Biogeosciences Discussions, 1, 755–802, 2004
www.biogeosciences.net/bgd/1/755/
SRef-ID: 1810-6285/bgd/2004-1-755

Biogeosciences
Discussions

Biogeosciences Discussions is the access reviewed discussion forum of *Biogeosciences*

Whole-system metabolism and CO_2 fluxes in a Mediterranean Bay dominated by seagrass beds (Palma Bay, NW Mediterranean)

F. Gazeau[1,2], C. M. Duarte[3], J.-P. Gattuso[2], C. Barrón[1], N. Navarro[3,5], S. Ruíz[3,6], Y. T. Prairie[4], M. Calleja[3], B. Delille[1], M. Frankignoulle[1], and A. V. Borges[1]

[1]Unité d'Océanographie Chimique (B5), MARE, U. Liège, B-4000 Sart Tilman, Belgium
[2]Lab. d'Océanographie, CNRS Paris 6, B.P. 28, F-06234 Villefranche-sur-mer Cedex, France
[3]IMEDEA (CSIC-UIB), Grupo de Oceanografia Interdisciplinar, Inst. Mediterráneo de Estudios Avanzados, C/Miquel Marqués 21, 07190 Esporles (Islas Baleares), Spain
[4]Dépt. Sc. Biologiques, U. Québec à Montréal, 8888, Centre-Ville, Montréal, H3C3P8, Canada
[5]present address: Área de Biodiversidad y Conservación, ESCET, Univ. Rey Juan Carlos, C/ Tulipán s/n, Móstoles 28933, Madrid, Spain
[6]present address: CLS Space Oceanography Division, Parc technologique du Canal, 8-10 Rue Hermès, 31526 Ramonville Cedex, France

Received: 1 September 2004 – Accepted: 6 October 2004 – Published: 26 October 2004

Correspondence to: F. Gazeau (gazeau@obs-vlfr.fr)

Abstract

The relationship between whole-system metabolism estimates based on planktonic and benthic incubations (bare sediments and seagrass, *Posidonia oceanica* meadows), and CO_2 fluxes across the air-sea interface were examined in the Bay of Palma (Mallorca, Spain) during two cruises in March and June 2002. Moreover, planktonic and benthic incubations were performed at monthly intervals from March 2001 to October 2002 in a seagrass vegetated area of the bay. From the annual study, results showed a contrast between the planktonic compartment, which was heterotrophic during most of the year, except for occasional bloom episodes, and the benthic compartment, which was slightly autotrophic. Whereas the seagrass community was autotrophic, the excess organic carbon production therein could only balance the excess respiration of the planktonic compartment in shallow waters (<10 m) relative to the maximum depth of the bay (55 m). This generated a horizontal gradient from autotrophic or balanced communities in the shallow, seagrass-covered areas of the bay, to strongly heterotrophic communities in deeper areas, consistent with the patterns of CO_2 fields and fluxes across the bay observed during the two extensive cruises in 2002. Finally, dissolved inorganic carbon and oxygen budgets provided NEP estimates in fair agreement with those derived from direct metabolic estimates based on incubated samples over the *Posidonia oceanica* meadow.

1 Introduction

The role of coastal ecosystems in carbon and nutrient fluxes can be conveniently summarised by their trophic balance, referring to the difference between the production of organic matter, as represented by the gross primary production (GPP) of the ecosystem and its degradation through community respiration (CR; Odum, 1956). Autotrophic systems, where GPP >|CR| (if CR is expressed in negative units), produce organic matter in excess and thereby act as sinks of inorganic nutrients and CO_2 from surrounding water. In contrast, heterotrophic ecosystems, where GPP <|CR|, rely on allochtonous inputs of organic matter and act as sources of inorganic nutrients and CO_2 to the surrounding water (Duarte and Prairie, 2004[1]).

The net flux of CO_2 across the air-water interface is modulated by this metabolic balance but also by external inputs of dissolved inorganic carbon (DIC; upwelling, river inputs), calcium carbonate ($CaCO_3$) precipitation/dissolution, and purely thermodynamic effects related to temperature changes or mixing of water masses with different chemical characteristics.

Coastal ecosystems contain highly productive communities, such as macrophyte beds which tend to be net autotrophic (Duarte and Cebrián, 1996; Gattuso et al., 1998; Hemminga and Duarte, 2000). As they also receive important inputs of organic matter from land, both GPP and |CR| tend to be elevated relative to open ocean waters (Duarte and Agustí, 1998; Gattuso et al., 1998; Hopkinson and Smith, in press).

Smith and Hollibaugh (1993) argued that coastal ecosystems are a heterotrophic compartment of the biosphere. In contrast, other authors suggested that they produce organic matter in excess relative to local demands (Duarte and Cebrián, 1996; Gattuso et al., 1998; Wollast, 1998) and then act as sources of organic matter for the open ocean (Wollast, 1998; Liu et al., 2000; Chen et al., 2003). Duarte and Agustí (1998) and Hopkinson and Smith (in press) concluded, on the basis of comparative analyses of several coastal communities, that the metabolic balance of coastal ecosystems would be dependent on their trophic status, with productive areas being more autotrophic.

However, oligotrophic coastal systems, with unproductive planktonic communities, often support highly productive benthic components. This implies that an assessment of their metabolism requires the integration of both benthic and planktonic compartments over relevant temporal and spatial scales. Nevertheless, an examination of coastal metabolism datasets (Duarte and Agustí, 1998; Gattuso et al., 1998; Hopkinson and Smith, in press) reveals that most coastal communities were examined at

---

[1] Duarte, C. M. and Prairie, Y. T.: Prevalence of heterotrophy in aquatic systems, Ecosystems, submitted, 2004.

small spatial scales (bottle incubations or benthic chambers) rather than based on research conducted at the ecosystem scale. This is largely attributable to the difficulties in encompassing the variability within ecosystems using discrete measurements and to extrapolate these estimates to large areas.

To overcome this problem, more integrative approaches, based on material mass balances at the ecosystem scale have been proposed (e.g. Land-Ocean Interaction in the Coastal Zone, LOICZ approach, Gordon et al., 1996). However, these methods require salinity gradients to compute water exchanges and are, therefore, best used in estuarine systems and cannot be readily used in other coastal areas.

Assessments of the spatial and/or temporal variability of dissolved oxygen (O_2) concentration and the partial pressure of CO_2 (pCO_2) may be also used to derive integrative estimates of net ecosystem production (NEP=GPP+CR). However, these estimates are not straightforward, as temperature changes, the history and residence time of water masses and other physical (e.g. Borges and Frankignoulle, 2001) and/or biogeochemical (e.g. Frankignoulle et al., 1996; Frankignoulle et al., 2001) factors may also affect O_2 concentration and pCO_2. For instance, the computation of the CO_2 air-water flux can be critical in the estimation of NEP based on DIC budgets (Gazeau et al., 2004[2]), especially in coastal environments such as estuaries where simple parameterisations of the gas transfer velocity as a function of wind speed have been shown to be site specific (Borges et al., 2004). Thus, both approaches have their own limitations and, to our knowledge, no comparison of NEP estimates derived from GPP and CR incubation measurements and inferred from CO_2/O_2 fluxes at the ecosystem scale have ever been made in the past.

In this paper, we estimated whole system metabolism for the Bay of Palma (Mallorca, NW Mediterranean) to test the coherence between the two approaches to quantify NEP. The study was based on an annual time series of benthic and planktonic

---

[2] Gazeau, F., Gattuso, J.-P., Middelburg, J. J., Barrón, C., Duarte, C. M., Schiettecatte, L.-S., Brion, N., Pizay, M.-D., Frankignoulle, M., and Borges, A. V.: Planktonic and whole-system metabolism in a nutrient-rich estuary (The Scheldt Estuary), Limn. Ocean., submitted, 2004.

metabolism at a fixed station over a seagrass meadow as well as extensive surveys in the bay at two contrasting periods of the annual cycle.

2 Methods

2.1 Study site

The Bay of Palma (Mallorca, NW Mediterranean) is an oligotrophic system with a surface area of 217 km^2, a width of 30 km and a mean depth of 28.5 m (Fig. 1). It receives negligible freshwater inputs and, in the absence of appreciable astronomical tides, exchanges with the offshore waters are dominated by wind stress (Ramis et al., 1990). The Bay of Palma contains extensive seagrass (*Posidonia oceanica*) meadows that extend down to 34 m depth and cover more than 30% of the bay (Fig. 1). As the water is rather clear (average ±SE extinction coefficient=0.06±0.02 m^{-1}, Navarro et al., 2004[3]), the sediment floor remains within the euphotic layer throughout the bay. The city of Palma de Mallorca (385 000 permanent inhabitants) supports intense tourism activities and a large harbour.

Benthic and planktonic metabolisms were estimated, using in situ incubations, at a fixed station from March 2001 to November 2002, and at a grid of stations during two cruises in March (EUBAL-I) and June 2002 (EUBAL-II). During these two cruises, gas fluxes and hydrography (current velocity) were also examined.

2.2 Hydrography, current velocity and residence time

Five CTD (Conductivity Temperature Depth) surveys were conducted in the Bay of Palma during each of the EUBAL-I (1, 3, 7, 11 and 12/03/2002) and EUBAL-II (19, 21, 25, 26 and 27/06/2003) cruises. During the first survey of EUBAL-I, a total of 32 CTD

---

[3] Navarro, N., Agustí, S., and Duarte, C. M.: Plankton metabolism and DOC use in the Bay of Palma, NW Mediterranean Sea, Microb. Ecol., submitted, 2004.

casts were performed with an average horizontal sampling resolution of 2.8×2.8 km. The other surveys consisted of 11 CTD casts each, reducing the sampling resolution to 5.2×5.2 km. Profiles were vertically averaged every 0.5 m. Direct current measurements were obtained on three surveys during EUBAL-I (1, 9 and 12/03/2002) and one survey during EUBAL-II (25/06/2002) with a ship-hull mounted 150 kHz RD instrument ADCP (Acoustic Doppler Current Profiler). This latter was set up to record currents from surface (10 m) to the bottom with a vertical resolution of 4 m and a 2 min ensemble period using the Transect Acquisition Software. In order to reduce the instrumental errors, raw ADCP data were averaged to 10 min ensembles. Absolute ADCP velocities were computed using bottom-tracking mode, which delivers accurate estimation of the ship velocity. Post-processing of ADCP data was carried out following the methodology described by Allen et al. (1997). Unfortunately, the ship was not equipped with a 3D GPS (Global Positioning System) that provides accurate heading to account for the gyrocompass error. Hence, a typical error for a conventional gyrocompass of 2° (Griffiths, 1994) is assumed in the post-processing of ADCP data. The maximum error velocity has been estimated at about 4 cm s^{-1}.

The CTD observations were interpolated over a regular 0.5×0.5 km grid, using an objective analysis based on Optimal Statistical Interpolation. The two main parameters of this scheme are the characteristic scale and the cut-off length scale. The first determines the influence between observations and the second gives the filtering of scales which were not resolved by the sampling strategy. For the first CTD survey of EUBAL-I (dense sampling), the characteristic scale was set-up to 5 km and the cut-off scale to 10 km. For the other CTD surveys (coarse sampling), the scale derived from statistics was 7.5 km and the cut-off length scale was set to 15 km. For further details about this technique refer to Pedder (1993).

In order to have a qualitative view of the general circulation in the Mallorca channel, a database of daily sea surface temperature (SST) was compiled, for the EUBAL-I period, from Advanced Very High Resolution Radiometer (AVHRR) obtained from Instituto Espanyol de Oceanografia (http://www.teledeteccion-oceanografica.net/).

2.3 Community metabolism

The community metabolism in a *Posidonia oceanica* meadow and unvegetated sediments were studied monthly from March 2001 to October 2002 using in situ benthic incubation chambers at the shallow (7 m depth) Posidonia station in the Western side of the bay (Fig. 1). Benthic incubations were set up in the vegetated (4 chambers) and unvegetated (3 chambers) sediment to estimate the net community production (NCP). The benthic chambers consisted of a PVC cylinder inserted in the sediment and a gas-tight polyethylene plastic bag fitted to the cylinder with a sampling port (Hansen et al., 2000). Water samples were withdrawn with syringes at the start of the incubation, just before sunset and right after sunrise. Samples for dissolved O_2 were transferred into Winkler bottles, fixed and measured by the Winkler technique following Carrit and Carpenter (1966) using an automated precise titration system (Mettler DL21 Auto-titrator) with potentiometric (redox electrode) end-point detection (Oudot et al., 1988). The average precision achieved in replicates was %CV=0.29. In order to express dissolved O_2 changes per unit area, the volume of water enclosed in the benthic chambers was estimated from the dilution of a phosphate solution (0.25 mol l^{-1}) in the benthic chambers and measurements of phosphate concentrations by spectrophotometry (Hansen and Koroleff, 1999) from samples collected after an equilibration period of 5 min. Dissolved O_2 changes, adjusted to 24 h, within the benthic chambers were used to calculate NCP. Further details and procedures are provided in Barrón et al. (2004[4]).

During both EUBAL cruises, the community metabolism of *Posidonia oceanica* meadow and unvegetated sediment communities were studied at Posidonia (7 m) and Cap Enderrocat stations (15 m) using in situ benthic incubations as described above. Moreover, during EUBAL-II, incubations of both communities were performed along a depth gradient at Posidonia station (4, 7, 15 and 22 m). The variation of benthic NCP

---

[4] Barrón, C., Duarte, C. M., Frankignoulle, M., and Borges, A. V.: Organic carbon metabolism and carbonate dynamics in a Mediterranean seagrass (Posidonia oceanica) meadow, Limn. Ocean., submitted, 2004.

with depth at this station was upscaled to the entire bay using estimates of the surface area of vegetated and unvegetated sediments based on the detailed study of Rey and Diaz del Rio (1984), using a Geographic Information System (ArcView 3.2 software package).

The planktonic metabolism was measured, at monthly intervals, from June 2001 to October 2002 at the Posidonia station. The water column was vertically mixed throughout the study, as evidenced by CTD profiles. Integrated (0 to 7 m) water samples were carefully siphoned into twelve 125 ml biological O_2 demand (BOD) bottles. Five replicates were used to determinate the initial O_2 concentration and seven replicate clear bottles were suspended in situ at a depth of 4 m and incubated for 24 h. NCP was calculated from the difference between final and initial O_2 concentrations measured as described above and integrated to a depth of 7 m.

Planktonic GPP and CR were measured at 4 stations in the bay during each of the EUBAL cruises (Fig. 1). Samples (5 replicates) were incubated in situ at 4 depths for 24 h in both transparent and dark 60 ml BOD bottles. O_2 concentrations were measured before and after incubation using an automated Winkler titration technique with potentiometric end-point detection. Analyses were performed with an Orion redox electrode (9778-SC) and a custom built titrator. Reagents and standardizations were similar to those described by Knap et al. (1996). Daily planktonic CR and NCP were estimated by regressing O_2 in the dark and transparent bottles against time, respectively. Daily GPP was estimated as the difference between NCP and CR.

At each station and incubation depth, samples were taken for chlorophyll *a*. Water was filtered through GF/F filters that were stored frozen until extraction and analysis by high-performance liquid chromatography (Barranguet et al., 1997). Light penetration in the water column was measured using a LI-COR quantum LI-1935A and a LI-1400 data-logger twice during each incubation period. During two surveys on each cruise, vertical CTD (SeaBird SBE19) profiles of fluorescence (Chelsea and Sea tech sensors during EUBAL-I and -II, respectively) were performed at 11 stations in the bay (Fig. 1), and were calibrated using concomitant measurements of surface chlorophyll *a* concentration (same method as above). Surface irradiance was measured every 15 min during each cruise using a LI-COR cosine corrected quantum sensor (LI-1925A) and a LI-1400 data-logger. Strong variations were observed during the first cruise, while during the second cruise light conditions were relatively constant (data not shown). As phytoplanktonic GPP is strongly dependent on the available light intensity, a correction was applied to compare results obtained under different light conditions during EUBAL-I. Relationships between daily GPP rates normalized per unit of chlorophyll *a* and the averaged daily irradiance were established for each station using the model of Platt et al. (1980). The resulting PI (production vs. irradiance) curves were then used to recalculate GPP for the mean daily surface irradiance over the whole campaign (421.5 μmol m^{-2} s^{-1}).

2.4 CO_2/O_2 fluxes and NEP estimates

Underway parameters (seawater pCO_2, O_2, salinity and in situ temperature) were sampled with a frequency of 1 min from the seawater supply of the ship (pump inlet at a depth of about 2 m) during six surveys of the EUBAL-I cruise (1, 3, 7, 9, 11 and 12/03/2002) and during five surveys of the EUBAL-II cruise (19, 21, 25, 26 and 27/06/2003). Total alkalinity (TA) and O_2 were sampled from the seawater supply to cover the spatial variability during the surveys (on average 10 samples per survey). Vertical profiles of pH, TA and O_2 were obtained at four reference stations (Fig. 1). During the EUBAL-II cruise, vertical profiles of pCO_2 were established during 24 h cycles at three reference stations (Posidonia, Bahia and Cap Enderrocat, Fig. 1). A non-dispersive infrared gas analyser (IRGA, LI-COR, LI-6262) was used to measure pCO_2 in wet air equilibrated with seawater. The IRGA was calibrated daily using three dry gas standards: pure nitrogen (0.0 ppm; Air Liquide Belgium) and two gas mixtures with a CO_2 molar fraction of 360.5 and 773.8 ppm (National Oceanic and Atmospheric Administration). The temperature at the outlet of the equilibrator was monitored with a platinum resistance thermometer (PT100, Metrohm) with an estimated accuracy of ±0.05°C and pCO_2 values were corrected for the temperature difference between in

situ seawater and water in the equilibrator using the algorithm proposed by Copin-Montégut (1988). The offset in temperature was typically 0.5°C. The accuracy of the pCO_2 measurement by equilibration is estimated to ±2 ppm (cumulated errors on temperature correction and instrument calibration). For further details on the equilibrator design and performance tests refer to Frankignoulle et al. (2001). A second IRGA was used to measure atmospheric pCO_2 sampled at the bow of the ship. Vertical pCO_2 profiles were established every 3.5 h with a resolution of 1 m, by pumping water from a given depth with a peristaltic field pump (ISCO 150) through a Liqui-Cel equilibrator (mini-module, 9″) at a rate of about 1.5 l min^{-1}. The pCO_2 was measured using a portable IRGA (EGM-3, PPSystems) with an estimated precision of ±2 ppm. TA was determined using the classical Gran electro-titration method, on 100 ml GF/F filtered samples with a reproducibility of ±2 μmol kg^{-1} and an estimated accuracy of ±3 μmol kg^{-1}. The measurement of pH was obtained using a combined electrode (Metrohm), calibrated on the Total Hydrogen Ion Concentration Scale (mol kg SW^{-1}), using the buffers proposed by Dickson (1993). The reproducibility of pH measurement is estimated to ±0.004 pH units. DIC was calculated from pCO_2 and TA (underway data) and from pH and TA (vertical profile data) with the dissociation constants of carbonic acid and borate from Roy et al. (1993), the dissociation constant of boric acid from Dickson (1990) and the CO_2 solubility coefficient of Weiss (1974). The accuracy of DIC computed from the pCO_2-TA and the pH-TA couples is estimated to ±5 and ±10 μmol kg^{-1}, respectively. DIC was normalized to a constant salinity according to:

$$DIC_{37} = 37\frac{DIC_{observed}}{Salinity_{observed}} \tag{1}$$

to remove the variations due to changes in salinity owing to mixing, evaporation or dilution. pCO_2 was normalized to a constant temperature using the algorithm proposed by Copin-Montégut (1988).

Discrete dissolved O_2 concentration was measured according to the Winkler method using a potentiometric end-point determination with an estimated accuracy of

±2 μmol kg^{-1}. Underway O_2 concentration was measured with a polarographic electrode (Oxyguard) calibrated against the discrete O_2 samples with an estimated accuracy of ±3 μmol kg^{-1}. Apparent oxygen utilisation (AOU) was computed using the concentration of O_2 at saturation calculated with the algorithm proposed by Benson and Krause (1984). Salinity and in situ temperature were measured using a SeaBird SBE21 thermosalinograph. Vertical profile data were obtained from a 12 bottle rosette coupled to a CTD (SeaBird SBE19). The estimated errors on salinity and in situ temperature measurements are ±0.05 and ±0.01°C, respectively. Wind speed was measured at approximately 10 m height with a Batos (5 s sampling interval during EUBAL-I) and Aanderaa (1 min sampling interval during EUBAL-II) cup anemometer.

The air-sea CO_2 flux (F; mmol C m^{-2} d^{-1}) was computed from the air-sea gradient of pCO_2 ($\Delta pCO_2 = pCO_{2\,water} - pCO_{2\,atmosphere}$; ppm), the gas transfer velocity (k; m d^{-1}) and the solubility coefficient of CO_2 (α; mmol m^{-3} ppm^{-1}), using equation:

$$F = \alpha k \Delta pCO_2 \tag{2}$$

As a convention, a positive flux corresponds to a source for the atmosphere. Computations were made using various algorithms of k as a function of wind speed (Liss and Merlivat, 1986; Wanninkhof, 1992; Wanninkhof and McGillis, 1999; Nightingale et al., 2000; McGillis et al., 2001), although, we mainly discuss the values computed with the parametrization by Wanninkhof and McGillis (1999) for a consistent comparison with values from the Dyfamed station (Bégovic and Copin-Montégut, 2002). For each survey, the $\alpha \Delta pCO_2$ data were interpolated on a grid of 0.0034° E×0.0025° N. To account for the strong non-linearity of the k parametrizations, the flux computations were carried out using hourly bins of wind speed (assuming that the whole area is uniformly submitted to wind speed measured anywhere during the survey) and then averaged for a given survey.

NEP over the *Posidonia oceanica* meadow was computed based on a DIC budget, according to the equation:

$$NEP_{DIC} = \rho h_{pos} \frac{\left(DIC_{bay'} + t_{bay'} \frac{F_{bay'}}{\rho h_{bay'}}\right) - \left(DIC_{pos} + t_{pos} \frac{F_{pos}}{\rho h_{pos}}\right)}{t_{pos}} \tag{3}$$

where NEP_{DIC} is expressed in mmol C m^{-2} d^{-1}, ρ is the water density (kg m^{-3}), DIC_* is DIC_{37} (mmol kg^{-1}), t_* is the water residence time (d), h_{pos} is the average water column height over the *Posidonia oceanica* meadow (m), $h_{bay'}$ is the average mixed layer depth in the Bay of Palma (excluding the *Posidonia oceanica* meadow, m), F_* is the air-sea CO_2 exchange computed using the Wanninkhof and McGillis (1999) k parametrization, subscript *pos* denotes data over the *Posidonia oceanica* meadow and subscript *bay'* denotes data over the rest of the Bay of Palma (excluding the *Posidonia oceanica* meadow).

An identical equation was used to computed NEP from O_2 concentrations (NEP_{O2} in mmol O_2 m^{-2} d^{-1}); the flux air-sea of O_2 was computed using the Wanninkhof and McGillis (1999) k parametrization and the Schmidt number (Sc) formulation for seawater given by Wanninkhof (1992), assuming a k dependency proportional to Sc$^{-0.5}$.

The relative water residence time over the *Posidonia oceanica* meadow and in the Bay of Palma (excluding the *Posidonia* meadow) were computed according to:

$$t_{pos} = t_{total} \frac{V_{pos}}{V_{total}} \tag{4}$$

$$t_{bay'} = t_{total} \frac{V_{bay'}}{V_{total}} \tag{5}$$

where V_* is the volume (km^3), t_* is the water residence time (d), subscript *total* denotes data in the whole Bay of Palma, subscript *pos* denotes data over the *Posidonia oceanica* meadow and subscript *bay'* denotes data over the rest of the Bay of Palma (excluding the *Posidonia oceanica* meadow).

3 Results and Discussion

3.1 Monthly metabolism at Posidonia station

The *Posidonia oceanica* community tended to be autotrophic and the bare sediment community tended to be heterotrophic during the study (Fig. 2a). The seagrass community ranged from heterotrophy with a lowest NCP in August 2002 (−24.7 mmol O_2 m^{-2} d^{-1}) to autotrophy with a highest NCP in April 2002 (88.8 mmol O_2 m^{-2} d^{-1}). The unvegetated sediment community ranged from heterotrophy (−4.8 mmol O_2 m^{-2} d^{-1} in April 2001) to autotrophy (NCP=5.0 mmol O_2 m^{-2} d^{-1} in July 2001). The benthic community metabolism at Posidonia station showed considerable variability along the study period, with the highest NCP found in spring and early summer (Fig. 2b). In contrast, the planktonic NCP showed no clear seasonality. Indeed, most monthly NCP estimates in 2001 indicated a heterotrophy while those in 2002 suggested an autotrophy. Overall, the NCP of the planktonic compartment averaged −4.6±5.9 mmol O_2 m^{-2} d^{-1}, indicating a metabolic balance (i.e. H_o: mean NCP=0, $P>0.05$), with a tendency towards heterotrophy whereas the benthic compartment was overall net autotrophic (16.2±5.2 mmol O_2 m^{-2} d^{-1}). NEP (sum of benthic and planktonic NCP) was dominated by the benthic compartment in spring and summer, and by the planktonic community in the fall and winter. At an annual scale, NEP was nearly balanced, with a tendency towards autotrophy (7.7±7.7 mmol O_2 m^{-2} d^{-1}).

3.2 Hydrography, water currents and residence time during EUBAL-I and -II cruises

The horizontal velocity fields based on the ADCP surveys during the EUBAL-I and -II cruises differed considerably. In March, the flow pattern was initially characterised by a clear clockwise circulation with maximum velocities of 19 and 22 cm s^{-1}, on 01/03 and 09/03/2002 respectively (Figs. 3a and b). The water entered the bay on its Western side, while the water outflow is dominant on the Eastern side. The circulation changed to the opposite direction towards the end of the cruise (12/03/2002; Fig. 3c)

when the flow pattern became anticlockwise and the flow intensified to reach a value of 40 cm s^{-1}. This flow reversion was consistent with a shift between the beginning and the end of the cruise, from a relatively cool, high-salinity (37.5 to 37.6) to a warmer and less saline water mass (+0.5°C; 37.2; Fig. 4). This pattern was evident both from CTD surveys and examination of AVHRR SST data (not shown).

The flow pattern during EUBAL-II was similar to the one observed at the end of EUBAL-I, with a general anticlockwise circulation (Fig. 3d). It should be noted that the current velocities were, on average, lower than those during EUBAL-I (6–7 cm s^{-1} vs. 20–24 cm s^{-1}).

The water residence time in the Bay of Palma was estimated from the current velocities recorded during each survey. The average water residence time was much shorter during EUBAL-I (2.5±0.2 d) than during EUBAL-II (10 d). Due to the low velocities and the consequent noise during EUBAL-II, the computed residence time is subject to a strong uncertainty.

3.3 Ecosystem metabolism during EUBAL-I and -II cruises

Integrated chlorophyll *a* concentrations at the incubated stations were on average significantly higher in March than in June, except at Posidonia station which presented similar values during both cruises (Table 1). Minimal and maximal concentrations were found, respectively, at Cap Enderrocat station in June (1.5 mg m^{-2}) and at Bahia station in March (17.3 mg m^{-2}). Light attenuation coefficients (K) were rather low (<0.16 m^{-1} during both cruises) with slightly higher values in March, except for Posidonia station.

During EUBAL-I, surface planktonic GPP rates ranged from 2.8 mmol O_2 m^{-3} d^{-1} (Posidonia) to 5.2 mmol O_2 m^{-3} d^{-1} (Cap Enderrocat) with an average value of 3.7±1.2 mmol O_2 m^{-3} d^{-1} (Fig. 5). During EUBAL-II, surface planktonic GPP rates were slightly higher (mean: 4.7±1.2 mmol O_2 m^{-3} d^{-1}) with a minimal value at Cap Enderrocat (3.3 mmol O_2 m^{-3} d^{-1}) and a maximal one at station 4 (6.3 mmol O_2 m^{-3} d^{1}). Average water-column planktonic CR strongly increased between March and June, from 1.5±0.8 mmol O_2 m^{-3} d^{-1} to 3.4±1.9 mmol O_2 m^{-3} d^{-1}, respectively. Higher vertical and horizontal gradients were found during the EUBAL-II cruise.

During EUBAL-I, maximal integrated planktonic GPP values were observed at stations Bahia and 4 (98 and 92 mmol O_2 m^{-2} d^{-1}) and the minimal one at Posidonia station (36 mmol O_2 m^{-2} d^{-1}, Table 2). During EUBAL-II, integrated planktonic GPP ranged from 29 mmol O_2 m^{-2} d^{-1} at Cap Enderrocat to 86 mmol O_2 m^{-2} d^{-1} at Bahia. Integrated planktonic CR showed a low spatial variability during the first cruise with a mean value of −35±7.4 mmol O_2 m^{-2} d^{-1}. In contrast, during the second cruise, strong geographical variations were highlighted with a minimal value measured at Posidonia (−45 mmol O_2 m^{-2} d^{-1}) and a maximal one at station 4 (−107 mmol O_2 m^{-2} d^{-1}). The planktonic compartment was autotrophic at all incubated stations during EUBAL-I while during EUBAL-II, two stations (Station 4 and Cap Enderrocat) presented a heterotrophic status.

Significant relationships were found between integrated planktonic GPP and integrated chlorophyll *a* concentration during both cruises (Fig. 6a). As chlorophyll *a* concentrations were estimated at 11 stations on two surveys during each cruise, these relationships were used to extrapolate GPP, integrated across the euphotic layer (34 m during EUBAL-I and 46 m during EUBAL-II) to the whole bay (Table 3). During both surveys in March, the lowest chlorophyll *a* values and consequently the lowest planktonic GPP were found at Posidonia and Cap Enderrocat stations while maximal rates were found in deep waters in the middle of the bay. During the second cruise, due to lower chlorophyll *a*concentrations, planktonic GPP were much lower and higher spatial variations were observed in comparison to March, reaching a mean value of 33±44 mmol O_2 m^{-2} d^{-1} (vs. 93±43 mmol O_2 m^{-2} d^{-1} during EUBAL-I). The highest values were generally estimated over the *Posidonia oceanica* meadow.

During the first cruise, for all stations investigated during the surveys, planktonic integrated CR rates were calculated by multiplying the mean volumetric rate observed during the incubations (−1.5±0.8 mmol O_2 m^{-2} d^{-1}) by the depth of each station. Planktonic integrated CR was, therefore, highest at deep stations reaching a maximal value

at station 8 (60 m depth; −89 mmol O_2 m^{-2} d^{-1}), but was always lower than planktonic GPP except for one station during the first survey (Cap Enderrocat). Consequently, the planktonic compartment was autotrophic during EUBAL-I with an average value of 46±41 mmol O_2 m^{-2} d^{-1}.

Due to the strong heterogeneity in CR observed during EUBAL-II at the four incubated stations, the same procedure was not applied. During this cruise, a significant relationship was observed between GPP and CR integrated across the water column, excluding the last incubated depth (Fig. 6b). It should be mentioned that CR rates measured near the bottom and therefore near the *Posidonia oceanica* meadow do not fit with this relationship. This suggests that near the bottom, planktonic CR may be fuelled by organic matter from the *Posidonia oceanica* meadow rather than by the planktonic production. Therefore, CR rates collected at the four incubated stations were upscaled only to the area covered by the *Posidonia oceanica* meadow, while integrated CR was calculated based on the estimated GPP in the rest of the bay where chlorophyll *a* and consequent GPP rates are much lower.

On average, integrated and extrapolated planktonic CR was similar during both cruises (−47±24 and −43±27 mmol O_2 m^{-2} d^{-1} in March and June, respectively). Therefore, due to a higher GPP during the first cruise, the planktonic compartment was autotrophic in March and heterotrophic in June (46±41 and −10±45 mmol O_2 m^{-2} d^{-1}, respectively).

Seagrass communities were autotrophic at all depths during both cruises, with the highest NCP found at the shallowest station (Table 4). In contrast, bare sediment communities remained net heterotrophic during both cruises, except for the shallowest community investigated during EUBAL-II (4 m). The upscaled results suggest that the NCP of the *Posidonia oceanica* meadow was marginally autotrophic during EUBAL-I (1 mmol O_2 m^{-2} d^{-1}) and significantly autotrophic, with an average NCP of 26 mmol O_2 m^{-2} d^{-1}, during EUBAL-II.

Combining these estimates with concurrent estimates of planktonic NCP over the *Posidonia oceanica* meadow, a NEP of 60 and 34 mmol O_2 m^{-2} d^{-1} was estimated in this area for EUBAL-I and -II, respectively.

Considering the entire bay, where the bare sediments and the seagrass meadow cover respectively 70 and 30% of its surface, benthic NCP was estimated at −1 and 7 mmol O_2 m^{-2} d^{-1} for EUBAL-I and -II, respectively. Therefore, a whole-system *NEP* of 45 and −3 mmol O_2 m^{-2} d^{-1} was estimated in March and June, respectively, indicating that the Bay of Palma acted as an autrotrophic ecosystem in March and as a heterotrophic one in June.

As mentioned previously, monthly time series were obtained at one station in the bay (Posidonia). The *NEP* measured at this station was 40 and 4 mmolO_2 m^{-2} d^{-1} during EUBAL-I and -II, respectively, while similar values (45 and −3 mmol O_2 m^{-2} d^{-1}) were reported for the entire bay during the same cruises (see above). Therefore, this suggests that the annual *NEP* estimated at Posidonia station (7.7 mmol O_2 m^{-2} d^{-1}; see above) might be a relatively confident indicator of the metabolism of the entire Bay of Palma over an annual cycle, although this extrapolation procedure could lead to a slight overestimate especially during low planktonic GPP periods as during EUBAL-II.

3.4 Spatial and temporal variations of *DIC*, AOU and air-sea CO_2 fluxes during EUBAL-I and -II cruises

The comparison of pCO_2 among cruises required the normalization to a constant temperature of 19°C ($pCO_{2(19°C)}$), as temperature strongly affects the equilibrium constants of *DIC* and, in particular, the solubility coefficient of CO_2, so that pCO_2 rises of about 4% when temperature increases of 1°C. Normalization of in situ pCO_2 ($pCO_{2(insitu)}$) values to a constant temperature allows to remove temperature effects and to focus on potential biological controls of pCO_2. No correlation was found between AOU and $pCO_{2(insitu)}$ (Fig. 7a) during the two EUBAL cruises taken together, while AOU and $pCO_{2(19°C)}$ (Fig. 7b) were strongly correlated which suggests that both variables were controlled by biological effects during these two cruises. The $pCO_{2(19°C)}$ and AOU values were on average lower during EUBAL-II than during EUBAL-I. This is related to

the longer residence time of the water mass in the bay during summer (Sect. 3.2) that leads to an enhanced impoverishment in CO_2 and enrichment in O_2 in June despite the fact that *NEP* was lower in June than in March (Sect. 3.3). The $pCO_{2(19°C)}$ and AOU values observed were much lower than those at the Dyfamed station (located in the open waters of the Ligurian Sea, about 620 km North from the Bay of Palma) for the corresponding periods. This suggests that in the Western Mediterranean Sea, the continental shelf is more productive than the open oceanic waters.

During both EUBAL cruises, TA was well correlated to salinity (Fig. 7c) suggesting that $CaCO_3$ precipitation/dissolution rates were too low and/or water residence time too short to significantly affect surface water TA values. The linear regression function based on data from both EUBAL cruises was very similar to that reported by Copin-Montégut (1993) for the Alboran Sea.

Strong spatial gradients of $pCO_{2(insitu)}$, $pCO_{2(19°C)}$ and AOU were observed during both EUBAL cruises (Fig. 8). During the six EUBAL-I surveys, $pCO_{2(insitu)}$, $pCO_{2(19°C)}$ and AOU surface distributions exhibited variable patterns with no recurrent spatial features. This suggests either highly variable *NEP* in space and time and/or the advection of water masses with different $pCO_{2(insitu)}$, $pCO_{2(19°C)}$ and AOU signatures. The latter explanation is consistent with shifts in the water mass and residual current patterns observed between the start and the end of the cruise (Sect. 3.2). During the EUBAL-II surveys, $pCO_{2(insitu)}$, $pCO_{2(19°C)}$ and AOU minima were systematically observed near-shore, above the *Posidonia oceanica* meadow (Fig. 8 and Table 5). Also, during the EUBAL-II surveys, lower near-shore values of $pCO_{2(insitu)}$, $pCO_{2(19°C)}$ and AOU were systematically observed on the Western side of the bay in comparison to the Eastern side (Fig. 8). This is consistent with the anti-clockwise pattern of residual currents (Fig. 3), leading to an impoverishment in CO_2 and an enrichment in O_2 as the water mass is advected above the *Posidonia oceanica* meadow. Also, a higher planktonic NCP was observed on the Western side of the bay during two EUBAL-II surveys, suggesting overall higher *NEP* on this side of the bay (Table 2).

The variability of the flux computations related to the choice of the *k* parametrization is huge as shown in other studies (e.g. Borges and Frankignoulle, 2002). The fluxes computed using the Wanninkhof and McGillis (1999) k parametrization were on average identical to those using the Liss and Merlivat (1986) k parametrization, and, corresponded to 57, 66 and 63% of those computed using, respectively, the k parametrization given by Wanninkhof (1992), Nightingale et al. (2000) and McGillis et al. (2001).

The Bay of Palma was a sink for atmospheric CO_2 during EUBAL-I (on average $-1.7\,\mathrm{mmol\,C\,m^{-2}\,d^{-1}}$) and a source during EUBAL-II (on average $2.7\,\mathrm{mmol\,C\,m^{-2}\,d^{-1}}$, Table 5). At the Dyfamed station, the CO_2 fluxes ranged between -2.9 and $-8.7\,\mathrm{mmol\,C\,m^{-2}\,d^{-1}}$ in March 1998–1999 and between 2.8 and $3.3\,\mathrm{mmol\,C\,m^{-2}\,d^{-1}}$ in June 1998–1999 (Bégovic and Copin-Montégut, 2002). The stronger fluxes at Dyfamed are related to higher wind speeds since the ΔpCO_2 are more marked in the Bay of Palma: -56 ppm during EUBAL-I (-39 ppm at Dyfamed in March 1998–1999) and 68 ppm during EUBAL-II (20 ppm at Dyfamed in June 1998–1999).

The temperature effect on the solubility coefficient of CO_2 strongly contributes to the seasonal variability of air-sea CO_2 flux in the Bay of Palma, as also shown in open oceanic waters (Dyfamed; Bégovic and Copin-Montégut, 2002) and other coastal waters (Bay of Calvi, Corsica; Frankignoulle, 1988) of the Western Mediterranean Sea. Indeed, pCO_2 and ΔpCO_2 values were higher during EUBAL-II than EUBAL-I, although, $pCO_{2(19^\circ C)}$ and DIC_{37} were actually lower during EUBAL-II (Table 5). Thus, the fact that the Bay of Palma is a source of CO_2 in June seems to be largely related to a temperature effect, since $pCO_{2(19^\circ C)}$ and AOU data were lower than in March (Fig. 7a, Fig. 8 and Table 5). At any rate, the contrasting role of the bay as a sink in March and a source in June is consistent with the positive NEP found in March and the net heterotrophy observed in June.

Our results also suggest that the potential impact of *Posidonia oceanica* meadows on the CO_2 air-sea flux budget in the Western Mediterranean continental shelf during summer could be small. The average CO_2 flux observed over the *Posidonia* meadow during EUBAL-II ($2.54\,\mathrm{mmol\,C\,m^{-2}\,d^{-1}}$; Table 5) was only 10% lower than that for unvegetated

areas during the same cruise ($2.76\,\mathrm{mmol\,C\,m^{-2}\,d^{-1}}$). As *Posidonia oceanica* meadows are believed to cover about 25% of the shelf area (Bethoux and Copin-Montégut, 1986), they can only decrease the summertime CO_2 emission from the Mediterranean continental shelf by a modest 2.5%.

3.5 DIC- and O_2-derived NEP estimates over the *Posidonia oceanica* meadow during EUBAL-II

NEP estimates over the *Posidonia oceanica* meadow during EUBAL-II based on surface water DIC_{37} and O_2 were highly variable and the ecosystem metabolism ranges from a distinctly autotrophic to a nearly balanced status (Table 6). The day-to-day variability of NEP seems to be mainly related to light availability, as there was a strong relationship between the NEP and surface irradiance (Fig. 9), which explained about 91 and 70% of the variance of, respectively, NEP_{DIC} and NEP_{O_2}. Based on these linear regressions and continuous surface irradiance measurements, NEP over the *Posidonia oceanica* meadow was integrated for the full duration of the EUBAL-II cruise (19–27 June): at $22\pm12\,\mathrm{mmol\,C\,m^{-2}\,d^{-1}}$ and $10\pm7\,\mathrm{mmol\,O_2\,m^{-2}\,d^{-1}}$ for, respectively, NEP_{DIC} and NEP_{O_2}. The difference between NEP_{DIC} and NEP_{O_2} could be related to net $CaCO_3$ production that was not included in the DIC budget. Net $CaCO_3$ production was measured using in situ benthic chambers on 20/06/2002 at station Posidonia, yielding a value of $15\,\mathrm{mmol\,C\,m^{-2}\,d^{-1}}$ for the *Posidonia oceanica* vegetated community and $1\,\mathrm{mmol\,C\,m^{-2}\,d^{-1}}$ for bare sediments of the Bay of Palma (Barrón et al., 2004[5]). Based on the relative sea-floor coverage by these benthic communities, the integrated net $CaCO_3$ production between the shore and 30 m depth is $10\,\mathrm{mmol\,C\,m^{-2}\,d^{-1}}$ and corresponds to the difference between NEP_{DIC} and NEP_{O2}.

NEP_{O_2} and NEP_{DIC} are well correlated and the slope of the linear regression (Ta-

---

[5] Barrón, C., Duarte, C. M., Frankignoulle, M., and Borges, A. V.: Organic carbon metabolism and carbonate dynamics in a Mediterranean seagrass (Posidonia oceanica) meadow, Limn. Ocean., submitted, 2004.

ble 6) gives an indication on the ΔO_2:ΔDIC ratios of both GPP and CR processes. The photosynthetic quotient (PQ) corresponds to the molar ratio of the release of O_2 to the consumption of DIC during photosynthesis while the respiratory quotient (RQ) corresponds to the molar ratio of the release of DIC to the consumption of O_2 during organic matter mineralization. As mentioned by Thamdrup and Canfield (2000), an important uncertainty in using O_2 uptake as a measure of mineralization in sediments lies in the assumption that anaerobic respiration and reoxidation of reduced inorganic species are at steady state. Holmer et al. (2003) reported that reduced sulfides are low both in the pore waters and in the particulate pools of seagrass sediments around Mallorca Island, suggesting that the previous assumption is realistic in these iron-poor and carbonate rich sediments. Therefore, in the present study, a RQ of 1 was assumed and the NEP_{O_2} vs. NEP_{DIC} ratio was used to compute a PQ value. The latter is slightly lower but not significantly different than 1. This would suggest that NEP over the *Posidonia oceanica* meadow is mainly related to the photosynthetic activity of the seagrass community. Indeed, one can compute a PQ of 1.06, based on the C:N:P elemental molar ratio of 956:39:1 reported by Atkinson and Smith (1983) for *Posidonia oceanica* leaves. The C:N:P elemental molar ratio of roots is 3550:61:1 (Atkinson and Smith, 1983) but the below-ground production of *Posidonia oceanica* is much lower than the above-ground production (about 10%; Duarte and Chiscano, 1999) and does not significantly affect the PQ estimate. Based on the C:N:P molar elemental composition of phytoplankton reported by Redfield (1963) and Hedges et al. (2002), the predicted PQ values are higher than 1, respectively, 1.30 and 1.45.

Error estimates on these NEP values (Table 6) are largely derived from the uncertainty on the water residence time. The analytical error on DIC_{37} and O_2 should not significantly affect the NEP estimates, since the variables used in the computations are averages of a large number of observations (assuming that analytical errors are random and not systematic). The air-sea flux correction also introduces a significant uncertainty in the computations. NEP_{DIC} computed using the air-sea CO_2 fluxes calculated with Wanninkhof and McGillis (1999) k parametrization corresponds on average

to 99.4, 102.7, 94.7 and 95.0% of NEP_{DIC} computed using the k parametrizations given by, respectively, Liss and Merlivat (1986), Wanninkhof (1992), Nightingale et al. (2000) and McGillis et al. (2001). NEP_{O_2} computed using the air-sea O_2 fluxes calculated with Wanninkhof and McGillis (1999) k parametrization corresponds on average to 98.5, 96.7, 96.5 and 97.2% of NEP_{O_2} computed using the k parametrization given by, respectively, Liss and Merlivat (1986), Wanninkhof (1992), Nightingale et al. (2000) and McGillis et al. (2001). The choice of the k parametrization for air-sea flux correction also affects the PQ estimate, the lowest one corresponding to the NEP computations using the Wanninkhof and McGillis (1999) k parametrization (Table 6) and the highest one (1.1±0.2) corresponding to the NEP computations using the Wanninkhof (1992) k parametrization. The less constrained uncertainty in the computations of NEP above the *Posidonia oceanica* meadow during EUBAL-II probably comes from the representativeness of the underway surface water data for the whole water column DIC_{37} and O_2. This approach is attractive because it is based on large data sets that adequately resolve the spatial variability, but it is based on the assumption that the variables are homogeneous in the water column (no vertical gradients).

Examination vertical profiles of DIC_{37} and O_2 at the four reference stations sampled during EUBAL-II (Fig. 10) shows that these vertical gradients are more marked for O_2 than DIC_{37} but they remain smaller than the spatial gradients, for both variables. We attempted to adjust the surface values of O_2 and DIC_{37} to represent the whole column values of these variables. Station 4 (located at the edge but outside the *Posidonia oceanica* meadow) was considered to represent the incoming water from the bay and the other three stations were considered to be representative of the *Posidonia oceanica* meadow. NEP computed from adjusted DIC_{37} and O_2 values, assuming that surface DIC_{37} is 1 and 4 μmol kg^{-1} (for the entire bay and *Posidonia oceanica* meadow, respectively) lower than whole column DIC_{37} and that surface O_2 is 9 and 4 μmol kg^{-1} (for bay and *Posidonia oceanica* meadow, respectively) lower than whole column O_2, were much larger than NEP estimates based on surface water values, but, the PQ value remains unchanged (Table 6). NEP estimates based on the adjusted DIC_{37} and O_2 values are also well correlated to surface irradiance (not shown), allowing the integration for the full duration of the EUBAL-II cruise (19–27 June) to yield estimates of 35±8 mmol C m^{-2} d^{-1} and 48±7 mmol O_2 m^{-2} d^{-1} for, respectively, NEP_{DIC} and NEP_{O2}. In this case, net $CaCO_3$ production cannot explain the difference between NEP_{DIC} and NEP_{O_2}, and the difference between NEP_{DIC} and NEP_{O_2} is probably mostly related to the error on the slope and y-intercept of the linear regressions as a function of surface irradiance that are higher for NEP_{O_2}. However, considering potential sources of error associated to each method, these estimates are in fair agreement with the NEP estimate based on the upscaled incubation measurements of 34 mmol O_2 m^{-2} d^{-1} over the *Posidonia oceanica* meadow during this cruise (Sect. 3.3).

3.6 Daily variations of *DIC* during EUBAL-II

The daily variations of DIC_{37} at stations Posidonia and Cap Enderrocat follow the daily oscillation expected from the diel alternation between photosynthesis and respiration; DIC_{37} decreases from dawn to dust and increases during the night (Fig. 11). However, at station Bahia, the DIC_{37} time-course during the 24 h cycle was erratic. This can be attributed to the fact that station Bahia is much deeper (33 m) than stations Posidonia (13 m) and Cap Enderrocat (16 m). It is then probable that due to the water column depth, the impact on water column DIC from metabolic activity is much smaller at station Bahia and is not discernable from the background noise.

The difference of average DIC values from the top half of the water column and from the bottom half of the water column (ΔDIC) provides qualitative information on the relative importance of metabolic rates from the planktonic and benthic compartments. During the 24 h cycle at Posidonia station, in the lower half of the water column higher average DIC values were observed during night-time while lower average DIC values were observed at the end of the day (Fig. 11). This suggests higher metabolic rates in the benthic compartment than in the planktonic one, at the Posidonia station. Indeed, the integrated metabolic rates measured by O_2 incubations show that, at this station,

benthic CR is about 1.8 times higher than planktonic CR and that benthic GPP is about 1.5 times higher than planktonic GPP. At station Bahia, the reverse trend in ΔDIC is observed, suggesting higher metabolic rates in the planktonic compartment compared to the benthic one. This conclusion is not surprising considering that reference station Bahia is deeper than reference station Posidonia and that benthic metabolic rates are expected to be lower due to stronger light-limitation.

Day-time net community production (NCP_d) was estimated from the time course of DIC values from dawn to dust. Considering the scatter in the data, a simple linear regression was used. We did not attempt to estimate CR because only 3 profiles were obtained at night. NCP_d estimates were in fair agreement with those based on O_2 incubations and reproduce the same spatial trend, with higher NCP_d at Posidonia station than at Cap Enderrocat station (Table 7). We can conclude that the daily DIC time-course approach can be used with confidence to estimate metabolic rates but its application is limited to relatively shallow waters (≤15 m).

4 Conclusions

Benthic areas dominated by the seagrass *Posidonia oceanica* are autotrophic, whereas unvegetated sediment is a net heterotrophic component of the metabolism of the Bay of Palma, except for the shallowest areas. The autotrophic nature of seagrass meadows is consistent with previous reports for these ecosystems (Duarte and Cebrián, 1996; Gattuso et al., 1998; Hemminga and Duarte, 2000; Barrón et al., 2004[6]). In contrast, the planktonic community is largely heterotrophic, except during phytoplankton blooms, as in March 2002 (EUBAL-I), the time of the spring bloom in the NW Mediterranean (Duarte et al., 1999). Consequently, even the shallow Posidonia station (7 m) was near metabolic balance at the annual time scale despite the contribution of the seagrass

---

[6] Barrón, C., Duarte, C. M., Frankignoulle, M., and Borges, A. V.: Organic carbon metabolism and carbonate dynamics in a Mediterranean seagrass (Posidonia oceanica) meadow, Limn. Ocean., submitted, 2004.

community. Moreover, the short water residence time in the bay suggests that the extended planktonic heterotrophic periods, that dominate most of the year, cannot be supported by carbon in excess accumulated during autotrophic periods. As such, the whole ecosystem might be, in general, heterotrophic, especially during summer, when the strong increase in ecosystem community respiration, driven by the rise of temperature, greatly exceeds ecosystem gross primary production. The heterotrophic nature of the ecosystem and the planktonic community must be supported by allochtonous organic carbon inputs, probably derived from the human population surrounding the Bay of Palma.

During the summer cruise, the spatial variability of pCO_2 and O_2 fields and the direction of CO_2 fluxes were consistent with net ecosystem production (NEP) derived from incubations. When the water residence time in the bay is long enough (10 d in June), a mass balance approach allowed the derivation of NEP estimates that are in fair agreement with those derived from direct metabolic estimates from incubated samples over the *Posidonia oceanica* meadow. However, such a mass balance approach would require a detailed physical study to improve the accuracy of the water residence time estimate. Air-water flux of CO_2 (or O_2) introduced a relatively small error on the NEP estimates based on this method, in contrast with other ecosystems characterized by much larger air-water fluxes such as estuaries (e.g. Gazeau et al., 2004[7]). Our results also provide evidence that simple day-night whole water column DIC variations may also be useful to derive NEP estimates in shallow water (<15 m) seagrass ecosystems.

Acknowledgements. This research was supported by the European Union in the framework of the EUROTROPH project (contract #EVK3-CT-2000-00040), and by a CNRS/CGRI/FNRS/CSIC cooperation. We thank the officers, crew and technical staff of the Tethys II and Mytilus for full collaboration during the EUBAL cruises, D. Tailliez for operating

---

[7] Gazeau, F., Gattuso, J.-P., Middelburg, J. J., Barrón, C., Duarte, C. M., Schiettecatte, L.-S., Brion, N., Pizay, M.-D., Frankignoulle, M., and Borges, A. V.: Planktonic and whole-system metabolism in a nutrient-rich estuary (The Scheldt Estuary), Limn. Ocean., submitted, 2004.

the rosette and CTD and processing the data during EUBAL-I, C. Copin-Montégut for providing the DYFAMED dataset, R. Biondo, E. Libert, R. Martínez, M.-D. Pizay, R. Santiago and J.-M. Théate for technical support. AVB and MF are, respectively a post-doctoral researcher and a senior research associate at the FNRS. CB was supported by a grant from the Balearic government, and NN was supported by a fellowship from the Spanish Ministry of Education, Culture and Sports.

References

Allen, J. T., Alderson, S. G., Ruiz, S., Nurser, A. G., and Griffiths, G.: Shipboard VM-ADCP observations during RRS Discovery cruise 224, Internal Document no. 21, Southampton Oceanography Centre, 1997.

Atkinson, M. J. and Smith, S. V.: C:N:P ratios of benthic marine plants, Limn. Ocean., 28(3), 568–574, 1983.

Barranguet, C., Herman, P. M. J., and Sinke, J. J.: Microphytobenthos biomass and community composition studied by pigment bimoarkers: importance and fate in the carbon cycle of a tidal flat, J. Sea Res., 38, 59–70, 1997.

Bégovic, M. and Copin-Montégut, C.: Processes controlling annual variations in the partial pressure of CO_2 in surface waters of the central northwestern Mediterranean Sea (Dyfamed site), Deep-Sea II, 49(11), 2031–2047, 2002.

Benson, B. B. and Krause, D. J.: The concentration and isotopic fractionation of oxygen dissolved in fresh water and seawater in equilibrium with the atmosphere, Limn. Ocean., 29(3), 620–632, 1984.

Bethoux, J. P. and Copin-Montégut, G.: Biological fixation of atmospheric nitrogen in the Mediterranean Sea, Limn. Ocean., 31(6), 1353–1358, 1986.

Borges, A. V. and Frankignoulle, M.: Short-term variations of the partial pressure of CO_2 in surface waters of the Galician upwelling system, Prog. Ocean., 51(2–4), 283–302, 2001.

Borges, A. V. and Frankignoulle, M.: Distribution of surface carbon dioxide and air-sea exchange in the upwelling system off the Galician coast - art. no. 1020, Global Biog., 16(2), doi:10.1029/20000GB001385, 2002.

Borges, A. V., Delille, B., Schiettecatte, L.-S., Gazeau, F., Abril, G., and Frankignoulle, M.: Gas transfer velocities of CO_2 in three European estuaries (Randers Fjord, Scheldt and Thames), Limn. Ocean., 49(5), 2004.

Carrit, D. E. and Carpenter, J. H.: Comparison and evaluation of currently employed modifications of the Winkler method for determining dissolved oxygen in seawater: a NASCO Report, J. Marine Res., 24, 286–319, 1966.

Chen, C. T. A., Liu, K. K., and Macdonald, R.: Continental margin exchanges, in: Ocean biogeochemistry, edited by: Fasham, M. J. R., Springer, 53–97, 2003.

Copin-Montégut, C.: A new formula for the effect of temperature on the partial pressure of CO_2 in seawater, Mar. Chem., 25, 29–37, 1988.

Copin-Montégut, C.: Alkalinity and carbon budgets in the Mediterranean sea, Global Biog., 7(4), 915–925, 1993.

Dickson, A. G.: Thermodynamics of the dissociation of boric acid in synthetic seawater from 273.15 to 318.15 K, Deep-Sea A, 375(5), 755–766, 1990.

Dickson, A. G.: pH buffers for sea water media based on the total hydrogen ion concentration scale, Deep-Sea I, 40(1), 107–118, 1993.

Duarte, C. M. and Cebrián, J.: The fate of marine autotrophic production, Limn. Ocean., 41(8), 1758–1766, 1996.

Duarte, C. M. and Agustí, S.: The CO_2 balance of unproductive aquatic ecosystems, Science, 281(5374), 234–236, 1998.

Duarte, C. M. and Chiscano, C. L.: Seagrass biomass and production: a reassessment, Aqua Bot., 65, 159–174, 1999.

Duarte, C. M., Agustí, S., Kennedy, H., and Vaqué, D.: The Mediterranean climate as a template for Mediterranean marine ecosystems: the example of the northeast Spanish littoral, Prog. Ocean., 44(1–3), 245–270, 1999.

Frankignoulle, M.: Field measurements of air-sea CO_2 exchange, Limn. Ocean., 33(3), 313–322, 1988.

Frankignoulle, M., Borges, A., and Biondo, R.: A new design of equilibrator to monitor carbon dioxide in highly dynamic and turbid environments, Water Res., 35(5), 1344–1347, 2001.

Frankignoulle, M., Gattuso, J.-P., Biondo, R., Bourge, I., Copin-Montégut, G., and Pichon, M.: Carbon fluxes in coral reefs. 2. Eulerian study of inorganic carbon dynamics and measurement of air-sea CO_2 exchanges, Mar. Ecol.-Pr., 145(1–3), 123–132, 1996.

Gattuso, J.-P., Frankignoulle, M., and Wollast, R.: Carbon and carbonate metabolism in coastal aquatic ecosystems, Ann. R. Ecol., 29, 405–434, 1998.

Gordon, D. C. J., Boudreau, P. R., Mann, K. H., Ong, J.-E., Silvert, W. L., Smith, S. V., Wattayakorn, G., Wulff, F., and Yanagi, T.: LOICZ biogeochemical modelling guidelines, LOICZ Reports & Studies, 5, 1–96, 1996.

Griffiths, G.: Using 3DF Ashtech GPS heading for improving underway ADCP data, J. Atmosp. Oc., 11, 1135–1143, 1994.

Hansen, H. P. and Koroleff, F.: Determination of nutrients, in: Methods of seawater analysis, edited by: Grasshoff, K., Kremling, K., and Ehrhardt, M., Weinheim, Wiley-VCH Verlag, 1999.

Hansen, J. W., Thamdrup, B., and Jørgensen, B. B.: Anoxic incubation of sediment in gas-tight plastic bags: a method for biogeochemical process studies, Mar. Ecol.-Pr., 208, 273–282, 2000.

Hedges, J. I., Baldock, J. A., Gelinas, Y., Lee, C., Peterson, M. L., and Wakeham, S. G.: The biochemical and elemental compositions of marine plankton: a NMR perspective, Mar. Chem., 78(1), 47–63, 2002.

Hemminga, M. A. and Duarte, C. M.: Seagrass Ecology, Cambridge University Press, Cambridge, 2000.

Holmer, M., Duarte, C. M., and Marbá, N.: Sulfur cycling and seagrass (*Posidonia oceanica*) status in carbonate sediments, Biogeochem., 66, 223–239, 2003.

Hopkinson, C. S. J. and Smith, E. M.: Estuarine respiration: an overview of benthic, pelagic and whole system respiration, in: Respiration in aquatic ecosystems, edited by: del Giorgio, P. A. and Williams, L. P. J., Oxford University Press, in press, 2004.

Knap, A. H., Michaels, A. E., Close, A., Ducklow, H. W., and Dickson, A. G. (Eds): Protocols for the Joint Global Ocean Flux Study (JGOFS) core measurements, JGOFS Report No 19. Bergen, Norway, Unesco, 1996.

Liss, P. S. and Merlivat, L.: Air-sea gas exchange rates: introduction and synthesis, in: The role of air-sea exchange in geochemical cycling, edited by: Buat-Menard, P., Dordrecht, D. Reidel Publishing Company, 113–127, 1986.

Liu, K. K., Iseki, K., and Chao, S. Y.: Continental margin carbon fluxes, in: The changing ocean carbon cycle: a midterm synthesis of the Joint Global Ocean Flus Study, edited by: Hanson, R. B., Ducklow, H. W., and Field, J. G., Cambridge University Press, 187–239, 2000.

McGillis, W. R., Edson, J. B., Ware, J. D., Dacey, J. W. H., Hare, J. E., Fairall, C. W., and Wanninkhof, R.: Carbon dioxide flux techniques performed during GasEx-98, Mar. Chem., 75, 267–280, 2001.

Nightingale, P. D., Malin, G., Law, C. S., Watson, A. J., Liss, P. S., Liddicoat, M. I., Boutin, J., and Upstill-Goddard, R. C.: In situ evaluation of air-sea gas exchange parameterizations using novel conservative and volatile tracers, Global Biog., 14(1), 373–387, 2000.

Odum, H. T.: Primary production in flowing waters, Limn. Ocean., 1(2), 102–117, 1956.

Oudot, C., Gerard, R., Morin, P., and Gningue, I.: Precise shipboard determination of dissolved oxygen (Winkler procedure) for productivity studies with a commercial system, Limn. Ocean., 33(1), 146–150, 1988.

Pedder, M. A.: Interpolation and filtering of spatial observations using successive corrections and Gaussian filters, Monthly Weather Review, 121, 2889–2902, 1993.

Platt, T., Gallegos, C. L., and Harrison, W. G.: Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton, J. Marine Res., 38, 687–701, 1980.

Ramis, C., Jansá, A., and Alonso, S.: Sea breeze in Mallorca. A numerical study, Meteor. Atm., 42, 249–258, 1990.

Redfield, A. C., Ketchum, B. H., and Richards, F. A.: The influence of organisms on the composition of sea-water, in: The sea, edited by: Hill, M. N., New York, Wiley, 2, 26–77, 1963.

Rey, J. and Diaz del Rio, V.: Cartographia de los fondos marinos de la bahia de Palma (Baleares, España): distribution de las praderas vegetales y sedimentos superficiales, International Workshop on Posidonia Oceanica Beds, Porquerolles, 1984.

Roy, R. N., Roy, L. N., Vogel, K. M., Porter-Moore, C., Pearson, T., Good, C. E., Millero, F. J., and Campbell, D. M.: The dissociation constants of carbonic acid in seawater at salinities 5 to 45 and temperatures 0 to 45°C, Mar. Chem., 44(2–4), 249–267, 1993.

Smith, S. V. and Hollibaugh, J. T.: Coastal metabolism and the oceanic organic carbon balance, Rev. Geophys., 31(1), 75–89, 1993.

Thamdrup, B. and Canfield, D. E.: Benthic respiration in aquatic sediments, in: Methods in ecosystem science, edited by: Sala, O. E., Jackson, R. B., Mooney, H. A., and Howarth, R. W., New York, Springer, 86–103, 2000.

Wanninkhof, R.: Relationship between wind speed and gas exchange over the ocean, J. Geophys. Res., 97(C5), 7373–7382, 1992.

Wanninkhof, R. and McGillis, W. R.: A cubic relationship between air-sea CO_2 exchange and wind speed, Geophys. Res. Lett., 26(13), 1889–1892, 1999.

Weiss, R. F.: Carbon dioxide in water and seawater: the solubility of a non-ideal gas, Mar. Chem., 2, 203–215, 1974.

Wollast, R.: Evaluation and comparison of the global carbon cycle in the coastal zone and in the open ocean, in: The Sea, edited by: Brink, K. H. and Robinson, A. R., John Wiley & Sons, New York, 10, 213–252, 1998.

Table 1. Characteristics of the incubation stations during the EUBAL cruises in 2002. Salinity and temperature values were averaged and chlorophyll *a* concentrations were integrated over the water column. *K* is the light attenuation coefficient.

Station	Date	Bottom depth m	Salinity	Temperature °C	Integrated chlorophyll *a* $mg\,m^{-2}$	*K* m^{-1}
EUBAL-I						
Posidonia	04/03/2002	18	37.61	14.4	4.2	0.15
Bahia	06/03/2002	35	37.65	14.3	17.3	0.14
Station 4	08/03/2002	37	37.53	14.3	16.7	0.11
Cap Enderrocat	10/03/2002	20	37.62	14	11.4	0.14
EUBAL-II						
Posidonia	20/06/2002	13	37.80	22.6	3.3	0.16
Bahia	22/06/2002	33	37.78	22.4	4.9	0.09
Station 4	18/06/2002	33	37.76	20.8	2.6	0.08
Cap Enderrocat	24/06/2002	16	37.76	23	1.5	0.09

Table 2. Integrated planktonic gross primary production (GPP), community respiration (CR) and net community production (NCP) at four stations during the EUBAL-I and -II cruises.

Station	Bottom depth m	GPP	CR	NCP
		mmol O_2 m^{-2} d^{-1}		
EUBAL-I				
Posidonia	18	36	−33	3
Bahia	35	98	−45	53
Station 4	37	92	−35	57
Cap Enderrocat	20	73	−27	46
EUBAL-II				
Posidonia	13	72	−45	27
Bahia	33	86	−75	11
Station 4	33	56	−107	−51
Cap Enderrocat	16	29	−59	−30

Table 3. Integrated chlorophyll *a*concentrations, planktonic gross primary production (GPP), community respiration (CR) and net community production (NCP) estimated on two surveys during each of the EUBAL cruises.

Station	Date	Integrated chlorophyll *a* mg m^{-2}	GPP	CR	NCP
			mmol O_2 m^{-2} d^{-1}		
Posidonia	07/03/2002	16	44	−33	11
Bahia	“	8	93	−45	48
Cap Enderrocat	“	3	20	−27	−7
4	“	15	84	−35	49
8	“	15	90	−89	1
18	“	14	78	−18	60
19	“	8	45	−16	29
20	“	15	86	−67	19
22	“	15	89	−49	40
23	“	15	89	−61	28
26	“	16	94	−74	20
Mean (±SD)	07/03/2002	13±4	74±25	−47±24	27±29
Posidonia	11/03/2002	7	42	−33	9
Bahia	“	30	175	−45	130
Cap Enderrocat	“	9	53	−27	26
4	“	35	204	−35	169
8	“	19	109	−89	20
18	“	12	72	−18	54
19	“	15	88	−16	72
20	“	24	140	−67	73
22	“	22	128	−49	79
23	“	16	92	−61	31
26	“	23	131	−74	57
Mean (±SD)	11/03/2002	19±9	112±50	−47±24	65±48
Posidonia	21/06/2002	2.1	41	−45	−4
Bahia	“	4.2	81	−75	6
Cap Enderrocat	“	0.5	9	−59	−50
4	“	0.8	16	−107	−91
8	“	0.5	12	−23	−11
18	“	4.1	80	−41	39
19	“	0.9	18	−37	−19
20	“	1	20	−28	−8
22	“	0.1	1	−16	−15
23	“	0.1	3	−17	−14
26	“	0.4	8	−20	−13
Mean (±SD)	21/06/2002	1.3±1.5	26±29	−43±28	−17±33
Posidonia	26/06/2002	2.1	40	−45	−5
Bahia	“	7.1	138	−75	63
Cap Enderrocat	“	0.5	10	−59	−49
4	“	0.8	15	−107	−92
8	“	0.3	6	−19	−13
18	“	8.5	165	−41	125
19	“	1.2	24	−37	−14
20	“	0.6	15	−25	−10
22	“	0.7	13	−24	−11
23	“	0.4	8	−21	−13
26	“	0.2	6	−19	−13
Mean (±SD)	26/06/2002	2±2.9	40±56	−43±28	−3±56
EUBAL-I Mean (±SD)	March 2002	16±7	93±43	-47±24	46±41
EUBAL-II Mean (±SD)	June 2002	1.7±2.3	33±44	−43±27	−10±45

Table 4. Mean (±SE) benthic net community production (NCP) in March (EUBAL-I) and June 2002 (EUBAL-II).

Cruise	Community	Depth (m)	NCP±SE mmol O_2 m^{-2} d^{-1}
EUBAL-I	*P. oceanica*	7	29.7±10.8
		15	17.1±3.3
	Sediment	7	−0.3±0.2
		15	−0.4±0.1
EUBAL-II	*P. oceanica*	4	44.2±13.6
		7	12.0±11.0
		15	24.6±3.9
		22	19.1±11.1
	Sediment	4	5.7±0.5
		7	−4.0±0.4
		15	−3.7±0.3
		22	−6.4±0.4

Table 5. Average ±SD of AOU, pCO_2, pCO_2 normalized to a constant temperature ($pCO_{2(19^\circ C)}$), DIC_{37} (computed from continuous measurements of pCO_2 and salinity, and TA-Salinity linear regression function in legend of Fig. 7), wind speed (u), the air-sea gradient of pCO_2 (ΔpCO_2), in the surface waters, and atmospheric CO_2 flux computed using the gas transfer velocity given by Wanninkhof and McGillis (1999) (F), over the *Posidonia* meadow and in the rest of the bay, on the surveys carried out during the EUBAL-I and -II cruises. Data were interpolated using the Kriging procedure on a grid of 0.0034° E×0.0025° N and averaged.

μmol kg^{-1}	AOU ppm	pCO_2 ppm	$pCO_{2(19^\circ C)}$ mmol kg^{-1}	DIC_{37} ppm	ΔpCO_2 m s^{-1}	u mmol C m^{-2} d^{-1}	F
Bay (excluding *Posidonia* meadow)							
01/03/2002	−4.6±2.3	324±3	386±4	2.142±0.002	−46±16	3.9±1.6	−1.0±0.9
04/03/2002	−10.5±1.8	320±2	384±3	2.140±0.002	−64±1	6.9±1.8	−5.8±4.5
07/03/2002	−2.4±0.6	320±1	388±2	2.144±0.001	−54±2	4.5±2.2	−1.9±2.3
09/03/2002	−0.8±0.9	320±1	386±3	2.143±0.001	−57±3	2.9±0.9	−0.4±0.3
11/03/2002	−3.2±0.5	320±1	381±2	2.140±0.001	−55±4	3.3±0.9	−0.5±0.4
12/03/2002	−4.2±0.9	321±2	380±2	2.140±0.001	−53±7	3.3±1.0	−0.5±0.5
19/06/2002	−15.8±3.5	420±7	363±7	2.121±0.004	50±12	4.7±2.1	1.7±1.4
21/06/2002	−13.3±3.3	426±10	361±7	2.120±0.004	52±18	4.1±2.2	1.6±2.0
25/06/2002	−10.0±2.4	442±10	361±5	2.118±0.003	82±10	6.3±1.4	5.9±3.4
26/06/2002	−10.5±4.0	444±11	358±8	2.116±0.005	77±20	3.6±1.2	1.1±1.1
27/06/2002	−10.8±1.1	443±3	360±1	2.119±0.001	83±3	5.4±1.4	3.6±2.5
Posidonia meadow							
01/03/2002	−6.1±2.4	323±2	384±3	2.141±0.002	−56±17	3.9±1.6	−1.0±0.9
04/03/2002	−14.8±2.7	316±3	379±4	2.138±0.002	−63±1	6.9±1.8	−5.7±4.5
07/03/2002	−2.0±1.6	323±5	395±6	2.147±0.003	−54±4	4.5±2.2	−1.9±2.4
09/03/2002	0.0±0.6	323±8	394±10	2.147±0.005	−58±9	2.9±0.9	−0.4±0.4
11/03/2002	−2.6±0.6	320±1	383±2	2.141±0.001	−64±8	3.3±0.9	−0.6±0.5
12/03/2002	−4.2±1.1	321±3	379±2	2.140±0.001	−59±12	3.3±1.0	−0.6±0.5
19/06/2002	−24.0±5.8	405±17	346±15	2.110±0.010	40±21	4.7±2.1	1.4±1.1
21/06/2002	−18.0±4.7	420±18	351±13	2.114±0.009	45±31	4.1±2.2	1.3±1.7
25/06/2002	−14.1±3.9	433±14	351±10	2.111±0.007	74±15	6.3±1.4	5.3±3.1
26/06/2002	−12.6±5.8	445±18	354±12	2.114±0.008	79±31	3.6±1.2	1.1±1.1
27/06/2002	−12.7±2.2	449±7	358±5	2.117±0.003	87±11	5.4±1.4	3.7±2.6

Table 6. Net ecosystem production (*NEP*) and the photosynthetic quotient (PQ), over the *Posidonia oceanica* meadow during the EUBAL-II cruise. DIC_{37} and O_2 data were interpolated as explained in legend of Table 5. Top half of the table corresponds to *NEP* computed from the observed surface distributions of DIC_{37} and O_2. Lower half of the table corresponds to *NEP* computed from the surface distributions of DIC_{37} and O_2 that were adjusted to account for their vertical gradients (see text for details). The uncertainty on *NEP* was computed assuming an error on t_{total} of ±1 d. The uncertainty on PQ corresponds to SE on the slope of the linear regression of NEP_{O_2} vs. NEP_{DIC}.

	NEP_{DIC}	NEP_{O_2}	PQ
mmol C m^{-2} d^{-1}	mmol O_2 m^{-2} d^{-1}		
Based on observed surface distribution			
19/06/2002	41±3	31±3	0.93±0.18 (r^2=0.926)
21/06/2002	25±2	10±1	
25/06/2002	27±2	9±1	
26/06/2002	9±1	2±1	
27/06/2002	7±1	−5±1	
Based on adjusted surface distribution to account for vertical gradients			
19/06/2002	59±4	77±7	0.92±0.18 (r^2 = 0.902)
21/06/2002	42±4	56±3	
25/06/2002	45±2	54±3	
26/06/2002	27±2	48±2	
27/06/2002	25±3	40±1	

Table 7. Day-time net community production (NCP_d) from the EUBAL-II cruise based on O_2 incubations in both planktonic and benthic compartments and based on the day-time *DIC* evolution. NCP_d is computed from the slope of the linear regression of water column averaged *DIC* values (the error estimate on NCP_d is based on SE on the slope).

	O_2 incubations			*DIC* evolution
	Planktonic NCP_d	Benthic NCP_d	NEP_d	NEP_d
	mmol O_2 m^{-2} d^{-1}			mmol C m^{-2} d^{-1}
Posidonia	2.9	3.7	6.6	15.0±2.1
Cap Enderrocat	−0.5	4.1	3.6	9.2±5.0

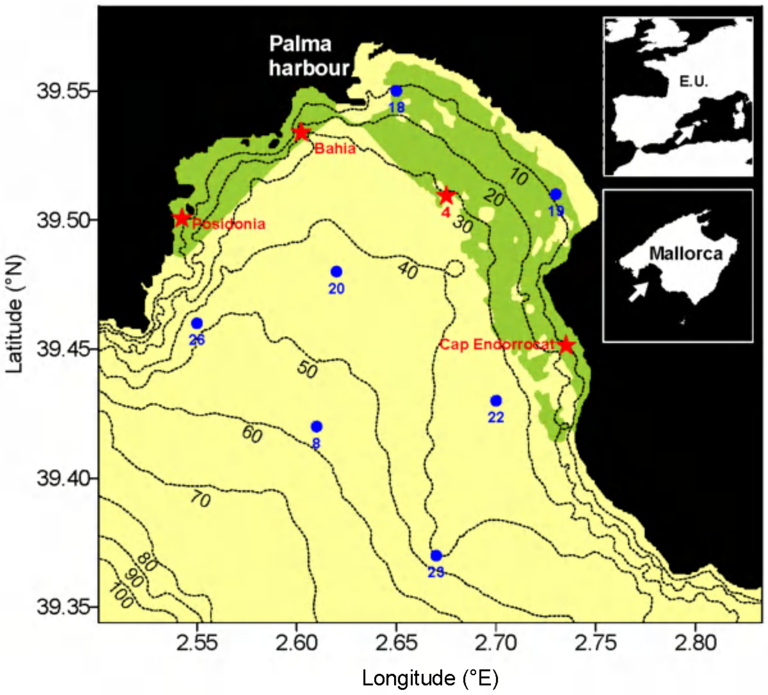


Fig. 1. Map of the Bay of Palma showing the bathymetry (dotted lines), the distribution of the *Posidonia oceanica* meadow (green area, adapted from Rey and Diaz Del Rio 1984), the four reference stations where incubations for metabolic processes were carried out (red stars) and stations where vertical profiles were carried out (blue circles).

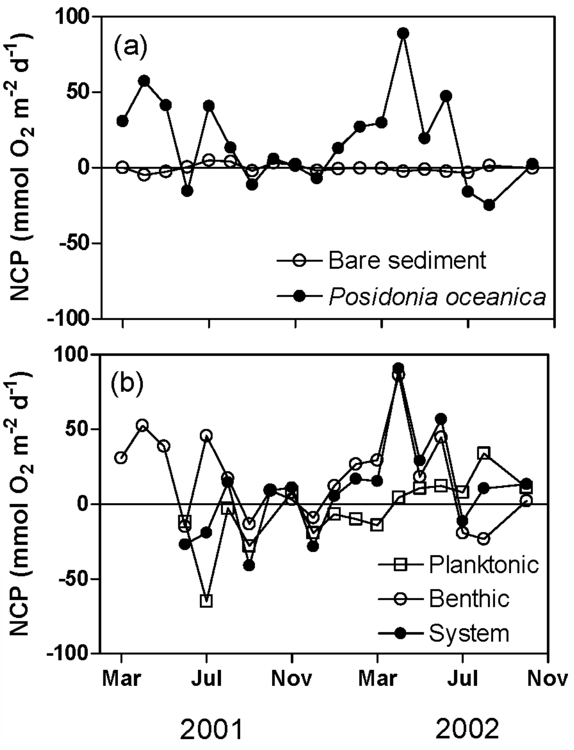
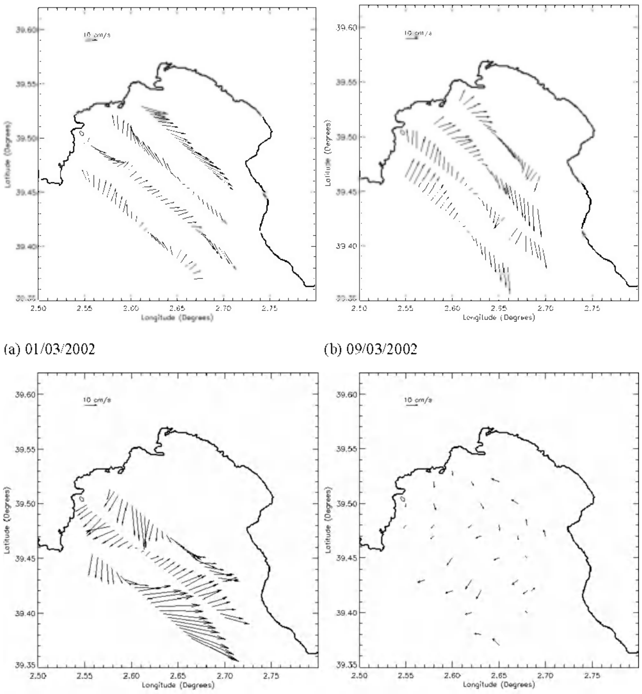


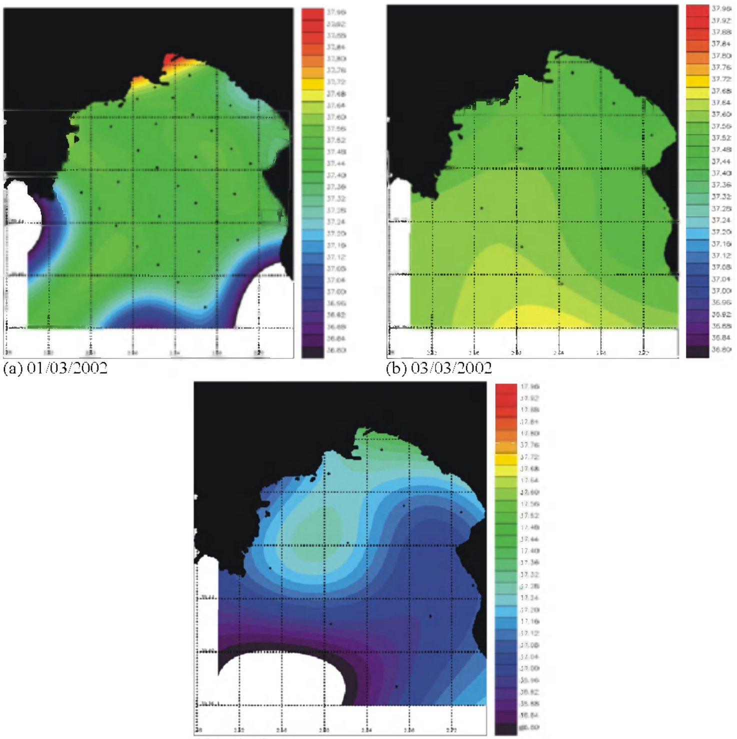
Fig. 2. **(a)** Monthly net community production (NCP) in the bare sediment and *Posidonia oceanica* communities. **(b)** Monthly NCP in the planktonic and benthic compartment as well as the combined net ecosystem production (system) at the Posidonia station (cf. Fig. 1).



(a) 01/03/2002 (b) 09/03/2002

(c) 12/03/2002 (d) 25/06/2003

Fig. 3. Velocity distribution during EUBAL-I at 14 m for **(a)** 01 March 2002, **(b)** 03 March 2002 and **(c)** 12 March 2002; and EUBAL-II at 10 m **(d)** for 25 June 2002.



(a) 01/03/2002 (b) 03/03/2002

(c) 12/03/2002

Fig. 4. Salinity distribution during EUBAL-I at 2 m for **(a)** 01 March 2002, **(b)** 03 March 2002; **(c)** 12 March 2002.

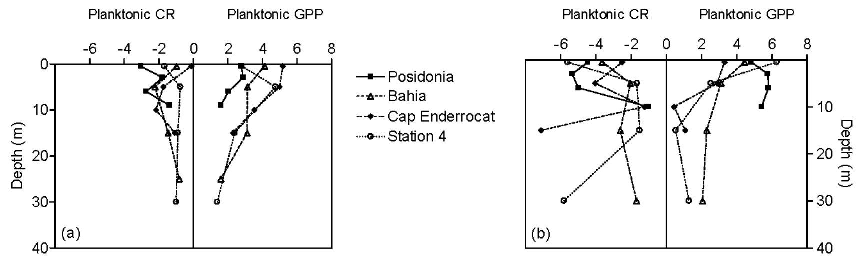


Fig. 5. Depth profiles of planktonic daily CR and GPP (mmol O_2 m^{-3} d^{-1}) measured at four stations in the Bay of Palma during **(a)** EUBAL-I and **(b)** EUBAL-II cruises (cf. Fig. 1).

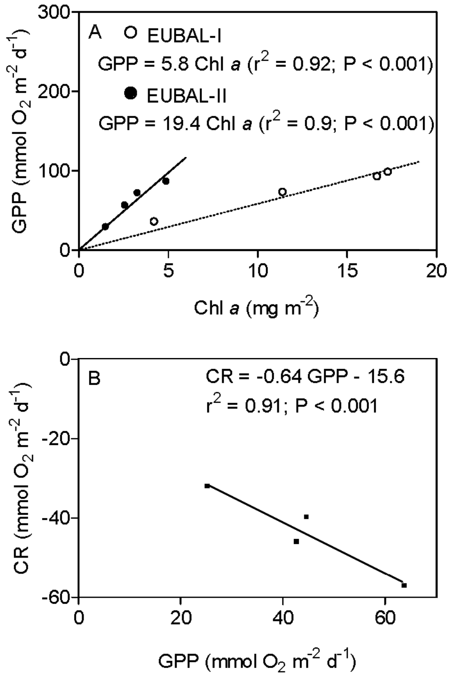


Fig. 6. **(a)** Linear relationships between integrated gross primary production (GPP) and integrated chlorophyll *a* concentrations (Chl *a*) at four stations (cf. Fig. 1) during EUBAL-I and II cruises. **(b)** Linear relationship between GPP and respiration (CR) integrated in the water column above the *Posidonia oceanica* meadow at four stations during the EUBAL-II cruise.

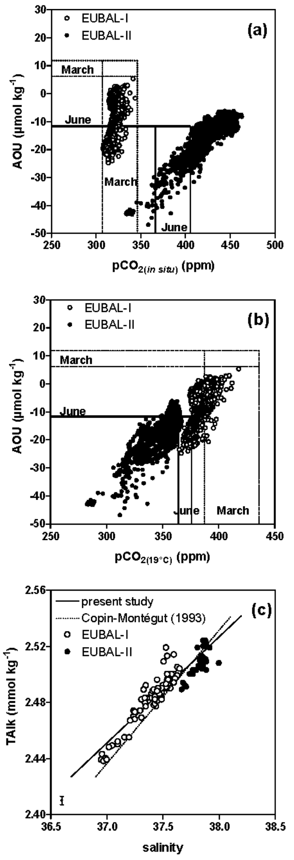


Fig. 7. **(a)** AOU (μmol kg^{-1}) versus $pCO_{2(insitu)}$ (ppm) and **(b)** AOU (μmol kg^{-1}) versus pCO_2 normalized to a constant temperature ($pCO_{2(19^\circ C)}$, ppm) in surface waters from all the surveys during the EUBAL-I and II cruises. The range of variation of AOU and $pCO_{2(19^\circ C)}$ at the Dyfamed station for the March 1998-99 and June 1998-99 periods (Copin-Montégut and Bégovic 2002; Bégovic and Copin-Montégut 2002) are indicated by the horizontal and vertical lines. **(c)** TA (mmol kg^{-1}) versus salinity in surface waters during the EUBAL-I and II cruises. Dotted line corresponds to the regression function reported by Copin-Montégut (1993) for the Alboran Sea (TA=−1.072 (±0.016)+0.09485 (±0.0004)×salinity) and the solid line corresponds to the regression function based on the EUBAL-I and II cruises (TA=−0.346 (±0.007)+0.0756 (±0.003)×salinity; r^2=0.869; n=119; $p<0.0001$). The error bar on the lower left corner of the plot corresponds to the estimated accuracy on TA measurements (b).

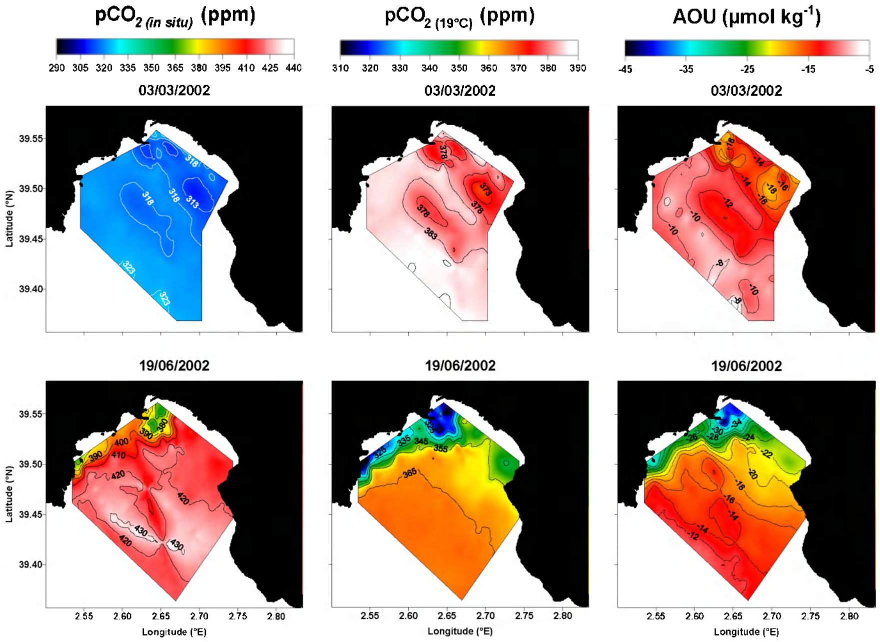


Fig. 8. Surface distributions of pCO$_{2(insitu)}$ (ppm), pCO$_2$ normalized to a constant temperature (pCO$_{2(19°C)}$, ppm) and AOU (μmol kg^{-1}) obtained on 3 March 2002 (EUBAL-I cruise) and 19 June 2002 (EUBAL-II cruise).

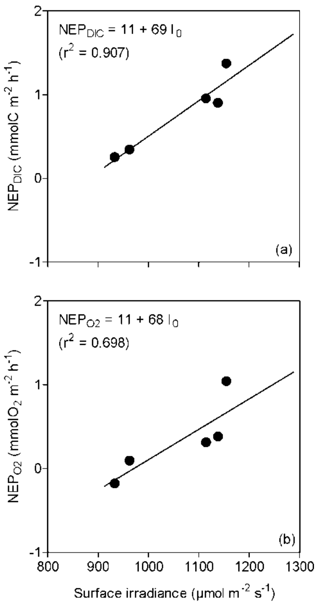


Fig. 9. NEP_{DIC} (A; mmol C m^{-2} h^{-1}) and NEP_{O_2} (B; mmol O$_2$ m^{-2} h^{-1}) over the *Posidonia oceanica* meadow versus surface irradiance (I$_0$; μmol m^{-2} s^{-1}) during the EUBAL-II cruise. NEP_{DIC} and NEP_{O_2} data were adjusted linearly to 12:00 Universal Time (UT; all surveys ended in mid-afternoon, ranging from 14:30 to 16:45 UT). Surface irradiance was averaged from dawn to 12:00 UT.

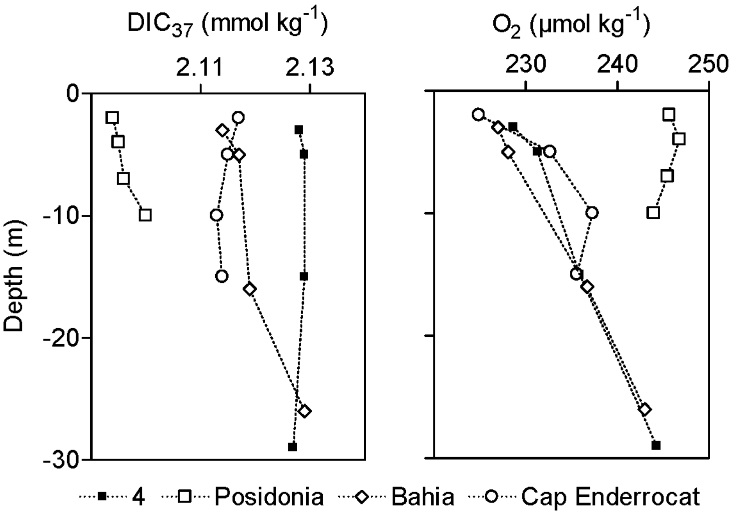


Fig. 10. Vertical profiles of *DIC* normalized to a constant salinity (DIC_{37} in mmol kg^{-1}) and O_2 (μmol kg^{-1}) at four reference stations (cf. Fig. 1).

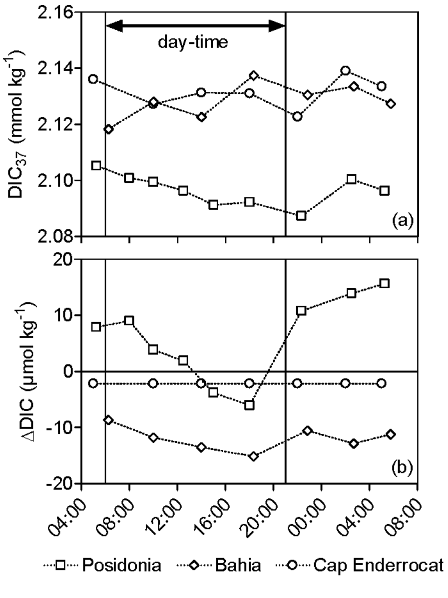


Fig. 11. (a) Variations of water column averaged *DIC* normalized to a constant salinity (DIC_{37} in mmol kg^{-1}) during 24 h at Posidonia (20–21 June), Bahia (22–23 June) and Cap Enderrocat (24–25 June; cf. Fig. 1). **(b)** Variations during the 24 h cycles of the difference of *DIC* (ΔDIC in μmol kg^{-1}) between the average value from the top half of the water column and the average value from the bottom half of the water column. *DIC* was computed from the pCO_2 measurements (vertical resolution of 1 m), TA values computed from the linear regression against salinity (legend of Fig. 7) and salinity and temperature profiles from CTD casts contemporary to the pCO_2 profiles. Time is in UT.