Duarte 2007) and the development of technology for the exosomatic combustion of excedentary organic carbon stored through geological time as coal, gas and oil, to derive energy. The burning of fossil fuels to derive energy can be equated to an exosomatic respiration process, as it consumes organic matter, excedentary from past periods of an autotrophic Biosphere, and oxygen to free energy and release  $CO_2$ , conducive to a net heterotrophic Biosphere as we will see below.

## 2.2. ECOSYSTEM METABOLISM AND C AND $O_2$ MASS BALANCES

H.T. Odum, on recognising the importance of ecosystem metabolism and the connection of carbon and oxygen fluxes through photosynthesis and respiration at the ecosystem level, proposed that ecosystem metabolism in aquatic ecosystems can be derived from changes in  $O_2$  by solving the mass balance equation (Odum 1958):

$$\frac{\partial O_2}{t} = P - R + f_{air-sea} + A_{input} \quad (2.3)$$

where  $\frac{\partial O_2}{t}$

indicates the rate of change in  $O_2$  concentration over time,  $P$  indicates gross primary production,  $R$  indicates community respiration,  $f_{air-sea}$  indicates the exchange of  $O_2$  between the water and the atmosphere and  $A_{input}$  represents the lateral exchanges of  $O_2$  with adjacent ecosystems; all with units  $\mu\text{mol } O_2 \text{ L}^{-1} \text{ h}^{-1}$ . The same equation can be formulated for  $CO_2$ , but changes in oxygen are faster and can be better resolved than those in  $CO_2$ . Changes in  $O_2$  along diel cycles in ecosystems can be derived from continuously recording instruments (figure 2.1), and the air-sea exchange of  $O_2$  can be derived from the differential in partial pressures between the air and the ocean surface and an exchange coefficient typically parametrised as a cubic function of wind velocity (Wanninkhof and McGillis 1999).  $R$  can be derived from the rates of decline in  $O_2$  (or increase in  $CO_2$ ) during the night and the rate of increase during the day provides the solution for  $P - R$  (figure 2.1). The term  $A_{input}$  can then be calculated as the residual in solving the equation, since this term is difficult to calculate directly.

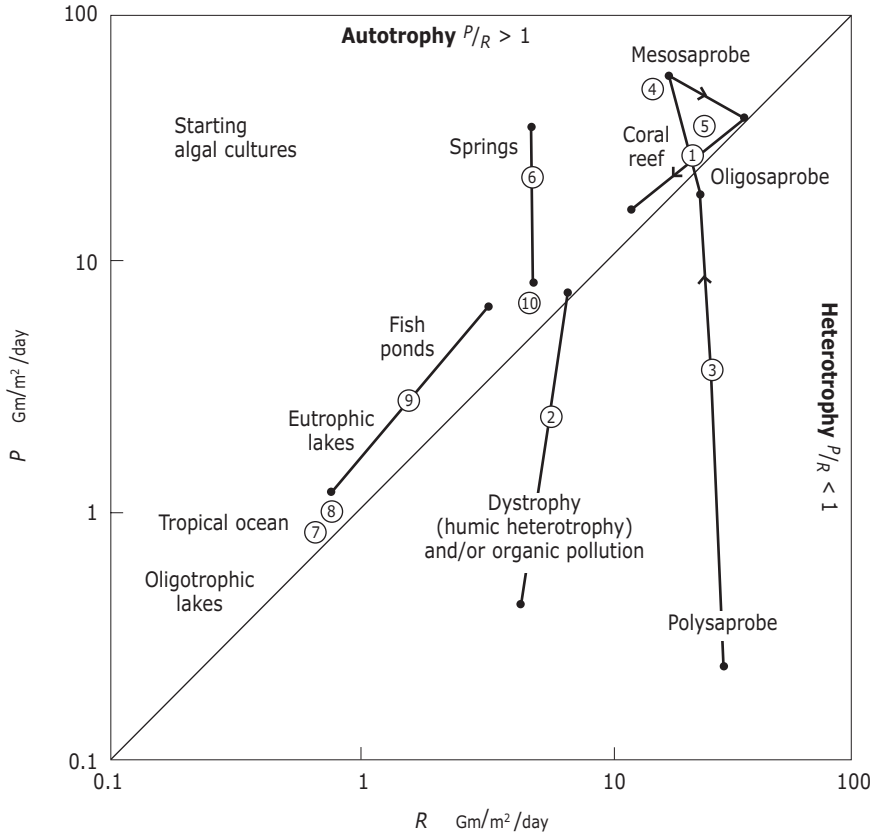
The terms of equation 2.3, when formulated on the basis of  $CO_2$ , encompass the subjects of most of the processes that are of interest to global biogeochemistry: the net rate of change in  $CO_2$ , essential to determine the role of ecosystems as sinks (positive rates of change) or sources (negative rate of change) of  $CO_2$ . The exchange with the atmosphere is the process responsible for the role of the ocean as a sink of  $CO_2$ . The inputs from adjacent ecosystems, including the inputs of materials delivered by rivers to the ocean demonstrates the connectivity between ecosystems. Whereas  $f_{air-sea}$  and  $A_{input}$  were presented by Odum (1958) as terms necessary to extract  $P$  and  $R$ , interest has shifted and attention is now focussed on how ecosystem metabolism, the balance between  $P$  and  $R$ , affects the exchange of  $CO_2$  between the water and the atmosphere ( $f_{air-sea}$ ).

### 2.3. PATTERNS IN THE ECOSYSTEM METABOLISM IN MARINE COMMUNITIES

On his first assessment, Odum (1956) characterised marine ecosystems as generally autotrophic, with coral reefs and the tropical ocean being slightly autotrophic, close to metabolic balance (figure 2.2). Indeed, the larger data set available half a century later supports the existence of a broad relationship between production and respiration in marine plankton communities (figure 2.3, Duarte and Agustí 1998; Robinson and Williams 2005).



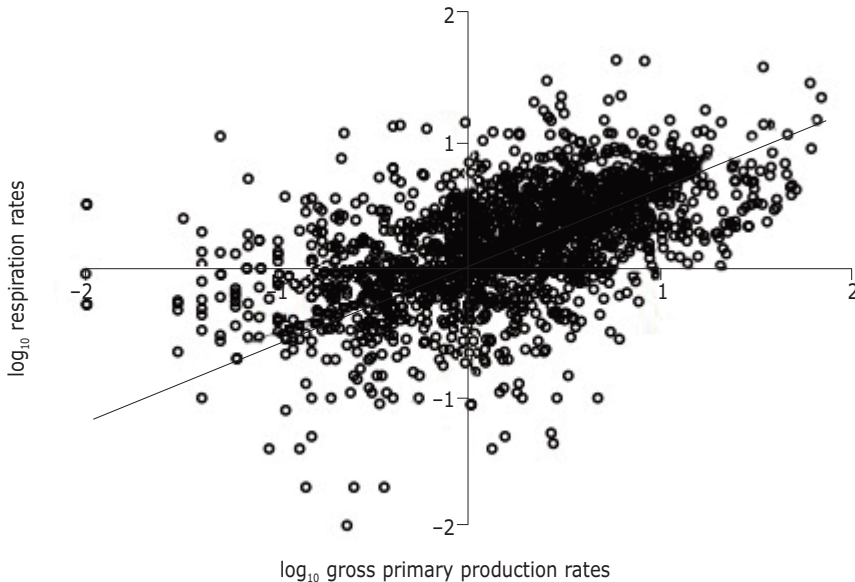
**Figure 2.2: The relationship between community production and respiration in a range of ecosystems**



Source: Odum 1956.

This relationship indicates that the respiration rates of plankton communities are not proportional to their gross primary production (Duarte and Agustí 1998), but that  $GPP \sim R^{0.62}$  (Robinson and Williams 2005) indicates that community respiration is highest for any given gross primary production in unproductive waters and that the  $P/R$  ratio increases with increasing production (Duarte and Agustí 1998; Robinson and Williams 2005). Indeed, the relationship between production and respiration implies that  $GPP = R$  at an average  $GPP$  of  $1.06 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$  and marine plankton communities with a lower  $GPP$  are, therefore, likely to be heterotrophic (Duarte and Regaudie-de-Gioux 2009). Examination of  $\text{CO}_2$  fluxes in the ocean indicates that the equatorial areas and the unproductive tropical gyres in the center of oceanic basins tend to be net sources of  $\text{CO}_2$

**Figure 2.3: The relationship between the respiration and gross primary production of plankton communities in the ocean (units  $\text{mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ ). The solid line shows the fitted, model II, regression equation.**

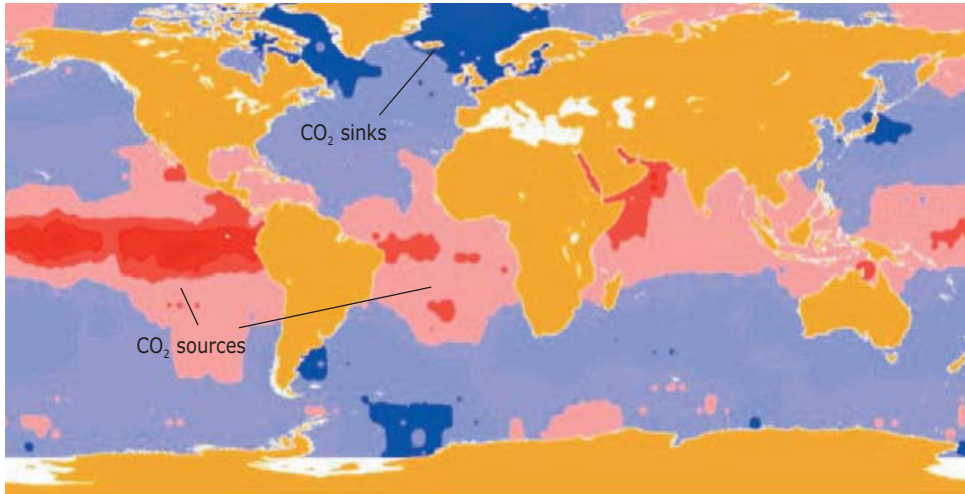


Source: Modified from Robinson and Williams 2005.

to the atmosphere (map 2.1), consistent with the net heterotrophy expected for communities in these ultraoligotrophic ecosystems (Prairie and Duarte 2005).

Heterotrophy was, in Odum's (1956) conceptualisation, a characteristic of a dysfunctional ecosystem, such as those affected by organic inputs (figure 2.2). Indeed, the oceanographic community has long assumed marine ecosystems to be autotrophic, with the implicit rationale that heterotrophic ecosystems cannot sustain harvests, such as fisheries sustained over centuries, nor can they export organic matter as plankton ecosystems in the ocean mixed layer, as was recorded by sediment traps collecting materials below the mixed layer (Duarte and Regaudie-de-Gioux 2009). Indeed, some graphical representations of the ocean carbon budget echo this belief, as no organic inputs to the open ocean, other than the riverine inputs to the coastal ocean, are included, such that the only material the open ocean exchanges with the atmosphere is  $\text{CO}_2$  (figure 2.4). These representations of the carbon cycle of the open ocean imply that it must be an autotrophic ecosystem, as heterotrophy can only be sustained if the stocks of organic carbon in the ocean

**Map 2.1: Air-sea fluxes of CO<sub>2</sub> in the ocean.** Intense blue colored indicates strong sinks whereas strong red colored indicates strong emissions of CO<sub>2</sub> to the atmosphere.

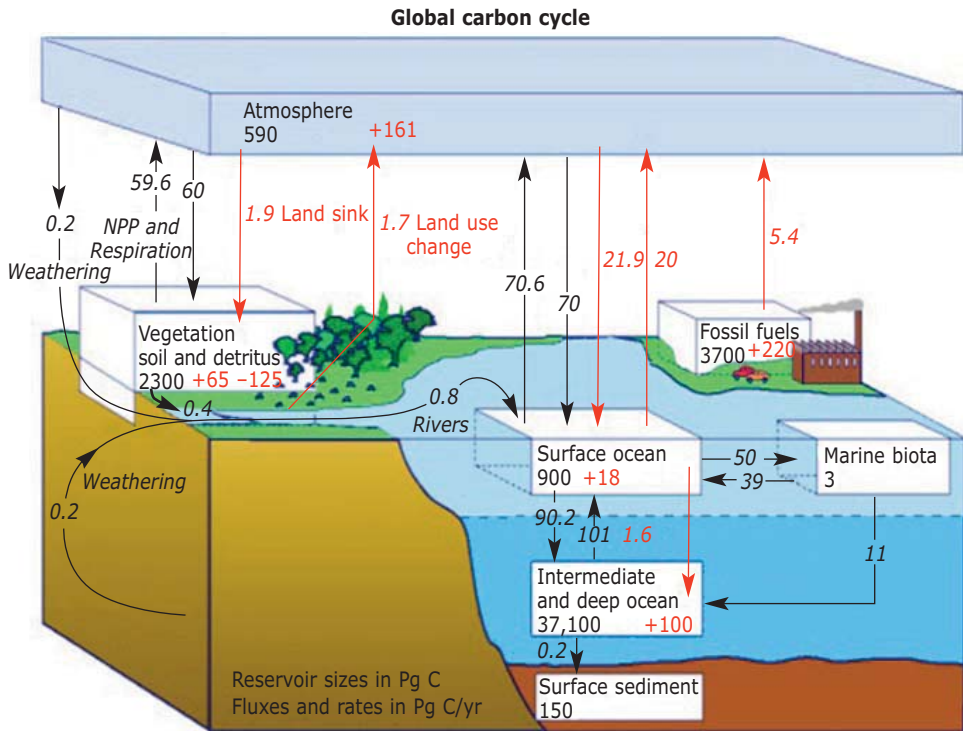


Source: Produced from the data base in Takahashi et al. 2002.

are not declining and if inputs of organic matter from other biosphere domains are significant, a possibility that is not included in these representations (figure 2.4).

Yet, the open ocean is believed to have been a weak source of CO<sub>2</sub> to the atmosphere during the Holocene, because sediment accumulation was lower than the riverine input of organic carbon (Siegenthaler and Sarmiento 1993) and is thought to have become a sink as a consequence of the human perturbation of the carbon budget (Siegenthaler and Sarmiento 1993; Sarmiento and Gruber 2002). Holocene CO<sub>2</sub> emission must have been supported by external inputs of organic matter, which can be delivered by the rivers and from atmospheric deposition. Whereas decades ago, riverine inputs of organic carbon were estimated at 0.8 Pg C yr<sup>-1</sup> (1 Pg = 10<sup>15</sup> g, Siegenthaler and Sarmiento 1993), there was until five years ago, not a single estimate of the atmospheric input of organic carbon to the ocean. Yet atmospheric organic carbon inputs to the ocean must be significant (del Giorgio and Duarte 2002), as rainfall contains organic carbon, aerosol—dust—depositing on the ocean contains organic carbon (Duarte et al. 2005), and many organic compounds exist in the atmosphere in a semivolatile form that can be transferred, through diffusive fluxes to the ocean (Dachs et al. 2005). Dachs et al. (2005) and Duarte et al. (2006) reported organic carbon inputs with dry aerosol dep-

**Figure 2.4: Global carbon budget showing preindustrial fluxes and those resulting from human perturbation.** Arrows show fluxes, in Pg C yr<sup>-1</sup>, and boxes contain pool sizes, as Pg C. Numbers and arrows in black show pre-industrial fluxes and those in red show the human perturbation. Black: pre-industrial; red: human perturbation.



Source: Reproduced from Sarmiento and Gruber 2002.

osition to average  $1 \text{ mmol C m}^{-2} \text{ d}^{-1}$ , and these have been calculated to deliver  $0.24 \text{ Pg C}$  annually to the ocean (Jurado et al. 2008). Dachs et al. (2005) reported a large air-sea exchange of volatile organic carbon, which could sustain an input of about  $25 \text{ to } 31 \text{ mmol C m}^{-2} \text{ d}^{-1}$  to the NE Subtropical Atlantic Ocean. This high atmospheric organic carbon input is likely to be representative of upper values for the ocean, as the NE Subtropical Atlantic is an area supporting particularly high atmospheric inputs (Jickells et al. 2005), but even input rates six fold lower than those reported for the Subtropical NE Atlantic will suffice to support an excess respiration over production in less productive regions of the ocean. The inventory of rates of organic carbon deposition to the ocean is as yet insufficient to attempt the calculation of a global flux. Efforts to assess air-sea exchanges of organic carbon are essential to resolve present inconsistencies in the metabolic and carbon budgets of the ocean.

Whereas the metabolic balance of oceanic planktonic communities remains unresolved, there is evidence that some coastal communities are strongly autotrophic. These are the vegetated coastal habitats formed by macrophytes, including seagrass meadows, salt-marshes and mangrove forests. These ecosystems rank amongst the most productive in the Biosphere and produce organic matter in excess of their respiration rates (Duarte and Cebrián 1998; Gattuso et al. 1998). Indeed, the excess production by these communities is so high that vegetated coastal habitats are important sinks for CO<sub>2</sub>, accumulating organic carbon in their sediments (Duarte et al. 2005).

#### **2.4. RESPONSES OF PLANKTON METABOLISM TO CLIMATE CHANGE**

The ocean has acted as a strong sink for CO<sub>2</sub> since human perturbations of the C cycle were initiated, removing atmospheric CO<sub>2</sub> at a rate of about 2 Gt C yr<sup>-1</sup> (Siegenthaler and Sarmiento 1993; Sarmiento and Gruber 2002). However, planktonic metabolism may shift in response to climate change. Warming of the oceans is expected to stimulate respiration rates over photosynthetic rates (Harris et al. 2006; López-Urrutia et al. 2006). A warming by 4 °C, as anticipated for the 21st Century, is expected to directly lead to a 16% decrease in *P/R* ratios (Harris et al. 2006), which may expand the area of the ocean occupied by heterotrophic communities acting as CO<sub>2</sub> sources to the atmosphere. Indeed, there is some evidence that the capacity of the ocean to act as a sink for CO<sub>2</sub> is weakening at present (Doney et al. 2009). In addition, there is evidence that ocean warming leads to a steep decline in seagrass meadows (Marbá and Duarte 2010), adding to the steady decline in this (Waycott et al. 2008) and other communities acting as strong carbon sinks (Duarte 2008). Moreover, a decline in the primary production of the ocean (Gregg et al. 2003) and an expansion of the unproductive gyres (Polovina et al. 2008) has been reported, although the causes for these trends remain unresolved.

Enhancing respiration and decreasing primary production can lead to large metabolic imbalances. Because gross ocean primary production and respiration involve large fluxes, a small, 10% imbalance suffices to generate a perturbation to the global carbon budget much larger than the anthropogenic perturbation that may, partially, be responsible for such changes, thereby accelerating the trend towards a CO<sub>2</sub>-rich and warmer Biosphere.





**Photo 2.3: Austral ice**



Whereas the complementarity between production and respiration sets bounds to this imbalance, the stocks of organic carbon, mostly in dissolved form and ocean sediments, are large enough to support an excess respiration over production for some decades. Hence, the metabolism of the ocean may represent a yet unrecognised tipping element in the Earth System. *Tipping elements* is a term used by Lenton et al. (2008) to describe subsystems of the Earth system that can be switched into a qualitatively different state by small perturbations, with the tipping point defined as the critical point at which the future state of the system is qualitatively altered. Hence, ocean metabolism may represent a tipping element that may be perturbed by climate change, where a relatively small perturbation may offset the close and delicate balance between production and respiration. Once ocean metabolism tips towards increased heterotrophy, the associated net emissions of CO<sub>2</sub> to the atmosphere will strengthen global warming, in turn strengthening respiration on a feed back loop that may accelerate climate change and its negative consequences for society (photo 2.3). It is fundamental to assess, through a combination of empirical cross-system comparisons and experimental analyses designed to test model predictions, what degree of global warming, if any, may tip the ocean ecosystem toward a net heterotrophic state.

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