Estimating carbon fluxes in a *Posidonia oceanica* system: Paradox of the bacterial carbon demand

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ABSTRACT

A mass balance ecosystemic approach, based on bacterial carbon demands and primary production data, was used to investigate if the bacterial community (freewater bacterioplankton and benthic bacteria of the oxygenated sediment layer) could be sustained by the main primary producers (*Posidonia oceanica* and its epiphytes, adjacent macroalgae and phytoplankton communities; hereafter called the *P. oceanica* system) of a non-eutrophic Mediterranean bay. Unexpectedly, the findings of this study differed from previous works that used benthic incubation chamber and O_2 optode methods. In this study, data were grouped in two categories, corresponding to two time periods, according to the seawater temperature regime (<18 °C or >18 °C): from May to October and from November to April. Between May and October, the produced benthic macrophyte tissues could not provide the carbon required by the bacteria of the oxygenated sediment layer, showing that the balance production of the investigated bay was clearly heterotrophic (*i.e.* negative) during this time period. In contrast, between November and April, benthic bacteria respiration nearly equated to carbon production. When integrating the open water carbon dynamics above the meadow in the model, a negative carbon balance was still observed between May and October, while a slight carbon excess was noticed between November and April. In the light of these findings, the carbon balance being negative on an annual basis, alternative carbon sources are required for the maintenance of the bacterial carbon production.

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1. Introduction

Aquatic ecosystems cover 70% of the planet Earth and among them, oceanic ecosystems are considered to act as CO_2 sinks. More especially, seagrass ecosystems play a major role as they are assumed to contribute up to 12% of the net organic carbon production of the ocean (Duarte and Cebrian, 1996) and are estimated to account for 40% of the carbon stored each year by coastal vegetation (Nelleman et al., 2009). Among the macrophyte systems that characterise the benthic environment of the Mediterranean Sea, the endemic seagrass *Posidonia oceanica* (L.) Delille covers large areas by forming dense meadows extending from the surface down to 40 m depth for an estimated surface area of around 50.000 km^2. *P. oceanica* belongs to one of the most productive marine ecosystems (Pergent et al., 1994) and is defined as a Low Nutrient High Chlorophyll system (LNHC; Gobert et al., 2002). Although *P. oceanica* shoots should provide the necessary amount of carbon to support the consumer community, several facts make this assumption questionable: (i) *P. oceanica* tissues are grazing resistant (Klap et al., 2000); (ii) *P. oceanica* has a high nutrient demand to support its high biomass and production (Alcoverro et al., 2000; Lepoint et al., 2004), and (iii) the export of *P. oceanica* tissues (i.e. wave and current induced transport of uprooted shoots and/or dead organic matter (leaves, roots and rhizomes) to adjacent ecosystems shores or deeper bottom) represents a loss of locked nutrients (Mateo et al., 1997; Romero et al., 1992, 1994; Rico-Raimondino, 1995).

Since the formulation of the microbial loop concept (Pomeroy,

1974; Azam et al., 1983), it is well known that a major part of the organic carbon coming from primary producers is channelled through the microbial compartment. Yet, bacterial decomposition of seagrass detritus may be constrained by the low nutrient content of the leaves, which translocate the major part of their nutrients (Alcoverro et al., 2000; Lepoint et al., 2002a,b) and micronutrients (Richir et al., 2013) into the root-rhizome system before their shedding. Thus the nutrient depleted seagrass detritus enables only low decomposition rates, making questionable if this decomposition occurs at a rate corresponding to the nutrient requirement of the system.

As marine seagrasses, often nutrient limited in an oligotrophic water column (Short, 1987; Powell et al., 1989; Short et al., 1990; Duarte, 1990; Perez et al., 1991), derive most of their nutrients from the sediment pool (Perez-Llorens and Niell, 1991), the quantification of growth rates of sediment bacteria may be a prerequisite for understanding the carbon dynamics of the system and related remineralisation processes. However, bacterial degradation in the P. oceanica system: i.e. P. oceanica shoots and its epiphytes is not restricted to seagrass derived particles only (Richir et al., 2012). The presence of epiphytic, macroalgal and phytoplanktonic particulate organic carbon is assumed to complement the seagrass detritus both in the water column and the sediment. Therefore, it is advisable to take into account major primary producer compartments of the systems adjacent to P. oceanica meadows and to investigate the growth dynamics of bacteria in the water/sediment compartments when trying to understand the carbon flow dynamics in the overall P. oceanica system.

The published information on carbon budgets and carbon balance estimations of P. oceanica system were mostly based on community measurements using in situ benthic incubation chambers and deployed O_2 optodes in the water column (Velimirov, 1986; Frankignoulle and Bouquegneau, 1987; Barrón and Duarte, 2009; Champenois and Borges, 2012). Most of those studies agree on the fact that P. oceanica forms net autotrophic systems, producing an excess of organic carbon relative to community respiration (Duarte and Cebrian, 1996; Gattuso et al., 1998; Duarte and Chiscano, 1999; Duarte et al., 2010). In the present investigation a different approach was used to assess and characterize the above mentioned carbon flow dynamics in non-eutrophic Mediterranean bays.

2. Material and methods

2.1. General approach

In this study, a mass balance analysis was performed from data collected between years 1978–2014 from a oligitrophic bay (the Bay of Calvi, Corsica, France). More precisely, data previously obtained on biomasses and primary production of the P. oceanica system, as well as on biomasses and production of bacteria from the oxygenated sediment layer within the P. oceanica meadow and the overlying water column, were used to calculate a carbon balance estimation, which constitutes a basis for the development of an energy flow model of the P. oceanica system in non-eutrophic Mediterranean bays.

Data on production and biomasses of sediment bacteria come from the present study, and corresponding values for the water column were derived from Velimirov and Walenta-Simon (1992, 1993). Data on P. oceanica were obtained from Bay (1978, 1984), Gobert et al. (1995), Gobert et al. (2002), Mesureur (1981) and ElKalay (2003). Epiphyte biomasses and production were obtained from 3 stations situated between 0.8 and 30.0 m depth (Dauby, unpubl. data) and data on benthic macroalgae were based on the investigation made by Jansens (2001).

Part of the collected data concerning bacteria of the water column and primary producers were heterogenous with respect to sampling stations and depth, but more homogenous with respect to season. Data were therefore related to the surfaces of specific depth ranges, sectioned into 10 m isobath steps, and to the corresponding volumes of the above water column in order to enable the development of a carbon balance model of the P. oceanica system. As for seasonality, all data were grouped into two time periods characterized by temperature regimes either below 18 °C – November to April – or above 18 °C – May to October (strongly stratified period with a marked thermocline).

2.2. Reference site: the Bay of Calvi

The Bay of Calvi opens northwest, has a surface area of 22 km² and an average depth of 40 m (maximum depth: 107 m). The seafloor drops gradually (2% slope) from south to northeast. An extensive P. oceanica meadow covers 5 km² of the sandy and rocky seafloor, reaching a depth of more than 38 m (Bay, 1984). The sea surface temperature ranges from 12 °C (February–March) to 26 °C (August–September) with an annual mean of 18 °C. The water column is strongly stratified from May to October, with the thermocline around 25–30 m depth (range: 20–50 m depth, depending on wind conditions). Water residence time in the bay varies from 5 days in winter to 10 days in summer (Norro, 1995; Mazzuca et al., 2013). Bathymetry (Fig. 1), water column volume and an estimation of the surface of the different habitats (Table 1) were calculated using the GIS software ArcGIS® 10, based on SHOM (French Hydrographic and Oceanic Marine Service) and Natura 2000 (aerial photographies, side scan sonar images and field observations) data (Annex 1).

2.3. Sediment bacteria

Four sampling events were realized to be representative of both time periods, namely in July 1997, June 1998 and June 1999 for water temperatures above 18 °C and in March 2000 for a temperature regime below 18 °C. For each sampling event, sediments were sampled in triplicate from 5 different depths (10, 15, 20, 25 and 38 m depth) in the Bay of Calvi by scuba diving. Sediment corers (inner diameter of 5 cm) were introduced by hand into the sediment to a depth of about 15 cm and withdrawn by applying a slow rotary movement in order to prevent resuspension of the upper sediment layer (Annex 2).

Bacterial numbers, cell volumes and biomasses in the first 2 cm of sampled sediment cores were determined according to the method described in Kirschner and Velimirov (1999). Cellular carbon content was calculated from estimated cell volumes according to Norland (1993). Bacterial production, based on ^{3}H-thymidine and ^{14}C-leucine incorporation, was assessed according to the protocol developed by Kirschner and Velimirov (1999; Annex 2).

2.4. The P. oceanica meadow

Posidonia oceanica leaf biomasses were determined by monthly or seasonal samplings of 10 orthotropic shoots at 10, 20 and 30 m depth and corresponding shoot densities were measured in 20 × 20 cm quadrats (n = 10; Gobert et al., 1995; Gobert et al., 2002). The leaf-blade net primary production was estimated at 10 m depth by the harvest method (Bay, 1984; Annex 3) and by leaf-tagging at 30 m depth (owing to the limitation of working time at this depth). Since 1975, no significant change of the shoot density was noticed (Bay, 1984; Soullard et al., 1994; Gobert et al., 2003), so mean shoot densities of P. oceanica ranging from 472 to 139 m⁻² at 10 and 30 m depth, respectively were used for the calculations.