Influence of giant kelp beds (*Macrocystis pyrifera)* on diel cycles of pCO_2 and DIC in the Sub-Antarctic coastal area.

B. DELILLE[1,2*], A.V. BORGES[1] and D. DELILLE[2]

[1] Unité d'Océanographie Chimique, MARE, Université de Liège, Allée du 6 août, 17, 4000 Liège, Belgium

[2] Presently at Département de Géologie et Océanographie, Environnements et Paléoenvironnements Océaniques, Université de Bordeaux 1, Avenue des Facultés, F-33405 Talence, France

[3] Observatoire Océanologique de Banyuls, Université P. et M. Curie, U.M.R./C.N.R.S. 7621, 66650 Banyuls sur mer, France

* Corresponding author: Bruno.Delille@ulg.ac.be, ph: +32 4 366 31 87, fax: +32 4 366 36 67

Abstract

The partial pressure of CO_2 (pCO_2) and dissolved inorganic carbon (DIC) were monitored in shallow coastal waters located inside and outside giant kelp beds (*Macrocystis pyrifera*) located in the Kerguelen Archipelago (Southern Ocean). Photosynthesis and respiration by microplankton and kelp lead to marked pCO_2 and DIC diel cycles. Daily variations of pCO_2 and DIC are significant in the spring and summer, but absent in the winter, reflecting the seasonal cycle of biological activity in the kelp beds. If the kelp beds seem to favour the onset of phytoplankton blooms, most of the primary production inside the kelp beds is due to the kelp itself. The primary production of *Macrocystis* kelp beds in the Sub-Antarctic high-nutrient, low-chlorophyll (HNLC) waters off the Kerguelen Archipelago is elevated and closely linked to light availability. This production is significant from October to March and reaches its climax in December at the solar radiation maximum.

Keywords: Primary production, Carbon dioxide, Kelp, Antarctic zone, Kerguelen, *Macrocyctis pyrifera*, 49° 27'S- 70° 03'E.

1. Introduction

Marine macrophytes (seagrasses and macroalgae) can be found in any shallow coastal aquatic system. They cover only 2 x 10^6 km^2 worldwide (Whittaker and Likens, 1973), but can act as an effective carbon sink because of their large biomass (estimated to be about two-thirds of oceanic plant biomass) and relatively

long turnover time (1 year) as compared to phytoplankton (1 week) (Smith, 1981). It has been pointed out that macrophytes have a great potential for biomass production and CO_2 uptake in a global context (Smith, 1981; Wilcox and North, 1988; Gao and McKinley, 1994; Duarte and Chiscano, 1999; Duarte et al., 2004). Nevertheless, little is known about the influence of macrophytes on dissolved inorganic carbon (DIC) dynamics, and their quantitative significance in the global carbon and CO_2 cycles remains poorly constrained (Gattuso et al., 1998; Duarte et al., 2004; Borges, 2005; Borges et al., 2005).

Frankignoulle and Distèche (1984, 1987) and Frankignoulle and Bouquegneau (1987, 1990) studied the impact of *Posidonia oceanica* seagrass meadows on the partial pressure of CO_2 (pCO_2) and the DIC dynamics in the Mediterranean Sea. The *Posidonia* meadows exert a strong influence on the pCO_2 of the surrounding waters, driving a diel signal of pCO_2 consistent with the solar radiation cycle. The diel and seasonal variations of the carbon budget show two yearly phases, with spring and summer photosynthesis resulting in a decrease of CO_2 and the winter decay of organic matter resulting in the release of CO_2. In the Bay of Palma (Spain), strong decreases in pCO_2 over *Posidonia* meadows have been reported due to the meadows' higher primary productivity compared to the surrounding oligotrophic waters (Gazeau et al., 2005). In the same area, Barrón et al. (2006) highlighted the strong influence of calcification by epiphythes and calcium carbonate ($CaCO_3$) dissolution on CO_2 dynamics in *Posidonia* meadows, which is in agreement with observations of other seagrass ecosystems (Morse et al., 1987; Ku et al., 1999; Delille et al., 2000; Burdige and Zimmerman, 2002; Yates and Halley, 2003; Yates and Halley, 2006). On the whole, *Posidonia oceanica* seagrass meadows appear to act as a sink for atmospheric CO_2. In the waters surrounding the Kerguelen Archipelago, it has been previously reported that the DIC and pCO_2 of the

waters above *Macrocystis* kelp beds are strongly influenced by the biological activity of the kelp, which, in turn, leads to a potential sink for atmospheric CO_2 (Delille et al., 1997; Delille et al., 2000).

The primary production in *Macrocystis* kelp beds is high and generally ranges from 1000 to 1300 gC m^{-2} y^{-1} (Mann, 1982; Wheeler and Druehl, 1986). Jackson (1977) measured primary production of up to 3400 gC m^{-2} y^{-1} off of southern California. Surveying DIC over macrophyte beds allows us to assess the net ecosystem production by mass balance (Gazeau et al., 2005). This is of particular interest in polar areas and particularly in the Southern Ocean, where dense population of highly productive macroalgae are present. This production, however, has seldom been estimated (Dunton and Dayton, 1995).

The purpose of the present paper is to examine the diel changes of pCO_2 and DIC both outside and inside a *Macrocystis pyrifera* giant kelp bed within the shallow waters of the Kerguelen Archipelago in order to understand the physical and biological processes controlling pCO_2 dynamics and to follow the seasonal evolution of kelp bed primary production.

2. Material and Methods

Sites and sampling. The Kerguelen Archipelago (Fig. 1) is usually cited in the literature as a Sub-Antarctic island. From a strictly oceanographic point of view, this archipelago is situated either in the Polar Frontal Zone (Sub-Antarctica) or Permanently Open Ocean Zone (Antarctica) depending on the position of the Polar Front with regards to the archipelago (e.g. Delille et al. 2000). A substantial portion of the coastlines of the archipelago is occupied by *Macrocystis pyrifera* kelp beds.

Samples were collected from January to December 1996 at the vicinity of the Cimetière Island in Morbihan Bay (MB), and in Brise-Lame Bay (BB) in the northern

part of the Kerguelen archipelago. 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 biomass (wet weight) of *Macrocystis pyrifera* in Morbihan Bay was assessed using remote sensing data as about 1100 kt, spread over an area of about 190 km² (Belsher and Mouchot, 1992). The average biomass within two-thirds of the area covered by *Macrocystis* kelp beds is 22.5 kg m^{-2} and can reach up to 26 kg m^{-2}. Brise-Lame Bay has a surface area of about 12 km² and is widely open. However, sampling sites were chosen in the most sheltered part of the bay that is surrounded by *Macrocystis pyrifera* kelp beds.

Two sampling stations were chosen at each site, one located inside and one outside the kelp beds. Surface waters were sampled at both stations every third hour for 24 hours starting from 21:00. Analyses began aboard the *R.V. La Curieuse* within 15 minutes of the sample collection. Diel surveys were numbered chronologically. As BB and MB denote, respectively, diel surveys were carried out in Brise-Lame Bay and at the Cimetière Island in Morbihan Bay.

Dissolved inorganic carbon. Inorganic carbon speciation was calculated from pH and total alkalinity (TA) measurements. TA was measured using the classical Gran electrotitration method on 100 ml GF/F filtered samples. The accuracy of measurements was ±4 μeq kg^{-1}. pH was measured using a commercial combination electrode (Ross type, Orion®) calibrated on the U.S. National Bureau of Standards (NBS) scale. The precision of pH measurements was ±0.01 pH units. CO_2 speciation was calculated with the CO2SYS Package (Pelletier et al., 1998), using the CO_2 acidity constants of Mehrbach et al. (1973) refitted by Dickson and Millero (1987), the CO_2 solubility coefficient of Weiss (1974), and the borate acidity constant of Dickson (1990). The total borate molality was calculated using the Uppström (1974) ratio to

salinity. Taking into account uncertainties for the pH, TA, temperature, and salinity, the errors in pCO_2 and DIC were ±14 µatm and ±9 µmol kg^{-1}, respectively. DIC was normalized to a constant salinity of 33.4, denoted as DIC_n. Normalized pCO_2 ($pCO_{2\,n}$) was computed at a constant temperature of 5°C based on normalized TA and DIC data at a constant salinity of 33.4.

Chlorophyll a (chl *a*)*.* Samples were pre-filtered through a 200 µm mesh to remove detritic material and larger biota, and then filtered by gentle vacuum filtration of 1 L of seawater through a Whatman® GF/F glass-fibber filter. The measurements of chlorophyll a were performed with a Perkin-Elmer® MPF 66 spectrofluorometer using the spectrofluorometric method developed by Neveux and Panouse (1987).

Related parameters. Salinity was determined with a Guildline® induction salinometer with a precision of 0.003 on the practical salinity scale. Solar radiation measurements were provided by MétéoFrance from a station located at Port aux Français (Morbihan Bay).

3. Results

Sea surface temperature (SST) ranged from 1.6°C in austral winter (from June to August) to 8.4°C in the summer (from December to March) inside the kelp bed. In the winter, the diel temperature changes were small compared to the summer. On repeated occasions (MB3, MB8, BB1 and BB5), the diel cycle of SST is more marked inside the kelp beds than outside the beds (Fig. 3), with a strong increase in SST during the day and a rapid decrease at dusk. SST was significantly higher inside the kelp bed as compared to outside the bed during the summer.

Two phytoplanktonic blooms occurred in September and December, while chl *a* was low from February to August. Chl *a* concentration was larger inside the kelp beds than outside in September. Diurnal changes in the chl *a* concentration (Fig. 4) were on some occasions large (up to 3.0 $\mu g\ L^{-1}$), but they did not exhibit clear or recurrent patterns.

The pCO_2 ranged from 170 μatm to 520 μatm outside the kelp beds, and from 80 μatm to 530 μatm inside the kelp beds in MB and BB (Fig. 2). Seasonal changes were similar at both sites in MB and LB. Values were below atmospheric equilibrium in the summer (January) and then increased from February to April. CO_2 over-saturation appeared in February outside the kelp beds and in March inside the kelp beds.

After a maximum in April, the pCO_2 decreased until July, and reached values close to atmospheric equilibrium during the winter. The decrease of pCO_2 during spring and subsequent CO_2 under-saturation began earlier and was more marked inside the kelp beds (August) than outside (September). Outside the kelp beds, the pCO_2 tended to increase during early November, while the pCO_2 continued to decrease inside the kelp beds to reach the lowest values by the end of December.

The magnitude of diel variations in $pCO_{2\,n}$ were on some occasions high, reaching 180 μatm outside the kelp beds, and 270 μatm inside the beds (Fig. 5). From August to February, the pCO_{2n} outside the kelp beds tended to reach minimum values between 12:00 and 18:00. However, recurrent diel cycles were hardly distinguishable, especially during the winter. In contrast, diel cycles inside the kelp beds exhibited a clear pattern from November to April, with a strong increase in the pCO_{2n} from 18:00 to 00:00 that rapidly led to the highest values between 00:00 and 06:00. The $pCO_{2\,n}$ started to decrease and reached its lowest values between 12:00

and 18:00. From May to July, no clear trends were observed in the diel changes of pCO_{2n}.

In accordance with the pCO_2, the DIC_n exhibited marked seasonal changes ranging from 2.03 mmol kg^{-1} to 2.13 mmol kg^{-1} outside the kelp beds, while values as low as 1.79 mmol kg^{-1} were observed inside the beds (Fig. 2). The DIC_n increased in late summer to reach a maximum in May, and decreased slightly until late August, when a sharp decrease in the DIC_n was observed. The DIC_n began to increase outside the kelp beds in November in parallel with the $pCO_{2\,n}$, whereas the DIC_n decreased inside the kelp beds until January.

While no obvious recurrent pattern was apparent outside the kelp beds, the DIC_n exhibited a clear diel cycle from November to April inside the beds (Fig. 6). The DIC_n increased steadily at night, reaching a maximum between 03:00 and 09:00. Then, the DIC_n decreased during the day, reaching its lowest values between 12:00 and 18:00. During the winter, the diel changes in the DIC_n were weak and did not show any obvious pattern, with the exception of the MB 7 cycle that exhibited a large decrease at 03:00 and a sharp increase at 18:00.

4. Discussion

Seasonal variations

The overall seasonal changes in the SST, pCO_2 and DIC_n outside the kelp beds in BB and MB are consistent with those reported in the Port aux Français station based on weekly monitoring carried out the same year by Delille et al. (2000) (Fig. 2). This suggests that the drivers of the seasonal variations in the pCO_2 and DIC_n are similar for all these sites. Planktonic photosynthesis during the spring and summer is

responsible for the marked decreases in both the DIC_n and pCO_2, while the autumnal decay of organic matter is responsible of the sharp increase in these two measures, leading to a strong CO_2 over-saturation.

In the winter, cooling leads to a steady decrease in the pCO_2, while air-sea exchanges enhanced by strong winds maintain values close to atmospheric equilibrium. In November and December, the pCO_2 increases outside the kelp beds, while remaining constant inside the bed due to primary production by macroalgae and enhanced planktonic primary production (Delille et al., 2000).

Kelp beds can affect phytoplankton abundance in several ways: reducing light availability (shadowing) or increasing it by reducing turbulence, decreasing (Delille et al. 1997, 2000) or increasing (Pakhomov et al. 2002) nutrient availability, or increasing grazing pressure (Field et al. 1980, Pakhmov et al. 2002). The large difference in chl *a* concentrations outside versus inside the kelp beds during the MB7 cycle might indicate that the kelp bed enhances phytoplankton growth (Fig. 4). This is consistent with the early onset of the spring phytoplanktonic bloom inside the kelp bed. However, in the Sub-Antarctic Prince Edwards Archipelago, Pakhomov et al. (2002) reported that kelp beds have little influence on chl *a* concentration, while Field et al. (1980) reported lower chl *a* concentrations within kelp beds in South Africa. Reconciling these contrasting results requires a robust assessment of phytoplankton abundance by cellular counts (chl *a* concentration as a tracer of phytoplankton abundance can be biased by material of macrophyte origin) and measurement of primary production.

Diel variations

The amplitude of the daily changes in the $pCO_{2\,n}$ and DIC_n are consistent with

previous observations in the Kerguelen Archipelago (Delille et al., 1997) but higher than those above the *Posidonia oceanica* meadows (Frankignoulle and Distèche, 1984; Frankignoulle and Bouquegneau, 1987, 1990). From spring to autumn, intense CO_2 uptake starts generally at dawn and reaches a maximum, on average, three hours before dusk. In some occasions, we observed a rapid increase at dusk followed by a plateau throughout the night (MB1, MB8, BB2), when the expected effect from respiration on $pCO_{2\,n}$ and DIC_n would be a steady increase from dusk to dawn. This could be explained by the fact that, during the daytime, the kelp bed reduces currents and wind stress, and acts as a black body at the surface, promoting an increase in SST (e.g. BB 5 cycle on figure 3) and, potentially, promoting the stratification of the near-surface water column. This would explain why SST can be 1.0°C higher inside the kelp beds as compared to outside the beds during daytime. At dusk, as the temperature drops, a rapid destratification of the near-surface water column would lead to a significant and rapid increase in the $pCO_{2\,n}$ and DIC_n.

DIC uptake by the Macrocystis

Even if kelp beds favour the onset of the spring phytoplankton bloom, the large diel changes in $pCO_{2\,n}$ and DIC_n are most likely related to macroalgae primary production. The high chl *a* concentrations are only observed between November and January, whereas the large diel cycles of $pCO_{2\,n}$ and DIC_n within the *Macrocystis* kelp beds are conspicuous from September to March (Fig. 2). Furthermore, chl *a* concentrations are similar inside and outside the kelp beds, except in September. Even if *Macrocystis* kelp beds reduce currents and decrease turbulence (Jackson and Winant, 1983), this positive effect on planktonic primary production is probably counteracted by the lower availability of light, competition for nutrients with the

macroalgae (Delille et al 1997, 2000), and higher grazing pressure (Pakhomov et al. 2002). To our knowledge, no study exists which addresses the effect of kelp beds on pelagic primary production. We therefore made the simple assumption that planktonic production is similar inside and outside the kelp bed, and correlates linearly with the chl *a* concentration.

In order to follow the seasonal changes in primary production of the kelp bed community, we roughly assessed the DIC uptake by the kelp bed community (DIC_{kelp}) from the amplitude of the daytime DIC_n decrease and removed the planktonic daytime DIC uptake according to the following formula:

$$\Delta DIC_{kelp} = \Delta DIC_{n\,inside} - \Delta DIC_{n\,outside} \times \frac{chl\,a_{inside}}{chl\,a_{outside}} \quad (1)$$

ΔDIC_{inside} and $\Delta DIC_{outside}$ are the amplitude of the daytime DIC_n decrease inside and outside the kelp bed, respectively. Cha_{inside} and $Cha_{outside}$ are the mean chl *a* concentrations inside and outside the kelp bed, respectively.

This approach is prone to several errors. We made the assumption that primary productivity is similar inside and outside the kelp bed. Planktonic production, which corresponds to the last term in the equation above, accounts for typically less than 20 percent of the overall DIC uptake. Any potential bias resulting from our assumption is therefore not significant in the assessment of ΔDIC_{kelp}. The air-sea exchange of CO_2 was not considered in the calculation due to the difficulty of estimating the gas transfer velocity above a *Macrocystis* kelp bed. The dense canopy of the *Macrocystis* kelp bed covers a substantial portion of the air-sea interface, which prevents air-sea gas exchanges. Furthermore, the dense canopy of *Macrocystis* kelp beds conspicuously dampens waves and the effect of wind stress on the air-sea interface. *Macrocystis* also produce large amounts of biofilms that impede air-sea exchange. These effects are likely to decrease air-sea CO_2

exchanges drastically. We assumed that the air-sea CO_2 exchange is negligible compared to the changes of CO_2 due to biological activity.

Significant advection at the daily scale of waters surrounding the kelp beds can also affect DIC. However, it has been repeatedly reported that *Macrocystis* kelp beds reduce water currents and exchanges with surrounding waters (Jackson and Winant, 1983; Pakhomov et al., 2002) and that the residence time of water within the kelp beds can reach several days (Jackson and Winant, 1983). Accordingly, the higher chl *a* concentrations inside the kelp beds observed during the MB7 cycle suggest that the residence time in the studied kelp beds is at least as long as the time needed for phytoplankton doubling.

Keeping in mind the potential biases mentioned above, it is possible, by integrating ΔDIC_{kelp} over the depth of the water column, to derive the “maximum net kelp community production” during the day. Maximum net kelp community production integrates primary production and the respiration of non-planktonic organisms (mainly the kelp and epiphyte communities) during daytime, when gross primary production outweighs community respiration. This leads to positive and elevated values of production. The assessment of the net primary production requires the computation of community respiration at night. However, the night de-stratification process prevents a robust computation of the respiration. Unfortunately, maximum net kelp community production is not readily comparable with conventional measurements which provide either net or gross primary production. Nevertheless, the assessment of ΔDIC_{kelp} allows us to consistently follow the seasonal changes of the primary production of the kelp.

During the winter, ΔDIC_{kelp} decreases in parallel with the decrease of solar radiation (Fig. 7). In the autumn and winter, when solar radiation is below the threshold of 10 MJ m^{-2} d^{-1}, the ΔDIC_{kelp} is undetectable In September, the ΔDIC_{kelp} increases sharply

together with solar radiation, reaching a maximum in December at the time when solar radiation is at its maximum. On the whole, significant CO_2 consumption and related primary production occur from September to March when solar radiation is above the threshold of 10 MJ m^{-2} d^{-1}.

By integrating ΔDIC_{kelp} over the depth of the water column (5 m), we derived an assessment of the maximum net kelp community production of *Macrocystis* kelp beds around 15 gC m^{-2} d^{-1} (ΔDIC_{kelp}= 250 µmol kg^{-1}, MB9 cycle) when solar radiation is at its maximum. This is higher than the gross primary production of the *Macrocystis pyrifera* kelp bed in California, which ranges from 3 to 12 gC m^{-2} d^{-1} (Mc Farland and Prescott 1959: Towle and Pearse 1973; Jackson 1987). This difference appears even more significant if we take into account that gross primary production is higher that maximum net kelp community production as it integrates both gross primary production and community respiration.

Karl et al. (2003) showed that poor time resolution surveys can significantly underestimate pelagic primary production. This should hold true for macroalgae production, since light and nutrient availability changes on a day-to-day basis. By integrating a total of 11 diel cycles, we captured the production of the kelp with a better time resolution than previous studies did (Mc Farland and Prescott 1959: Towle and Pearse 1973; Jackson 1987). This can explain why we observed higher production in the Kerguelen Archipelago compare to the California coast. In another way, primary production of *Macrocystis* kelp beds can be enhanced in the Sub-Antarctic area as compared to the California coast. Indeed, net production of *Macrocystis laevis* Hay in the Prince Edward Islands derived from growth measurements was estimated to be 7.7 gC m^{-2} d^{-1} and 11.5 gC m^{-2} d^{-1} during the months of April and August (Attwood et al. 1990). These measurements were carried out while the production of the kelp was dampened by low light availability so that

these values are at the lower end of the annual range of net production. Hence, the net primary production is potentially significantly higher in the summer, and gross primary production of *Macrocystis* in the Prince Edward appears to be significantly higher than the measurements reported in California.

5. Conclusion

Nitrate concentrations in Morbihan Bay can exceed 20 µg L^{-1} and this nutrient is only briefly exhausted in the spring (Delille et al., 2000). Hence, the main limiting factor for *Macrocystis* growth in the HNLC waters of the Kerguelen Archipelago appears to be light availability rather than macronutrient availability, as suggested by the close link between primary production and light availability we report here. This is also in agreement with the model output of Jackson (1987) regarding Californian kelp beds.

Estimates of production by the *Macrosystis* kelp bed are above the range from 0.01 gC m^{-2} d^{-1} to 5.0 gC m^{-2} d^{-1} of the average maximum above-ground production of 29 marine seagrass species reported by Duarte and Chiscano (1999) and in the upper end of the range of the benthic net production compiled by Charpy-Roubaud and Sournia (1990) and Gazeau et al. (2004). These comparisons should be taken with caution due to the potential biases because of the difference in the experimental approaches. Nevertheless, this highlights the significance of primary production by *Macrocystis* kelp beds, particularly in high-nutrient, low-chlorophyll (HNLC) Sub-Antarctic regions of the Southern Ocean.

Macrocystis kelp beds would therefore act as effective sinks for atmospheric CO_2 by drastically decreasing DIC. However, related air-sea CO_2 transfer occurs outside the kelp bed when surface waters flow outward, rather than within the kelp bed where the dense canopy dampens gas fluxes across the air-sea interface. A rigorous

assessment of CO_2 fluxes driven by *Macrocystis* kelp beds would therefore require an extended pCO_2 survey of the surrounding waters coupled with an assessment of water mass advection.

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Figure captions

Figure 1. Brise-Lame Bay and Morbihan Bay in the Kerguelen Archipelago. The sampling sites are indicated by stars.

Figure 2. Mean and amplitude of diel changes in the temperature (SST), chlorophyll *a* (chl *a*), partial pressure of CO_2 (pCO_2) and dissolved inorganic carbon normalized to a constant salinity of 33.4 (DIC_n). The vertical bars indicate the range of diel change (maximum and minimum values). The average values from the diel cycle inside and outside kelp beds are represented as follows: circles - Morbihan Bay (MB), squares - Brise-Lame Bay (BB). Due to logistical constraints, MB measurements were not carried out during the autumn, while BB measurements were carried out mostly during the summer and autumn. The average values from both sites were merged into a composite annual cycle indicated by the long dashed line in order to cover one annual cycle satisfactorily. The dotted line is the annual cycle at the Port aux Français station from Delille et al. (2000). The horizontal dotted line represents the atmospheric pCO_2 at Amsterdam Island (361 µatm, V. Kazan, personal communication).

Figure 3. Diel changes in the sea surface temperature (SST) in Morbihan Bay (MB) and Brise-Lame Bay (BB) inside and outside the kelp beds. Daytime is indicated in grey on the lines.

Figure 4. Diel changes of chlorophyll a (chl *a*) in Morbihan Bay (MB) and Brise-Lame Bay (BB) inside and outside kelp beds. Daytime is indicated in grey on the lines.

Figure 5. Diel changes in the partial pressure of CO_2 normalised to a constant temperature of 5°C and salinity of 33.4 ($pCO_{2\,n}$) in Morbihan Bay (MB) and Brise-Lame Bay (BB) inside and outside the kelp beds. Daytime is indicated in grey on the lines.

Figure 6. Diel changes in the normalized DIC at a constant salinity of 33.4 (DIC_n) in Morbihan Bay (MB) and Brise-Lame Bay (BB) inside and outside the kelp beds. Daytime is indicated in grey on the lines.

Figure 7. Seasonal variations in solar radiation in Morbihan Bay and ΔDIC_{kelp} in Morbihan Bay (circles) and Brise-Lame Bay (squares).

Fig. 1

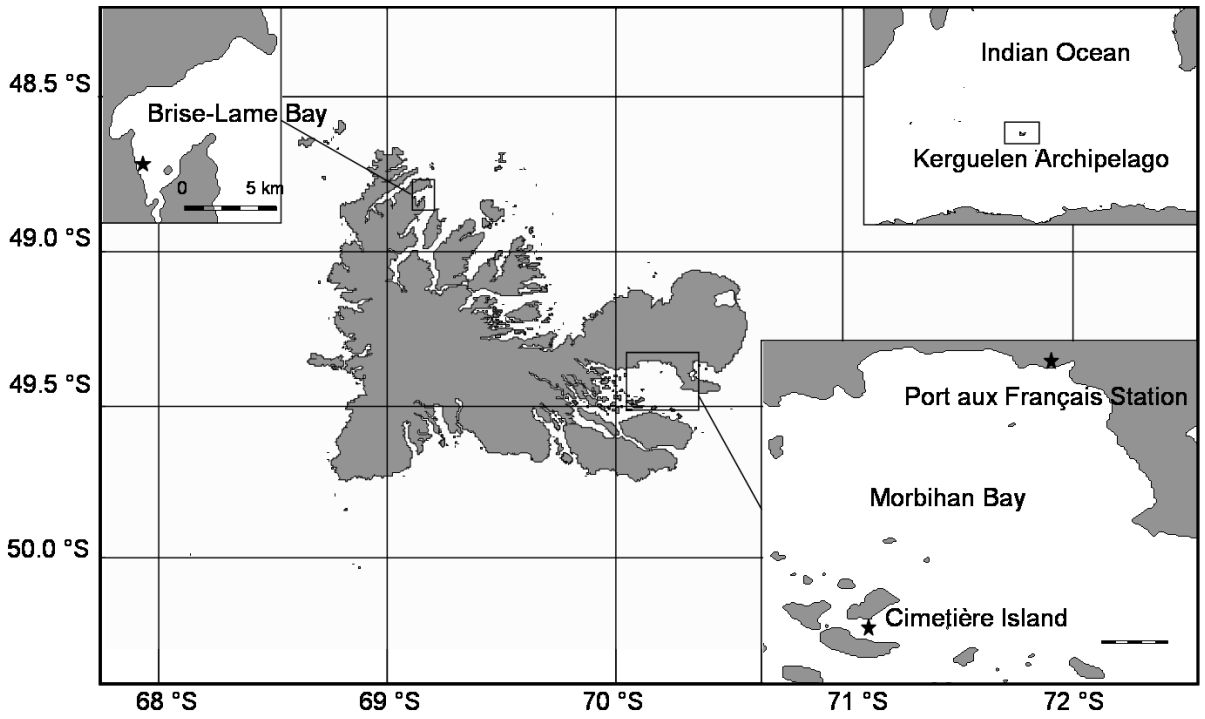

Indian Ocean
Kerguelen Archipelago
Brise-Lame Bay
0
5 km
Port aux Français Station
Morbihan Bay
Cimetière Island
48.5 °S
49.0 °S
49.5 °S
50.0 °S
68 °S
69 °S
70 °S
71 °S
72 °S

Fig. 2

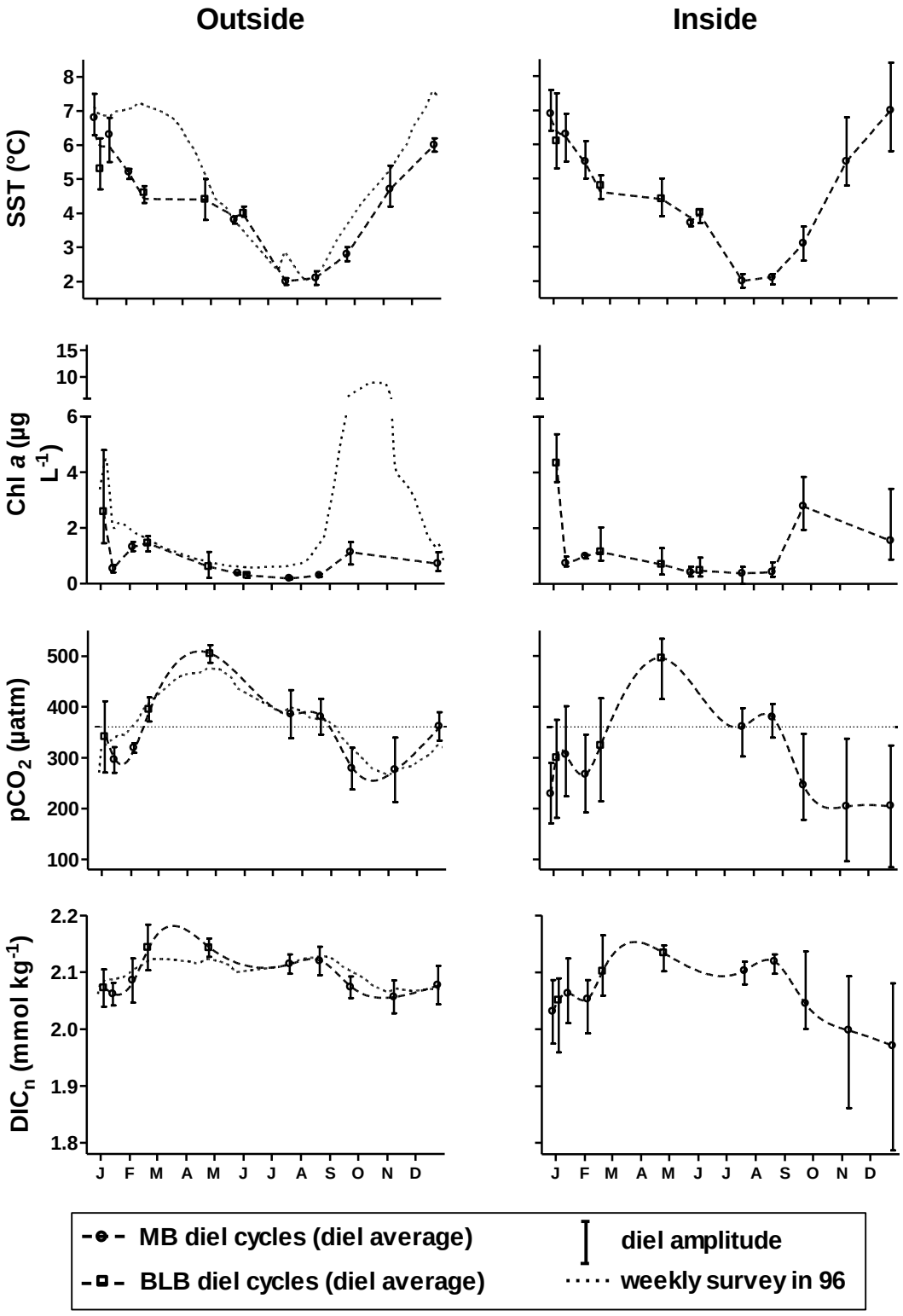

Outside
Inside
SST (°C)
Chl a (µg L-1)
pCO2 (µatm)
DICn (mmol kg-1)
J F M A M J J A S O N D
MB diel cycles (diel average)
BLB diel cycles (diel average)
diel amplitude
weekly survey in 96

Fig. 3

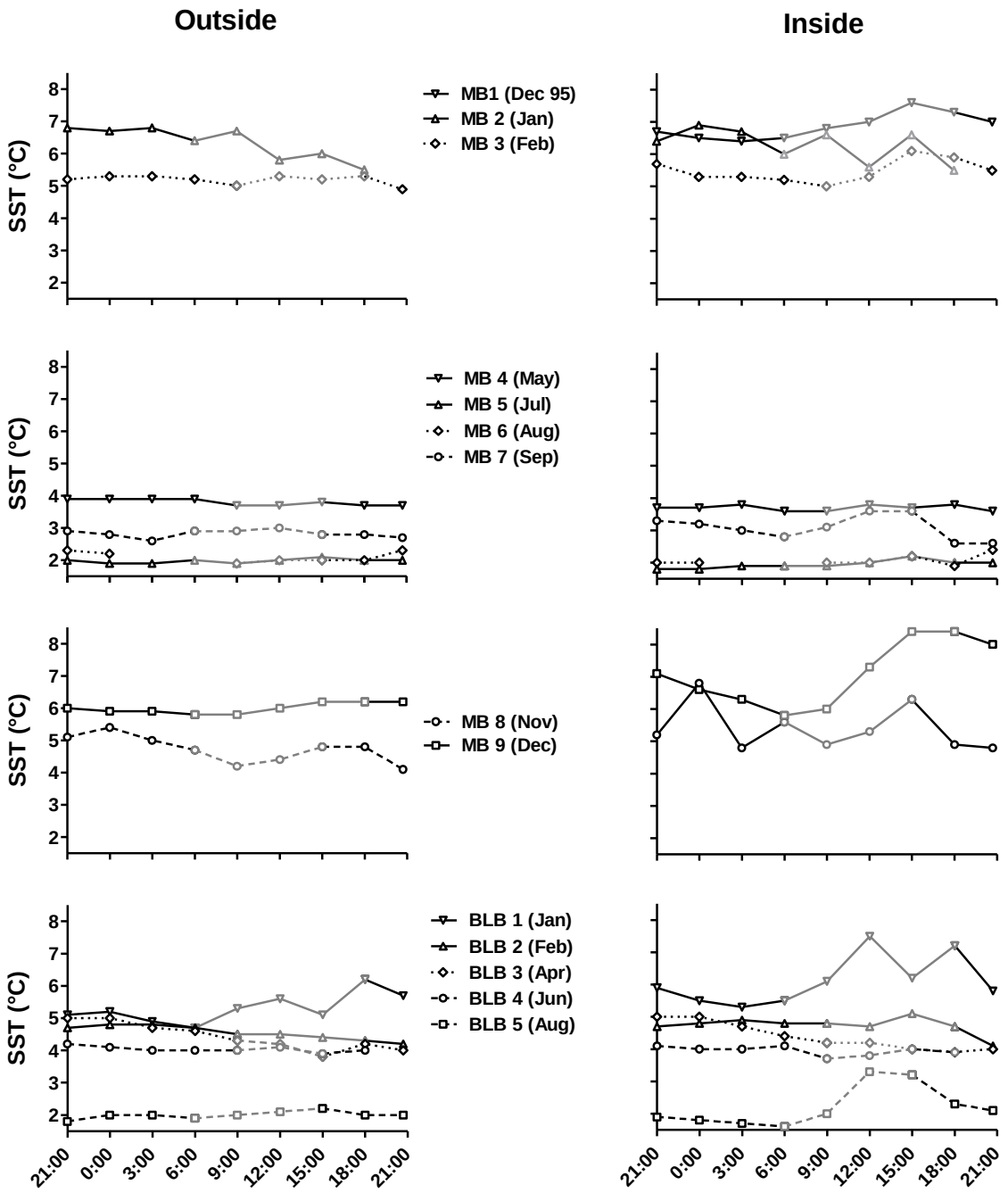

Outside
Inside
SST (°C)
MB1 (Dec 95)
MB 2 (Jan)
MB 3 (Feb)
MB 4 (May)
MB 5 (Jul)
MB 6 (Aug)
MB 7 (Sep)
MB 8 (Nov)
MB 9 (Dec)
BLB 1 (Jan)
BLB 2 (Feb)
BLB 3 (Apr)
BLB 4 (Jun)
BLB 5 (Aug)
21:00
0:00
3:00
6:00
9:00
12:00
15:00
18:00
21:00

Fig. 4

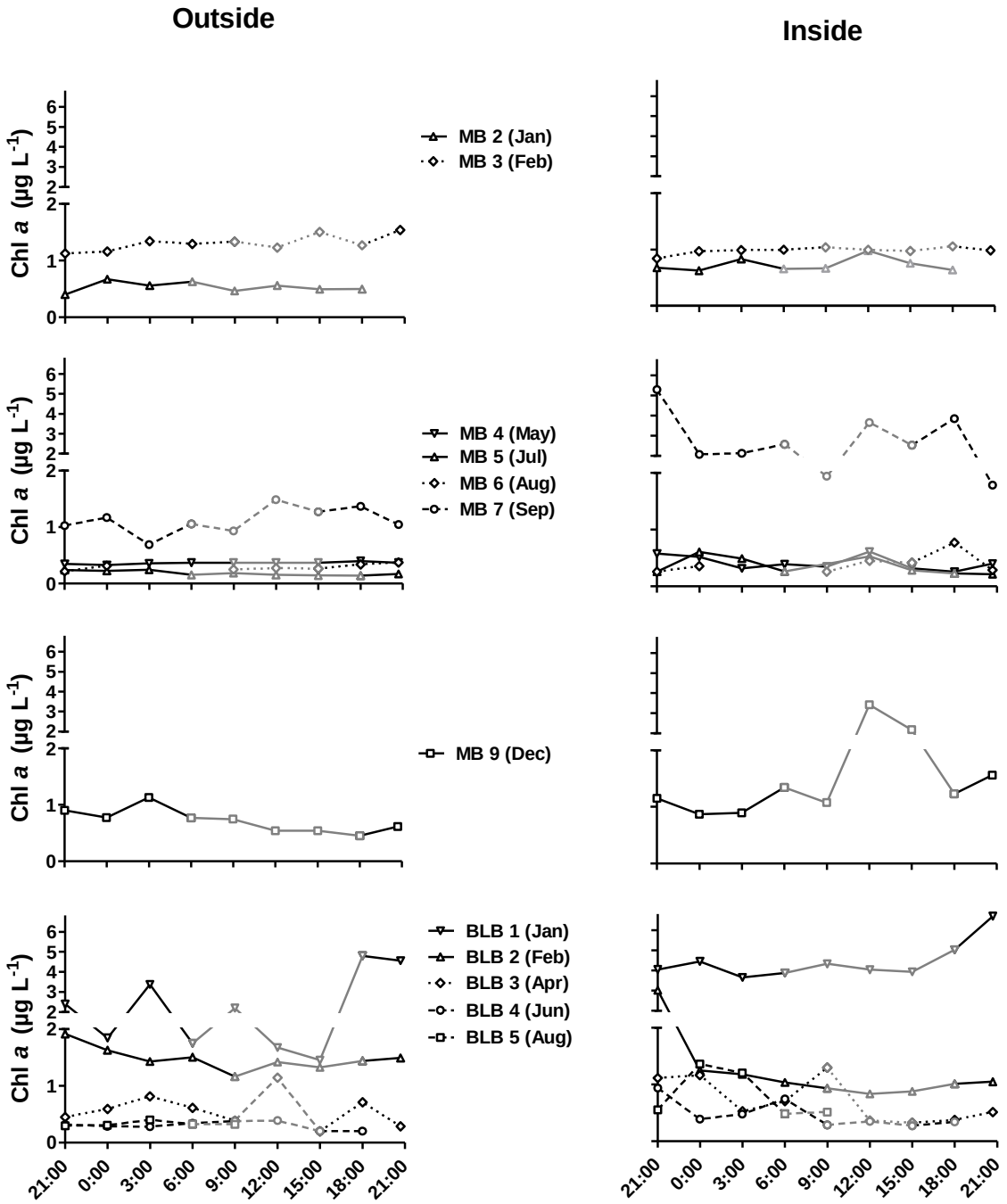

Outside
Inside
Chl a (µg L-1)
MB 2 (Jan)
MB 3 (Feb)
MB 4 (May)
MB 5 (Jul)
MB 6 (Aug)
MB 7 (Sep)
MB 9 (Dec)
BLB 1 (Jan)
BLB 2 (Feb)
BLB 3 (Apr)
BLB 4 (Jun)
BLB 5 (Aug)
21:00
0:00
3:00
6:00
9:00
12:00
15:00
18:00
21:00

Fig. 5

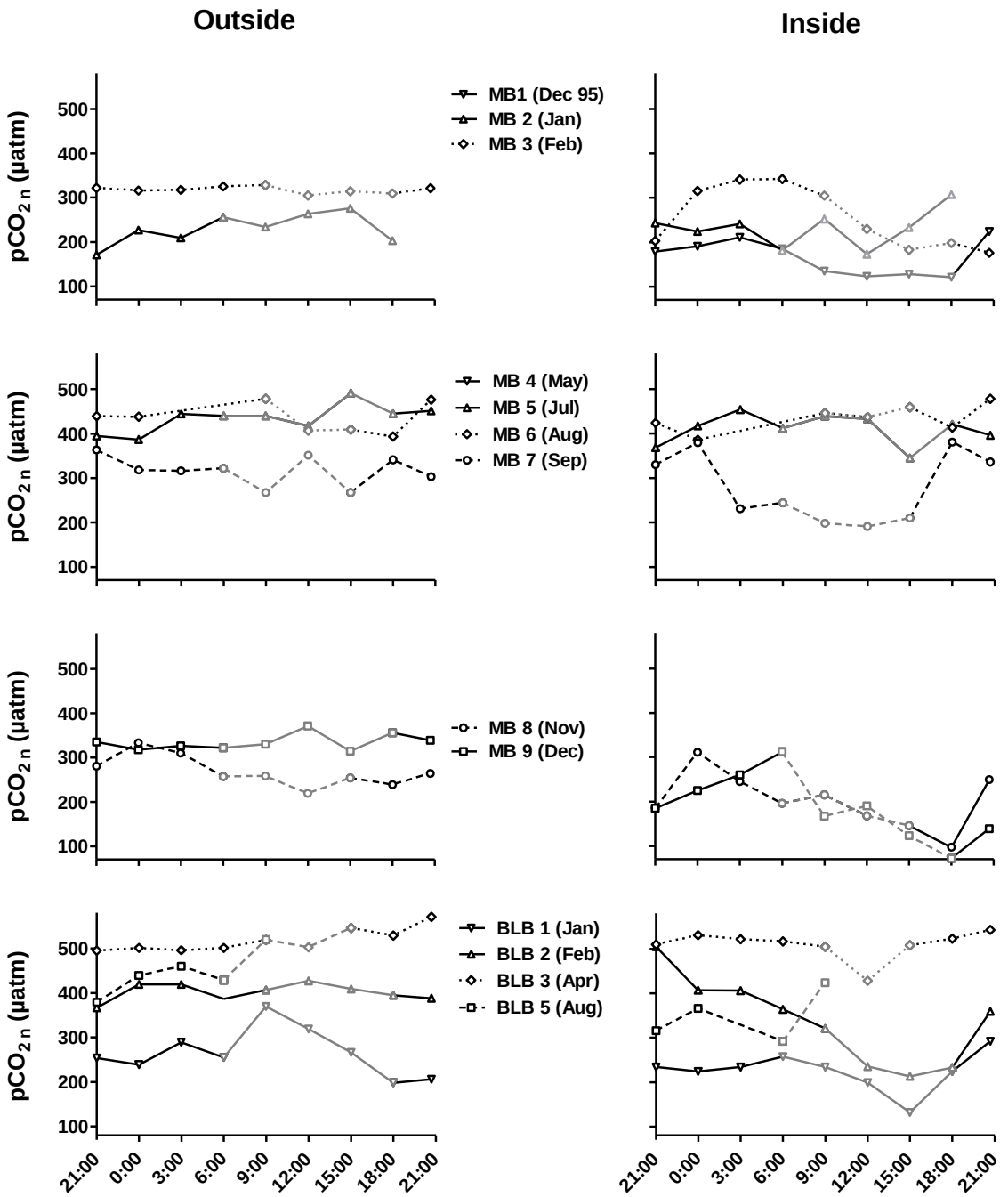

Outside
Inside
pCO2n (µatm)
MB1 (Dec 95)
MB 2 (Jan)
MB 3 (Feb)
MB 4 (May)
MB 5 (Jul)
MB 6 (Aug)
MB 7 (Sep)
MB 8 (Nov)
MB 9 (Dec)
BLB 1 (Jan)
BLB 2 (Feb)
BLB 3 (Apr)
BLB 5 (Aug)
100
200
300
400
500
21:00
0:00
3:00
6:00
9:00
12:00
15:00
18:00
21:00

Fig. 6

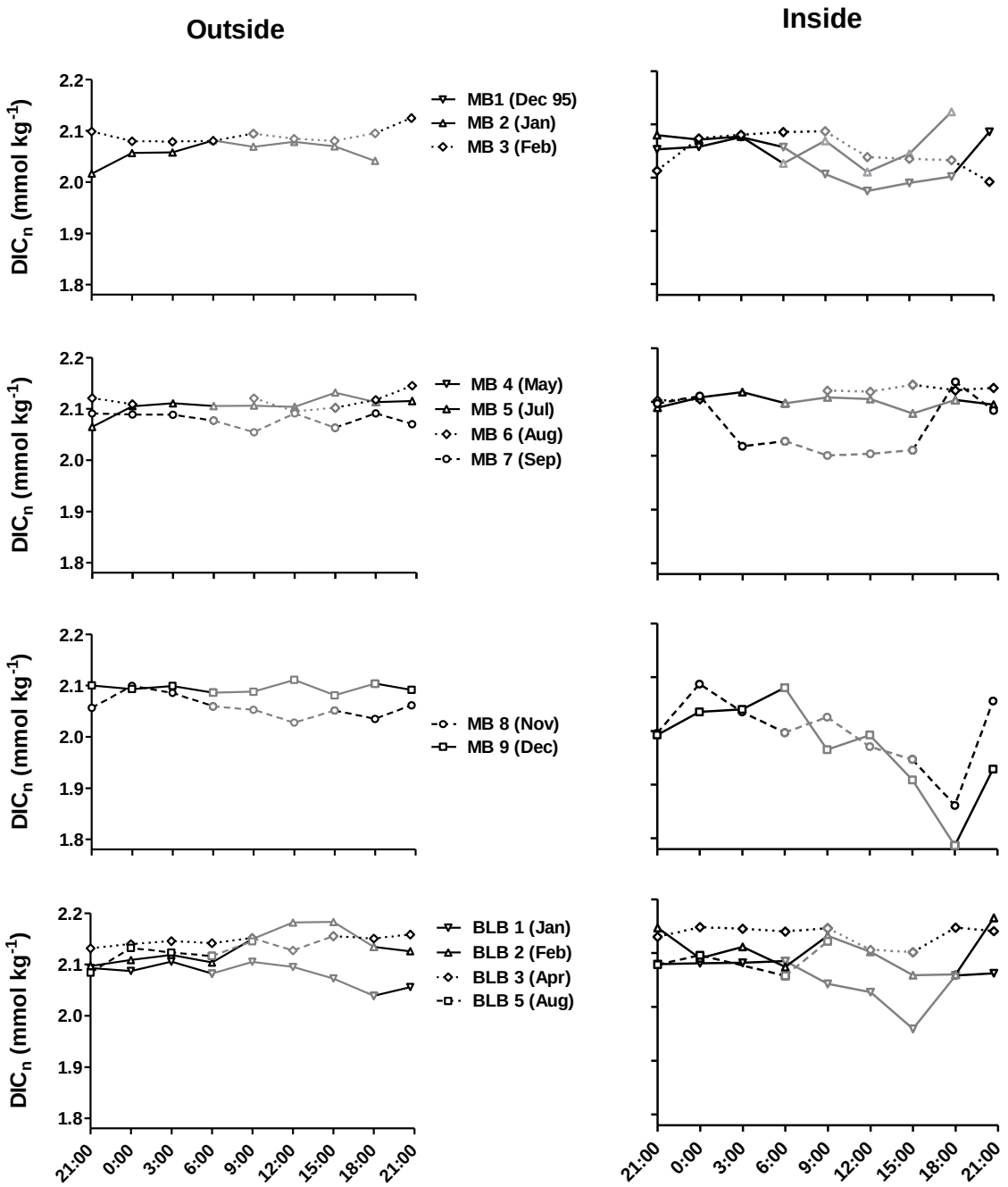
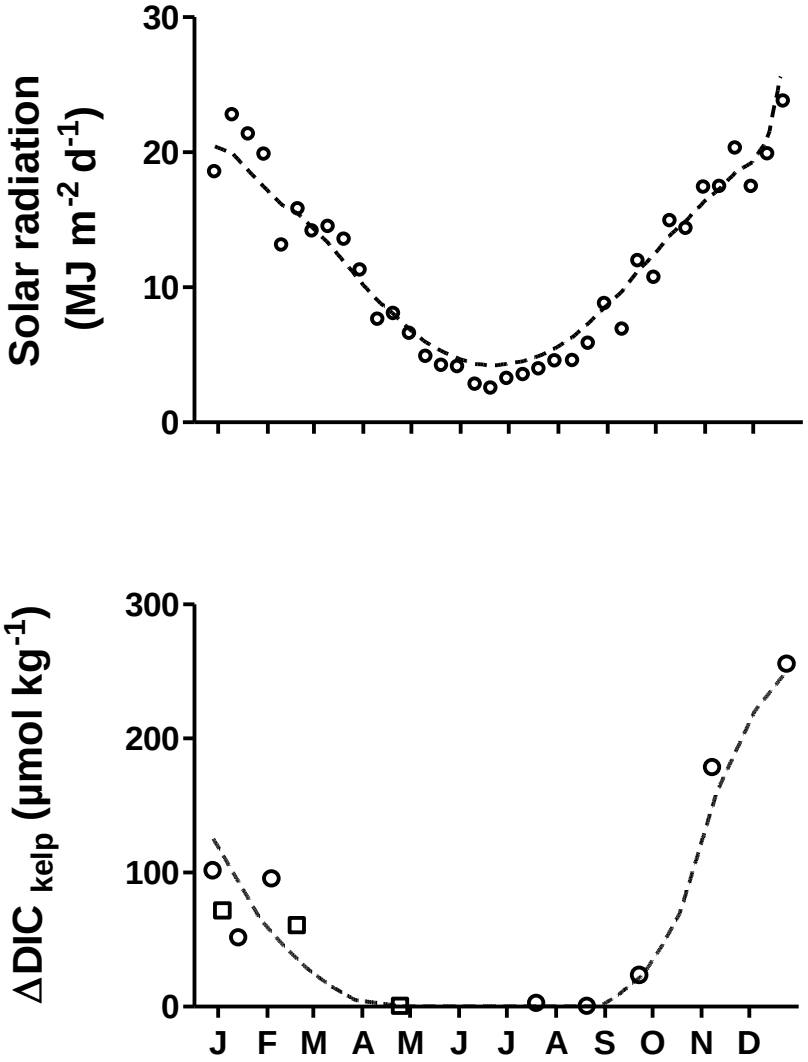

Outside
Inside
DIC$_n$ (mmol kg^{-1})
2.2
2.1
2.0
1.9
1.8
MB1 (Dec 95)
MB 2 (Jan)
MB 3 (Feb)
MB 4 (May)
MB 5 (Jul)
MB 6 (Aug)
MB 7 (Sep)
MB 8 (Nov)
MB 9 (Dec)
BLB 1 (Jan)
BLB 2 (Feb)
BLB 3 (Apr)
BLB 5 (Aug)
21:00
0:00
3:00
6:00
9:00
12:00
15:00
18:00
21:00

Fig. 7


Solar radiation (MJ m-2 d-1)
30
20
10
0
ΔDIC kelp (µmol kg-1)
300
200
100
0
J F M A M J J A S O N D