B. Delille · D. Delille · M. Fiala · C. Prevost
M. Frankignoulle

Seasonal changes of pCO₂ over a subantarctic Macrocystis kelp bed

Abstract The partial pressure of carbon dioxide (pCO₂), calculated from pH and total alkalinity measurements, was monitored together with chlorophyll a and bacterioplankton biomass in shallow coastal water located inside and outside a giant kelp bed (Macrocystis pyrifera) situated in the Kerguelen Archipelago, Southern Ocean. In spite of large changes over a short time-scale, pCO₂ variations over the year are large and exhibit a seasonal pattern in which the different stages of the annual biological turnover are well marked. The overall pattern of pCO₂ variations is related to biological activity (development of both photosynthesis and respiration) during almost the whole year. However, physical and thermodynamical constraints exert a strong influence on pCO₂ at meso time-scale (10 days) and/or when biological activity is weak. Macrocystis acts to maintain pCO₂ below saturation almost the whole year and large undersaturations (pCO₂ as low as 20 µatm) were observed within the kelp bed. Furthermore, primary production of Macrocystis covers a period of 8 ~ 9 months a year from winter to late summer and the kelp bed seems to favour the spring phytoplanktonic bloom. The buffer factor β indicates that, outside the kelp bed, inorganic carbon dynamics are mainly influenced by air-sea exchange and photosynthesis without calcification. Inside the kelp bed, β suggests calcification by the epiphytic community.

Introduction

In coastal areas, many factors play a role in the changes of pCO₂. As in the open ocean, warming and cooling of surface water, wax and wane of plankton blooms, wind velocity and lateral advection all influence pCO₂, but other complex processes, such as exchanges with the shallow sediment, outflows of fresh water, tidal mixing and coastal upwellings may strongly affect the carbon budget of the water column (Wollast 1991; Bakker et al. 1996; Frankignoulle et al. 1996a, 1996b; Borges and Frankignoulle 1999). The role of shelf seas in global cycling is indeed still poorly understood (Inoue and Sugimura 1988; Kempe and Pegler 1991; Wollast 1991; Bakker et al. 1996; Frankignoulle et al. 1996a, 1996b; Gattuso et al. 1998; Wollast 1998; Borges and Frankignoulle 1999).

Because of its inaccessibility, the Southern Ocean is the least documented ocean (Metzl et al. 1995; Bakker et al. 1997). With the exception of the works of Metzl et al. (1991), Poisson et al. (1993) and Louanchi et al. (1999), which gave observations above the Kerguelen Plateau, previous studies of pCO₂ in the Southern Ocean did not investigate subantarctic coastal areas. Recently Delille et al. (1997) carried out measurements of pCO₂ and related parameters over diel cycles inside and outside a kelp bed in the Kerguelen Archipelago. However, there is no other study about dissolved CO₂ in the coastal areas of the Subantarctic Zone (SAZ) and Polar Frontal Zone (PFZ).

A substantial proportion of these coastlines is occupied by highly productive giant kelp bed, Macrocystis pyrifera. This marine macroalga is one of the largest and grows up to 50 m in length, forming undersea forests in hard-bottom subtidal areas of subantarctic islands (Sfriso et al. 1987; Lavery and McComb 1991; Hanisak 1993). Macroalgae have a great potential for biomass production and CO₂ uptake (Smith 1981; Wilcox and North 1988; Gao and McKinley 1994). Smith (1981) pointed out that the coastal marine macrophytes

B. Delille (✉) · M. Frankignoulle
Unité d’Océanographie Chimique, Mécanique des Fluides Géophysiques, Institut de Physique, Bât B5, Université de Liège, 4000 Sart Tilman, Belgium
E-mail: Bruno.Delille@ulg.ac.be
Fax: +32-4-3662355

D. Delille · M. Fiala · C. Prevost
Observatoire Océanologique de Banyuls, Université P., et M. Curie, U.M.R./C.N.R.S. 7621, 66650 Banyuls sur mer, France
ecosystems, including both macroalgae and seagrasses, occupy only about 2 × 10⁶ km² but could act as an effective carbon sink because of their biomass (estimated to be about two-thirds of oceanic plant biomass) and relatively high turnover time (about 1 year) compared to phytoplankton (about 1 week). However, with the exception of works of Frankignoulle and Distèche (1984, 1987) and Frankignoulle and Bouquegneau (1987, 1990), little is known about the influence of macrophytes on pCO₂ and their quantitative significance in the global carbon (Gattuso et al. 1998). Moreover, productivity of Macrocystis is high and ranges from 1000 to 1300 g C m⁻² year⁻¹ (Mann 1982; Wheeler and Druel 1986) but Jackson (1977) also measured productivity up to 3400 g C m⁻² year⁻¹ off southern California. Kelps act to reduce currents within the kelp bed and decrease exchanges with surrounding waters (Jackson and Winant 1983). The authors noticed that residence time of water within the kelp bed may be long compared to some biological processes like nitrate uptake by the kelp, phytoplankton doubling and some larval development time. They also pointed out that such reduced currents would allow nutrients to recycle internally and plankton populations to exist solely within. However, in contrast to the numerous studies on the biology and primary productivity of polar microalgae, high-latitude macroalgae have been little studied, although dense populations of highly productive seaweeds are known from the Southern Ocean (Dunton and Dayton 1995).

The purpose of this paper is to examine the seasonal changes of pCO₂ both outside and inside a M. pyrifera giant kelp bed, in order to understand the role of physico-chemical and biological processes with regard to pCO₂ within shallow water of the Kerguelen Archipelago, and the influence of Macrocystis kelp bed on pCO₂. The present study was undertaken as a part of a program designed to elucidate the annual pattern of pCO₂ in the coastal area of the northern part of the Southern Ocean, as well as the role played by the Macrocystis kelp bed with regard to atmospheric pCO₂.

**Materials and methods**

**Sampling**

Measurements were carried out from December 1995 to December 1997 in Morbihan Bay (Fig. 1), Kerguelen Archipelago, Southern Ocean (Indian sector). Usually, the Kerguelen Archipelago is cited in the literature as a subantarctic island (Belkin and Gordon 1996; Delille et al. 1997; Razouls et al. 1997). However, from a strict oceanographic point of view, this archipelago is situated either in the PFZ or in the Antarctic Zone, depending on the position of the Polar Front with regard to the island. One should note that this latter position is still a matter of debate (Belkin and Gordon 1996; Park and Gambéron 1997). Located in the southeast of the archipelago, Morbihan Bay (about 600 km²) opens to the ocean through the Royal Pass, which is 12 km wide and 40 m deep. The bay is always free of ice. Satellite data processing has permitted estimation of the biomass (wet weight) of *M. pyrifera* at about 1100 kt, spread over an area of about 190 km² in the Morbihan Gulf in 1988 (Belcher and Mouchot 1992). Samples were collected in the vicinity of the base of “Port Aux Français” in Echouage Cove («400 × 300 m), which is open to dominant winds. Coastlines of the cove are partly surrounded by a *M. pyrifera* kelp bed. Two sampling sites were chosen, one inside and one outside the kelp bed. Both sites were sampled every 10 days, at the same time of the day (between 1.45 p.m. and 2.15 p.m.) in order to reduce the influence of diel cycles. Samples were taken from the surface from the same water mass, and attention was paid to avoid degassing. Analyses were begun in the base laboratory within 30 min after sample collection.

Salinity was determined with a Guildline induction salinometer whose accuracy was 0.003 on the practical salinity scale. Solar radiation and wind velocity measurements were provided by Météo-France.

**Inorganic carbon**

The inorganic carbon speciation was calculated from pH and total alkalinity (TAik) measurements. TAlk was measured using the classical Gran electrometric method on 100-mG F/F filtered samples. The accuracy of measurements was 4 µeq kg⁻¹. pH was measured using commercial combination electrodes (Ross type, Orion), calibrated according to the NBS scale. The accuracy of pH measurements was ± 0.01 pH units. CO₂ speciation was calculated using the CO2SYS Package (Lewis and Wallace 1998), the CO₂-acidity constants of Mehrbach et al. (1973) refitted by Dickson and Millero (1987), the CO₂ solubility coefficient of Weiss (1974), the borate acidity constant of Dickson (1990a) and the SO₄⁻ dissolution constant of Dickson (1990b). The total borate molality was calculated using the Uppström (1974) ratio to chlorinity. As silicates and phosphates concentrations were available in 1996 and partially in 1997, they were included in the calculations. Taking into account uncertainties of pH, TAlk, temperature, salinity, silicate and phosphate concentrations, the errors in pCO₂ and DIC were 14 µatm and 9 µmole kg⁻¹, respectively.

**Bacterial abundance**

Bacterial abundance was determined by acridine orange direct counts (AODC) (Hobbie et al. 1977). A minimum of 300 fluorescing cells with a clear outline and definite cell shape were counted as bacterial cells in 10 random microscope fields.

**Chlorophyll**

Phytoplankton was studied using chlorophyll a concentration. All samples were prefiltred through a 200-µm mesh to remove detritic