The diel carbon cycle of the Biosphere 2 ocean

Colm Sweeney *  

Columbia University, Lamont Doherty Earth Observatory, Palisades NY 10964, USA

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Abstract

The purpose of this study was to find the dominant processes affecting the diel carbon cycle of the Biosphere 2 ocean from July 27, 1995 to August 14, 1995. Despite excessively low nitrate (< 0.05 μmol l⁻¹) and phosphate (0.00–0.04 μmol l⁻¹) values, the Biosphere 2 ocean not only showed large daily TCO₂ changes of 30.5 ± 7.0 μmol kg⁻¹ but also a net production of organic carbon and CaCO₃ during the period of this study. A model used to predict pCO₂ values based on measured O₂ concentrations suggested CaCO₃ precipitation and organic carbon production were dominating the average diel ocean pCO₂ signal while the gas exchange with the atmosphere was relatively insignificant to the pCO₂ in the Biosphere 2 ocean. In the first 4 days of the experiment, the alkalinity decreased at a calculated rate of about 10 μeq kg⁻¹ d⁻¹ while in the following 10 days the model indicated that the alkalinity was nearly constant. The model also confirmed that the positive net production of organic carbon effectively held the pCO₂ in the Biosphere 2 ocean below equilibrium with the atmosphere. Although changes in the gas exchange had a small effect on the diel amplitude of pCO₂ (255 ± 84 μatm), changes in the photosynthetic quotient (PQ) were more significant. A PQ of 1.0 was used in the model to match calculated pCO₂ with measured pCO₂ of the Biosphere 2 ocean. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Biosphere 2; Carbon; Gas exchange; Diel; pCO₂; Ocean

1. Introduction

The focus of this study is to understand the major factors that control the carbon chemistry of the Biosphere 2 ocean. As with many coral reefs (Gattuso et al., 1993) and marsh embayments (Nixon et al., 1976), Takahashi et al. (1995) found that
Biosphere 2’s ocean was extremely depleted in nutrients. While nitrate values were found to be below the measurement blank (0.05 μmol kg⁻¹) and phosphate values varied from 0.00 to 0.04 μmol kg⁻¹, there were still large diel changes in oxygen (Langdon and Sweeney, 1995) and total CO₂ (TCO₂) values. In the absence of nutrients we can consider three dominating processes that might affect both the amplitude of the diel signal and the amount of TCO₂ stored in the ocean: gas exchange; photosynthesis; respiration; and CaCO₃ precipitation and dissolution. These three processes are the basis for our carbon cycle model of the Biosphere 2 ocean (Fig. 1).

1.1. Gas exchange

The first element of the TCO₂ budget in the Biosphere 2 ocean is the gas exchange rate. To calculate the effect of gas exchange we used the stagnant film model which separates the well mixed atmosphere and ocean reservoirs with the gradient in the thin film of thickness $z$ (m). Each gas has a particular molecular
diffusivity, \( D \) (m\(^2\) day\(^{-1}\)), within the thin film. The flux (mol m\(^{-2}\) d\(^{-1}\)) of CO\(_2\) into the ocean can then be represented by the equation:

\[
\text{Flux CO}_2 = \frac{D}{z} \alpha (\Delta p \text{CO}_2)
\]

(1)

Where \( \alpha \) is the solubility constant (mol atm\(^{-1}\)) of CO\(_2\) gas (Weiss, 1974). The \( \Delta p \text{CO}_2 \) (\( \mu \text{atm} \)) gradient in the micro layer is calculated using the equation:

\[
\Delta p \text{CO}_2 = p \text{CO}_2 \text{ atm} - p \text{CO}_2 \text{ sw}
\]

(2)

In which \( p \text{CO}_2 \text{ atm} \) (\( \mu \text{atm} \)) and \( p \text{CO}_2 \text{ sw} \) (\( \mu \text{atm} \)) are the measured partial pressure of CO\(_2\) in the atmosphere and seawater, respectively.

In this model the rate at which CO\(_2\) gas moves into the ocean is determined by \( D/z \) (m/d), the gas transfer coefficient (piston velocity, Broecker and Peng, 1971, 1974, 1982). With the gas transfer coefficient, we can calculate the time it will take for a gas to reach equilibrium using the depth of the mixed layer, \( h \).

In Biosphere 2 ocean we were able to calculate the gas transfer coefficient by artificially supersaturating the ocean with oxygen (to about 250 \( \mu \text{M} \)) and then allowing the value to relax back to a steady state value. The gas transfer coefficient, \( k \) (\( = D/z \)), was then calculated by regressing \( \ln(C_t - C_f) \) against time, where \( C_t \) is the concentration of oxygen at time \( t \) and \( C_f \) is the concentration of oxygen at steady state (Langdon and Sweeney, 1995). The average depth was assumed to be 3.6 m (Atkinson, et al., 1999)

\[
k = \frac{h}{(t_2 - t_1)} \ast \ln \left( \frac{C_1 - C_f}{C_2 - C_f} \right)
\]

(3)

Since the gas transfer coefficient for oxygen was calculated to be 2.1 \( \pm \) 0.2 m d\(^{-1}\) we were able to calculate the gas transfer coefficient for CO\(_2\) by using the diffusivity of each gas at a constant temperature:

\[
k_{\text{CO}_2} = k_{\text{O}_2} \ast \left( \frac{D_{\text{CO}_2}}{D_{\text{O}_2}} \right)^{1/2}
\]

(4)

Because the temperature of the gases were the same we assumed that the kinematic viscosity of water is constant (with constant temperature and salinity) so \( (D_{\text{CO}_2}/D_{\text{O}_2}) \) can be calculated using the relative ratio of the Schmit numbers for CO\(_2\) gas and O\(_2\) gas (Wanninkhof, 1992). This gives a gas transfer coefficient for CO\(_2\) of 2.0 \( \pm \) 0.2 m d\(^{-1}\) at 26.0\(^\circ\)C.

1.2. Photosynthesis and respiration

In the Biosphere 2 ocean, incubations experiments indicated that the benthic community, the plant matter growing around the edges and at the bottom, seem to be the dominant factor affecting the TCO\(_2\). The pelagic community, normally a dominant source and sink of TCO\(_2\) in the ocean, does not play an important role in Biosphere 2 ocean. Langdon and Sweeney (1995) used 12 h bottle incubation experiments to estimate that pelagic species of phytoplankton account for about 8% of the net photosynthesis observed in the ocean.

In low nutrient but highly productive environments such as coral reefs it has been shown that the plant organisms generally rely on recycled nutrients. In particular,
uptake of NH$_3$ increases in place of NO$_3^-$ which yields a photosynthetic quotient (PQ) of about 1.1 in many algae (Laws, 1991) and as low as 1.0 in coral reef environments (Porter, 1980; Barnes, 1983; Barnes and Devereux, 1984). With a PQ of 1.1, the algae in the Biosphere 2 ocean will take up one mole of CO$_2$ for every 1.1 moles of O$_2$ that they produce assuming that the only available nutrients in the system are those provided by NH$_3$ and not NO$_3^-$.

The Biosphere 2 ocean is unique because there is no wave action forcing the surface water oxygen above a saturated concentration. This allows us to assume that oxygen concentrations are only changing as a result of organic carbon production, oxidation or gas exchange. Since it has been observed (Fig. 2) that the average daily oxygen concentration in Biosphere 2 ocean is above saturation at 26°C, Langdon and Sweeney (1995) have estimated a positive net production rate of O$_2$ to be 10.8 m mol kg$^{-1}$ d$^{-1}$. This would imply that organic carbon was also produced at a rate of 10.8 μmol kg$^{-1}$ d$^{-1}$ with a PQ of 1.0. A net positive production implies that the TCO$_2$ is being constantly reduced throughout the study and may only be balanced by input of CO$_2$ gas from the atmosphere or dissolution of CaCO$_3$.

1.3. CaCO$_3$ precipitation and dissolution

Between March and June of 1995, Takahashi et al. (1995) made pCO$_2$ and TCO$_2$ measurements in Biosphere 2 ocean which demonstrated a 0.77 equivalents change in alkalinity for every mole of TCO$_2$ consumed. This implied that there were 0.39 mol CaCO$_3$ precipitated for every mol of TCO$_2$ consumed. Takahashi et al. (1995) also observed that the mean rate of decrease in alkalinity was 19 μeq kg$^{-1}$ d$^{-1}$ (9.5 μmol of TCO$_2$ kg$^{-1}$ d$^{-1}$). Without an adequate time series of TCO$_2$ measurements to calculate alkalinity changes during the full 14 day experiment in August 1995, we
have used estimated changes in alkalinity and measured changes in O₂ to predict pCO₂. The predicted pCO₂ was then compared with the measured value during the study period.

2. Methods

All measurements referred to in this experiment were done from July 19, 1995 (Julian day (JD) 200) to August 23, 1995 (JD 235) from a sampling platform in the Biosphere 2 ocean. In that time the salinity and temperature were held constant at 36.2 ± 0.5 psu and 26.0 ± 1.0°C through the use of heat exchangers and additions of fresh water. Initially, an airlift was used to insure proper circulation of water throughout the ocean was achieved during additions of 37.6 kg Na₂CO₃·xH₂O. On July 27, 1995 (JD 208) at 0655 the airlift was turned off and left off until August 14, 1995 (JD 226) at 1000. The model used data collected from July 27, 1995 (JD 208) through August 12, 1995 (JD 222) when the airlift was off.

The mole fraction of CO₂ in dry air 1 m above the Biosphere 2 ocean was made using a non-dispersive infrared gas analyzer (LICOR Model LI-6251). Calibration of the instrument was performed using four Biosphere 2 supplied CO₂ standards. Each standard was calibrated at Lamont using a gas chromatograph equipped with a flame ionization detector. The gas chromatograph was calibrated using a coulometer and P-V-T measurements of pure CO₂ gas (99.998%). The pCO₂ in air was computed using the measured barometric pressure, water vapor pressure at the seawater temperature, and the barometric pressure. The precision of the measurement is estimated to be about ± 0.5% of the measured value.

Measurement of the pCO₂ sea water was done by pumping water from 1 m below the surface into a 20 l equilibrator chamber through a shower head (25–30 l min⁻¹) which facilitated rapid exchange of CO₂ between the liquid and the gas phase. The equilibrated air was then passed through a infrared gas analyzer (LICOR Model LI-6251) alternatively with the atmospheric pCO₂ gas samples. Calibration of the infrared analyzer done using Biosphere 2 supplied CO₂ standards (as described above). Each value was measured over a 3 min time interval. The pCO₂ in the seawater was computed using the measured barometric pressure, water vapor pressure at the equilibration temperature, and the barometric pressure. The precision of the measurement is estimated to be about ± 0.5% of the measured value.

TCO₂ samples were collected in 250 ml Pyrex glass bottles sealed with a ground glass stopper that had been lubricated by silicon grease. Each sample was initially collected in a 5 l Niskin bottle at 1 m depth. Five hundred ml of seawater were allowed to drain into the sample bottles through a 0.6 m of bubble-free Tygon tubing. The tubing was then removed from the bottle leaving a small amount of head space between the stopper and the liquid. Once the sample was removed from Biosphere 2 each sample was poisoned with 250 µl of 50% saturated mercuric chloride to prevent any biological alteration of the sample. This experimental procedure yielded an average standard deviation in replicate samples of ± 2.0 µmol kg⁻¹.
In this study all values of alkalinity have been calculated using methods similar to those described by Peng et al. (1987). For the above calculations the following equilibrium constants were used: the solubility of CO$_2$ in water measured by Weiss (1974), the dissociation constants of CO$_3^{2-}$ and HCO$_3^-$ tested by Mehrbach et al. (1973) and the boric acid dissociation constant measured by Dickson (1990). Alkalinity can be calculated using measured values of TCO$_2$ and pCO$_2$ at a given salinity, temperature and nutrient levels to an accuracy of about 30 µeq kg$^{-1}$ (Takahashi et al. 1995). However, the calculated value will give a precision of about 2 µeq kg$^{-1}$.

Oxygen values were collected by an ENDECO 1133 pulsed oxygen sensor placed 1 m below the Biosphere 2 ocean surface. The electrode was calibrated against daily oxygen samples analyzed by Winkler titrations (Strickland and Parson, 1972). The oxygen sensor took a sample of the oxygen every 4 min and an analog voltage was logged by Biosphere 2's data acquisition system every 15 min. Chris Langdon reported that the calibration accuracy was ± 3.7 µM during the period of July 26–29. Calibrations made after that time have increased to ± 8.9 µM.

The light measurements were made with a Licor sensor with PAR quantum response and a cosine collector. This sensor was located at a depth of 2.15 m.

3. Results and discussion

3.1. Field results

On July 24, 1995 (JD 205) at 1545 the first of two additions of Na$_2$CO$_3$·xH$_2$O were added to the Biosphere 2 ocean to maintain a supersaturated concentration of aragonite. Before the two additions of Na$_2$CO$_3$·xH$_2$O, the average TCO$_2$ measured was 1819.0 ± 18.5 µmol kg$^{-1}$ and the pCO$_2$ had an average daily value of 817 ± 51 µatm. By July 27, 1995 (JD 208) at 0655 all of the 37.6 kg Na$_2$CO$_3$·xH$_2$O had been completely mixed (confirmed by measurements of TCO$_2$ in two different areas in the Biosphere 2 ocean) and the airlift was turned off. With the addition of Na$_2$CO$_3$·xH$_2$O the average daily pCO$_2$ had fallen down to 646.8 ± 55.2 µatm (Fig. 3a) and the average TCO$_2$ rose to a value of 1928.9 ± 18.4 µmol kg$^{-1}$ (Fig. 3b).

From July 27, 1995 (JD 208) to August 1, 1995 (JD 213), we continued to sample for TCO$_2$ measurements (Fig. 3b) at times that corresponded to daily maxima and minima of pCO$_2$. Over this 6 day period the TCO$_2$ of the Biosphere 2 ocean showed a daily amplitude of 30.5 ± 7.0 µmol kg$^{-1}$. While the average TCO$_2$ remained fairly constant throughout this period, the calculated alkalinity decreased from a high of 2128 ± 9 µeq kg$^{-1}$ to a low of 2084 ± 9 µeq kg$^{-1}$ (Fig. 3c). This trend was interrupted by one cloudy day (JD 210) which increased the average TCO$_2$ by almost 20 µmol kg$^{-1}$ and increased the alkalinity by about 14 µeq kg$^{-1}$ in the next 2 days. After August 1, 1995 (JD 213) measurements of TCO$_2$ were not taken until after the airlift was turned back on August 14, 1995 (JD 226). On August 19, 1995 (JD 231) the TCO$_2$ was as high as 2050 µmol kg$^{-1}$ and the calculated alkalinity had risen to 2137.7 ± 0.3 µeq kg$^{-1}$ with the airlift on.
The trend in alkalinity that was calculated from the time that the airlift was turned off until a final measurement was made 6 days later (Fig. 3c) illustrated that the calcification process in the Biosphere 2 ocean was not consistent. Further measurements before a final addition of Na₂CO₃·xH₂O on August 19, 1995 (JD 231) indicated a net increase in measured TCO₂ and calculated alkalinity from the time the airlift was turned off on July 27, 1995 (JD 208). Although it was possible that turning the airlift back on enhanced gas exchange and increase the TCO₂ measured, the increased gas exchange should not effect the calculated alkalinity. The only way to increase the alkalinity would be through dissolution of CaCO₃ in the Biosphere 2 ocean.

Because of the addition of Na₂CO₃·xH₂O before the experiment, Fig. 4 showed that the Biosphere 2 ocean was super-saturated with respect to both calcite and aragonite based on solubility constants for aragonite used by Mucci (1983). We assumed that the Ca²⁺ concentration was 8.5 mmol kg⁻¹ based measurements made by Takahashi et al. (1995) on June 23, 1995. The only other source of alkalinity might have been from the sediments. Oxidation of organic carbon in the sediments might have led to dissolution in the of CaCO₃ in the pore waters.

The fact that we calculated a net increase in alkalinity over the course of the experiment was even more paradoxical when we considered how much Amphora, a calcareous algae, was harvested from the Biosphere 2 ocean during the month of

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**Fig. 3.** Biosphere 2 Ocean Study—data collected from July 19, 1995 (JD 200) to August 23, 1995 (JD 235) for a) pCO₂ (b) total CO₂ and (c) calculated alkalinity.
Fig. 4. Aragonite saturation curve for Biosphere 2 ocean—saturation values (−) at 10.5, 9.5 and 8.5 mmol Ca\(^{2+}\) kg\(^{-1}\). These values are calculated based on constants used by Mucci (1983) at a salinity 36.2 pss and a temperature of 26.0°C. The points represent measured pCO\(_2\) values and calculated alkalinity values using constants from Peng et al. (1987).

August. Rosenthal (personal communication) reported that in the month of August, 1995 about 60 kg of *Amphoroa* was harvested from the Biosphere 2 ocean. If we assumed that the dry weight of *Amphoroa* was 90% CaCO\(_3\), the volume of Biosphere 2 was $2.6 \times 10^6$ l (Atkinson et al., 1999) and the harvesting of the *Amphoroa* was maintaining a steady state of growth, the alkalinity would be decreasing at a rate of 13 μeq kg\(^{-1}\) d\(^{-1}\) due to *Amphoroa* alone. This rate of decrease from *Amphoroa* in month August 1995 was 68% of alkalinity decrease that Takahashi et al. (1995) observed from March through June—a significant contribution. Unfortunately, at no time during our experiment did we see the alkalinity decrease at such a high rate.

3.2. Modelling results

With the help of a model of the carbon system in the Biosphere 2 ocean we have tried to reconstruct how alkalinity might have changed during a 14 day period that the airlift was off. Fig. 4a shows the first model run which predicted the pCO\(_2\) of the Biosphere 2 ocean based on the change in oxygen measured in the ocean (Fig. 2). The model used the calculated gas exchange values for both O\(_2\) and pCO\(_2\) and a PQ value of 1.0 to estimate the change in the pCO\(_2\) every 15 min from July 27, 1995 (JD 208) to August 10, 1995 (JD 222). Although there was a large increase in the observed pCO\(_2\) in latter half of the time series, it was not reflected in the modelled pCO\(_2\) values (Fig. 5a). Without changing the PQ ratio or the gas exchange, the only way to increase the pCO\(_2\) was to decrease alkalinity. As Fig. 3c indicates, there was an average decrease in alkalinity of about 10 μeq kg\(^{-1}\) d\(^{-1}\) for
the first 4 days of the experimental period. When we made a similar correction for alkalinity for the whole experimental period we saw a dramatic change in the modelled pCO₂ values (Fig. 5b). In the period of time that the 10 μeq kg⁻¹ d⁻¹ decrease in alkalinity was actually observed (JD 208–212) we saw a very good match between the modelled pCO₂ and the real pCO₂ measurements. Beyond Julian day 212, the modelled pCO₂ in Fig. 5b quickly increase in value while the measured values plateau. Without TCO₂ measurements after Julian day 213, we were unable to document the actual changes in alkalinity; however, the plateau in the measured pCO₂ values indicate that alkalinity may have been constant after the first 4 days. This result was confirmed in Fig. 5c, which showed a very close fit between the modelled pCO₂ and the measured pCO₂ values, when the alkalinity was held constant after the fourth day of the experimental period. The increase in alkalinity calculated on Julian day 213 (Fig. 3c), further demonstrated that it was unlikely that alkalinity continued to decrease at the initial rate of 10 μeq kg⁻¹ d⁻¹.

Although the correction for the alkalinity in the first 4 days of the experimental period does help to explain the major differences between the modelled data and the measured data, there is still small inconsistencies in the daily amplitude of the diel signal. The smaller amplitude observed in the modelled pCO₂ value could be explained by the fact that the rate of CaCO₃ precipitation or dissolution was not

![Fig. 5. pCO₂ Model results—pCO₂ values ( – ) calculated based on the change in O₂ values every 15 min compared with observed results ( ). This model assumes a piston velocity of 2.1 m d⁻¹ for O₂ and 2.0 m d⁻¹ for CO₂ along with a PQ value of 1.0. (a) Alkalinity constant (b) decrease in alkalinity (10 μeq kg⁻¹ d⁻¹) and (c) decreasing alkalinity (10 μeq kg⁻¹ d⁻¹) for the first four diel cycles followed by a constant alkalinity.](image-url)
Fig. 6. The effect of a change in the PQ ratio—this figure shows the change in amplitude of the diel pCO₂ values calculated from the change in dissolved oxygen in the Biosphere 2 ocean based on changes in the PQ ratio. The alkalinity in this model decreases for the first 4 days at a constant rate of 10 μeq kg⁻¹ d⁻¹ and then levels off at a constant value. The piston velocity is set at 2.5 m d⁻¹ for CO₂.

canstant throughout a diel period as has been pointed out by many investigations into the coral reef calcification rates (Barnes, 1982; Barnes and Chalker, 1990). In the model we assumed a constant rate of CaCO₃ precipitation which has no diel variability. If precipitation was more rapid at night we might expect to see larger amplitudes in the pCO₂ signal, however, this would contradict the prevailing theory that light enhances calcification rates in coral reefs (Barnes and Chalker, 1990). Fig. 6 illustrates that by decreasing the photosynthetic quotient there was a consequential increase amplitude of the modelled pCO₂ values. It would appear that PQ values that match the amplitude of the measured pCO₂ curve are below values observed in the natural environment (values tend to be between 1.0 and 1.4) (Porter, 1980; Barnes, 1983; Barnes and Devereux, 1984; Laws, 1991). Fig. 7a illustrates that an increase in gas exchange will not affect the amplitude of the pCO₂ values but will bring the average daily values to a steady state more quickly.

By starting with a decreasing the alkalinity value followed by a constant alkalinity value after the first 4 days in the Biosphere 2 ocean model, we were able to match the measured and calculated value of ocean pCO₂ based on the changes in oxygen measured over the study period. However, it is important to address how net production of organic carbon effects the pCO₂ value. Fig. 7b illustrated that with no net production of organic carbon the ocean pCO₂ moved into equilibrium with the atmospheric pCO₂. With a net production of organic carbon Fig. 7c showed that the ocean pCO₂ decreased until it reached a steady state where the amount of CO₂ being added to the ocean through gas exchange equaled the amount being taken out of through organic carbon production. This relationship can be seen in Fig. 3a which showed the ocean pCO₂ maintained an average value that was below that of the atmospheric pCO₂—indicating that there was a net positive production of organic carbon.
Fig. 7. Normalized models—(a) pCO\textsubscript{2} modelled with changes in gas exchange—this shows the pCO\textsubscript{2} value calculated from changes in O\textsubscript{2} concentrations in a system with no net organic carbon or CaCO\textsubscript{3} production. Shows pCO\textsubscript{2} (---) values based on a piston velocity of 2.5 m d\textsuperscript{-1}. The solid curve illustrates a piston velocity of 10 m d\textsuperscript{-1}. The atmospheric pCO\textsubscript{2} in this model has average value represented by the solid horizontal line and a daily amplitude of 410 μatm. (b) pCO\textsubscript{2} model with no production—this model shows the how the pCO\textsubscript{2} in the ocean changes in relation to the atmospheric pCO\textsubscript{2} if there is no net production of organic carbon. (c) pCO\textsubscript{2} model with Normal Biosphere 2 organic production—this model run shows that given a normal gas transfer coefficient (2.5 m d\textsuperscript{-1}) and a typical August net productivity (14 μmol Corg kg\textsuperscript{-1} d\textsuperscript{-1}) the pCO\textsubscript{2} value will decrease until it has reached an equilibrium value.

4. Conclusion

It was apparent from this study that changes in alkalinity played a major role in the average daily pCO\textsubscript{2} values measured in the Biosphere 2 ocean; however, it was unclear what caused these alkalinity changes. While harvests of Amphoroa indicated that the alkalinity may have decreased by as much as 15 μeq kg\textsuperscript{-1} d\textsuperscript{-1} throughout the month of August, the model showed very erratic shifts in alkalinity which were dominated by periods of constant alkalinity values. If the Amphoroa growth were constant in the ocean during the experimental period then we would have to assume that there was a balancing flux of carbonate ion from the sediment caused by organic carbon oxidation in the sediment. It is also possible that the actual harvesting of Amphoroa from the benthic layer may have enhanced the flux of high alkaline pore water into the overlying water. In the future, the harvesting of Amphoroa will have to be more carefully monitored to determine its affect on the alkalinity in Biosphere 2 ocean.
In addition to the effects of alkalinity, it also has been demonstrated that there was a net production of organic carbon in Biosphere 2 ocean during the study period. We have shown that the organic carbon production was high enough to force the ocean pCO$_2$ below atmospheric pCO$_2$ values despite the effects of gas exchange. We can therefore conclude that gas exchange does not play a very significant role in Biosphere 2 ocean.

References


