Carbon remineralization rates in marine sediments beneath areas of high and low primary productivity in the Galapagos Archipelago

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Non-Technical Summary

Since the last glacial period, which ended ~10,000 years ago, a significant increase in atmospheric carbon dioxide (CO$_2$) levels has occurred, in part due to human-influenced activities. Since the world’s oceans act as a sink for CO$_2$, prediction of future levels of atmospheric CO$_2$ depends on understanding the magnitude of this sink. As organisms in ocean surface waters photosynthesize, they take up CO$_2$ and convert it to organic carbon. When these organisms die, they sink out of the surface. Although not all of the carbon within the dead organisms makes it to the seafloor, the amount that does either becomes buried in the sediments or is remineralized. Remineralized carbon has the potential to return to the atmosphere as CO$_2$, while buried carbon does not contribute to atmospheric CO$_2$ levels for as long as it remains buried. This study was carried out in the Galapagos Islands in January 2006 to determine sedimentary carbon remineralization rates and compare them among regions of differing chlorophyll $a$ concentrations and rates of primary production (photosynthesis). Relatively high rates of carbon remineralization, and correspondingly shallow oxygen penetration depths, were expected underlying areas of greater primary production. Depth profiles of oxygen concentration in sampled sediments were generated using an oxygen microelectrode. These profiles were used to calculate the rate of oxygen consumption in the sediments. The Redfield ratio, which is a standard that relates carbon and oxygen concentrations, was then used to convert oxygen consumption rates to rates of carbon remineralization. Chlorophyll $a$ and primary production rates were gathered from fellow researchers. It was found that sediments beneath regions of relatively high primary production exhibited higher carbon remineralization rates and correspondingly shallower oxygen penetration depths than sediments beneath regions of low primary production, as hypothesized. Thus, sedimentary carbon remineralization in the Galapagos Islands reflects regional variability in surface-water processes.
Acknowledgements

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Abstract

Predictions of future atmospheric CO₂ levels require accurate quantification of the flux of carbon from ocean waters to the sea floor. Carbon that is remineralized has the potential for release back to the atmosphere, while carbon sequestered in the deep sea is isolated from the atmosphere for thousands of years to millennia. To assess the significance and magnitude of this process and its relationship to primary production around the Galápagos Islands, box cores were obtained at three stations west and two stations east of Isla Isabela in January 2006 while aboard R/V Thomas G. Thompson. Sedimentary oxygen concentration profiles, measured using an oxygen microelectrode, were modeled using the computer program PROFILE. Total sediment oxygen consumption rates were calculated from the depth-integrated oxygen profiles, and the Redfield ratio was used to convert oxygen consumption rates to carbon remineralization rates. Stations west of Isabela had carbon remineralization rates and oxygen penetration depths of 1.4x10⁻⁶ μmol cm⁻² s⁻¹ and 7.2 mm, respectively. Stations east of the island had carbon remineralization rates and oxygen penetration depths of 0.62x10⁻⁶ μmol cm⁻² s⁻¹ and 10.9 mm. These values are in accord with west-east variation in surface water chlorophyll content and primary productivity measurements. Greater carbon remineralization rates and shallower oxygen penetration depths were found underlying regions of high productivity (average of 13.6 μmol C L⁻¹ d⁻¹) on the west side, than low productivity (6.5-9.4 μmol C L⁻¹ d⁻¹) on the east side of Isabela. Thus, sedimentary carbon remineralization in the Galapagos Islands reflects regional variability in surface-water processes.
**Introduction**

Quantifying the flux of carbon from the ocean’s surface to the sea floor is necessary in order to predict future levels of atmospheric carbon dioxide (Jahnke et al. 1990). Since the last glacial period, atmospheric CO$_2$ has increased 85 ppm, which is thought to be due to the global anthropogenic input of CO$_2$. The extent to which CO$_2$ is removed from the atmosphere and subsequently stored in ocean sediments is dependent upon (1) photosynthetic carbon fixation in the euphotic zone, (2) transfer of some fraction of this fixed carbon out of the euphotic zone as export production, and (3) long-term carbon burial in marine sediments (Devol and Hartnett 2001). Carbon remineralized in the sediments has the potential to be released back into the atmosphere, whereas carbon that escapes remineralization will effectively be isolated from the atmosphere for as long as it remains buried.

Continental margins offer one of the largest sinks of carbon; more than 90% of all organic carbon burial presently occurs in continental margin sediments due to the relatively large input of fresh organic matter when compared to deep-sea sediments (Hedges and Keil 1995; Hartnett and Devol 2003). Organic matter delivered and incorporated into marine sediments is mineralized via multiple microbial pathways that oxidize it through the reduction of O$_2$, NO$_3$, oxides of Mn and Fe, and SO$_4$ (Thamdrup and Canfield 1996). It has been suggested that oxygen consumption is most important in deep-sea sediments, and that the importance of NO$_3$ and SO$_4$ oxides as electron acceptors increases in continental slope and shelf sediments (Murray and Kuivila 1990). In sediments on continental margins at depths greater than 1000 m, the largest component of the total carbon oxidation rate is due to oxygen (Hartnett and Devol 2003), suggesting that oxygen consumption can be used as a reasonable proxy for overall carbon remineralization under these circumstances.
High primary production in surface waters can potentially result in the transport of an increased amount of organic matter to the seafloor, when compared to areas of low production. However, it is important to note that other factors contribute to the distribution of surface-originating organic matter among marine sediments, such as the depth of the water column. As organic matter sinks through the water column, a majority of it is biologically oxidized, resulting in a decreasing carbon rain rate with depth and only a small portion being available for sediment burial. Supporting this, Murray and Kuivila (1990) observed a decrease in organic carbon in sediments with increasing distance from the continental margin, and therefore depth. It has been suggested that this relationship determines the quantity and time scale at which carbon is sequestered in the deep ocean (i.e. shallower regeneration depths will result in shorter sequestration times; Devol and Hartnett 2001).

As organic matter in the sediments is decomposed, dissolved oxygen is consumed. Therefore, oxygen penetration depths are likely to vary with changes in organic matter deposition, degradation and the bottom-water O$_2$ concentration (Cai and Sayles 1996). Cai and Sayles (1996) compared oxygen penetration in marine sediments and found that a site at which additional organic material was disposed in the form of sewage exhibited a much shallower oxygen penetration depth than those at uncontaminated sites. These data suggest that, when compared to areas with low organic matter deposition, those with high organic matter deposition will exhibit shallower oxygen penetration through the sediments, indicative of higher carbon remineralization rates in the oxygenated portion of the sediments. It is important to note, however, that other factors may also be important, in particular whether the sediments are disturbed. Bioturbation, or the disturbance of sediments by burrowing organisms, can greatly affect the distribution of oxygen in marine sediments (Mermillod-Blondin et al. 2005).
This study addressed two main questions: (1) Do sediment oxygen profiles and carbon remineralization rates vary in Galapagos Island sediments; (2) Is there a correlation between these variations and chlorophyll a concentrations or primary production in the overlying water column? During non-El Nino years, the Galapagos Islands exhibit chlorophyll a concentrations that are higher than the global average (0.5 – 1.5 mg m\(^{-3}\), with the highest values occurring to the west of the islands; Torres 2002). Historically, high productivity and chlorophyll a concentrations have been observed on the western side of Isabela Island, where the Equatorial Undercurrent brings nutrient-rich water to the surface (Feldman 1986; Martin et al. 1994). However, since the distribution of organic matter in marine sediments is not solely dependent on overlying primary production, reflecting other processes such as water depth, sedimentation rate, and biological activity, chlorophyll a concentration and rates of primary production are unlikely to explain all of the variance in sediment oxygen profiles.

**Methods**

In order to determine sedimentary carbon remineralization rates and compare them among regions of differing chlorophyll a concentrations and primary production, observations were made from 20-28 January 2006, a non-El Nino year, aboard *R/V Thomas G. Thompson*. Five sample stations, two east and three west of Isabela Island (Table 1, Fig. 1), were selected primarily according to the expected availability of sediment and regional patterns of chlorophyll a distribution (typically highest west of Isabela Island; Feldman 1986, Martin et al. 1994). For the purposes of this study, and due to their close proximity, all data from stations 1, 2 and 3 were averaged and are collectively referred to as station BI. A significant amount of time was spent both in the two weeks prior to the cruise, and during the cruise, mapping the seafloor in search of
sediments suitable for sampling. Upon arrival at each station, the 3.5 kHz sub-bottom profiler was utilized to confirm the existence of sediments prior to deploying the box core.

Once on site, chlorophyll \( a \) concentrations at the chlorophyll \( a \) maximum were estimated using the CTD-associated fluorometer (calibrated to the extracted chlorophyll \( a \) values of Snow (2006)) in casts to 200 m (stations 1 and 3) or to the bottom (stations 2, 4 and 5). The spade box core was then deployed to collect one sediment sample at each station. Once the box core was recovered, it was immediately and gently sub-sampled with PVC core liner tubes (7.6 cm diameter, 17.8 cm length). Four replicate sub-samples from each box core were taken in order to obtain an average carbon remineralization rate for sediments at each station. Overlying water was not recovered from any core deployment, and presumably leaked from the bottom and lower sides of the box core, due to the apparent integrity of the top layer of sediment. The CTD was therefore utilized to collect bottom-water at stations 2, 4 and 5. The water was then gently added to the respective sub-samples, taking care to avoid disturbing the top layer of sediment. The bottom-water collected at station 2 was used for stations 1, 2 and 3 (collectively BI) and was refrigerated at 5\(^\circ\)C until needed. Analysis indicated that the oxygen concentration of the bottom-water did not significantly change over the course of refrigeration. All sub-samples were refrigerated at 5\(^\circ\)C until bottom-water was available.

A polarographic oxygen-needle microelectrode was used to determine the dissolved oxygen profile for sediment samples (Revsbech et al. 1980). Profiles for all sediment samples were recorded immediately upon retrieval of CTD bottom-water (typically within one hour after core recovery) to minimize the effects of transporting the core out of its natural environment, including changes in atmospheric oxygen supply. A Ag/AgCl electrode was used as a reference during measurements and an electric potential between the silver reference electrode and the
glass-insulated platinum electrode was produced via a small black box connected to the electrodes. The electrodes were calibrated prior to boarding the ship using air-saturated seawater (20% O₂) and nitrogen-purged seawater (0% O₂). In order for the two electrodes to come into electrical equilibrium, oxygen was reduced at the platinum cathode and silver was oxidized at the reference anode. This movement of electrons produced a current, which was measured with a microvolt ammeter. The microelectrode was inserted into the core from above with the assistance of a micromanipulator attached to a ring stand. An average current reading was obtained from the overlying water, which closely represented the actual oxygen concentration in the water at the seafloor. After defining the average water oxygen concentration, the microelectrode was carefully lowered to the point where the tip of the microelectrode just touched the sediment surface. A significant deflection in the electrode current occurred at this point, and was used to confirm that the electrode was in fact at the surface of the sediment. The electrode was lowered into the core at 0.25 mm increments and volt ammeter readings were recorded at each interval. Probing continued until the current reading reached zero or remained constant for four 0.25 mm intervals. This value was called “zero” and was used to convert obtained current readings to oxygen concentrations by the following equation (Nuwer, J., pers. comm.):

\[
\frac{C_s[V] - Z_v[V]}{C_w[V] - Z_v[V]} \times C_{bw} [\mu mol \, kg^{-1}] = [O_2] \, \mu mol \, kg^{-1}
\]

where \( C_s \) is the current reading at each sediment interval, \( Z_v \) is “zero,” \( C_w \) is the current reading of the overlying water in the sub-core and \( C_{bw} \) is the oxygen concentration of the bottom water.

In-situ bottom water oxygen concentrations and temperatures were acquired from CTD sensors (error of CTD oxygen sensor was -0.083, with respect to measurements of Gilmore (2006) (Werdeman 2006)) on casts performed at stations 2, 4 and 5. The values obtained from the cast
performed at station 2 were assumed to be representative for stations 1, 2 and 3 due to their close proximity. Figure 2 illustrates typical distributions of $O_2$ with depth. The depth-integrated oxygen consumption rate in sediments was calculated (using the computer modeling program PROFILE; Berg et al. 1998) by integrating the obtained oxygen concentration profile as a function of depth and calculating the diffusion gradient across the sediment-water interface. This diffusion gradient represents the total flux of $O_2$ into the sediments, therefore reflecting the total oxygen consumption within the sediments. The diffusion coefficient of oxygen in sediment ($D_s$) was calculated using the estimated porosity ($\phi$) of deep-sea sediments (0.8; Nuwer, J., pers. comm.) and the diffusion coefficient of oxygen in water ($D$) at a given temperature ($D$ is a linear function of temperature; Pilson (1998)) via the equation:

\[
D_s = \phi^2 \times D
\]

Knowing the gradient of oxygen consumption in the sediments as well as the respective $O_2$ diffusion coefficient allowed for the calculation of the $O_2$ consumption rate (Murray and Grundmanis 1980). Oxygen was then converted to carbon via the modified Redfield ratio of $C_{106}:O_{138}$ (Hedges et al. 2002) to estimate the rate of carbon remineralization.

Measurements of chlorophyll $a$ and primary production were made by collaborators T. Snow and B. Gilmore using standard techniques. All sediment cores were visually examined for changes in color and the presence of benthic organisms and shell fragments. Sediment grain size was estimated by A. Cougan for stations 4 and 5.

**Results**

Stations 1, 2, 3 and 5 exhibited relatively uniform profiles (Fig. 3A-C and Fig. 4B), similar to the undisturbed profile of Sayles, F.L. and Goudreau, J. (unpubl.; Fig. 2A). However,
the oxygen concentration profiles through the sediments at station 4 were more sporadic (Fig. 4A), with multiple subsurface variations, including one apparent burrow effect (compare sub-core 1 in Fig. 4A to Fig. 2B). The greatest rate of carbon remineralization, $1.4 \times 10^{-6} \, \mu\text{mol cm}^{-2} \, \text{s}^{-1}$, along with the shallowest oxygen penetration depth, $7.2 \pm 0.6 \, \text{mm}$, was exhibited at station BI. Station BI also had the highest surface chlorophyll $a$ and primary production values (Table 2). The lowest rate of carbon remineralization, $0.62 \times 10^{-6} \, \mu\text{mol cm}^{-2} \, \text{s}^{-1}$, and the deepest oxygen penetration depth, $12.1 \pm 2.0 \, \text{mm}$, were exhibited at station 5. Due to evidence of bioturbation, calculations for station 4 excluded sub-core 1; remineralization rates and O$_2$ penetration depths were intermediate between stations BI and 5 (Table 2).

Primary production rates were higher on the west side of Isla Isabela ($13.6 \, \mu\text{mol C L}^{-1} \text{d}^{-1}$) than the east side ($6.5$-$9.4 \, \mu\text{mol C L}^{-1} \text{d}^{-1}$). Stations BI and 5 had similar chlorophyll $a$ concentrations ($0.6$ and $0.5 \, \mu\text{g L}^{-1}$, respectively) that were about twice as high as station 4 ($0.3 \, \mu\text{g L}^{-1}$). Chlorophyll $a$ size-fractionation data revealed that surface waters to the west of Isabela Island were dominated by large phytoplankton (greater than $20 \, \mu\text{m}$ and primarily diatoms), while surface waters to the east of Isabela Island were dominated by small phytoplankton (less than $2 \, \mu\text{m}$) and diatoms were rare (Snow 2006).

The visual analysis of sediment cores revealed that benthic organisms were present in sediments at all stations. The density of benthic organisms decreased with core depth in all cases, with most organisms usually concentrated in the top $3 \, \text{cm}$. Tube worm casings and small worms (usually less than $1 \, \text{mm}$ in diameter) were visible in cores from stations 1, 2 and 3. The surface-most layer of sediments at stations 1, 2 and 3 were usually smooth in texture, with few areas of variations in height (lumpiness), and contained no visible color changes throughout the samples. The surface-most layer of sediment at Station 4 was not flat, but contained many
perturbations in height. Though similar in color to stations 1-3, sediments at station 4 were characterized by distinct color changes with depth. A rough grain size analysis revealed changes in texture within the upper 15 cm as well, ranging from fine silt to fine sand (Cougan 2006). Tube worm casings and worms similar in size to stations 1-3 were seen. Sediments at station 5 held small (less than 3 mm in length) bivalve and snail shells, small worms and casings similar in size to previous stations. No obvious color changes were visible, but estimated grain size analysis revealed variations in grain size from very fine clay at the surface to silt below 8 cm (Cougan 2006). The surface-most layer was similar in texture to sediments from stations 1-3, containing few height variations.

Discussion

Although the lowest chlorophyll \( a \) concentrations and rates of primary production occurred at station 4, the subsurface variations and apparent burrow effect, both implying disturbed sediments, suggest that station 5 provides a more reliable measure of carbon remineralization on the east side of Isla Isabela, and thus a better comparison to the high production and high chlorophyll \( a \) station, BI (Fig. 5). This is because profiles (and therefore remineralization rates) were defined based on the assumption that molecular diffusion and microbial remineralization were the only transport processes of oxygen in the system. The visual analysis of cores suggested that similar amounts of macroscopic biological activity were occurring in sediments at all stations. Based on the oxygen profiles of all stations (Fig. 3 and Fig. 4) it appears that bioturbation is most influential in sediments at station 4. Stations 1 and 5 show a comparatively steady decline in oxygen concentration with depth, which suggests that oxygen penetration through the sediments is controlled by diffusion and microbial
remineralization (Keil, R., pers. comm.). On the other hand, station 4 exhibits multiple subsurface variations which suggest that diffusion and remineralization are not the only factors influencing oxygen distribution in these sediments. While the assumption of oxygen distribution processes was supported at stations BI and 5 by the lack of evidence of biological effects, implying that remineralization rate calculations at these stations were likely accurate, a more accurate oxygen penetration depth and carbon remineralization rate at station 4 would need to consider the effect of bioturbation in the analysis of profiles and the resulting calculations. A portion of this error was likely accounted for with the elimination of the most disturbed, sub-core 1 in calculations, but the remaining variations in the other sub-cores were still a likely greater source of error in analysis of station 4 sediments than at other stations. The distinct layering of station 4 sediment may also help explain its sporadic oxygen distribution. Variations in oxygen concentration may be a result of varying grain sizes or chemical make-ups in the different layers. For example, the average depth to which oxygen penetrated in station 4 sediments was to the bottom of the first color-distinguishable layer, which is consistent with known electron acceptance patterns (Thamdrup and Canfield 1996). Further studies could be done in which exact grain-size analysis and more extensive examination of biota and chemical composition of sediments are performed. A better understanding of these areas would offer better constraints from which to draw comparisons among sediments underlying areas of high and low productivity.

The data show that shallower oxygen penetration depths and greater rates of carbon remineralization are associated with areas of higher primary production, which may reflect greater deposition of organic matter to marine sediments. Supporting this supposition, Gehlen et al. (1997) analyzed the effect of increasing amounts of organic carbon on $O_2$ consumption rates,
which have been converted to carbon remineralization rates for the purpose of this study. Gehlen et al.'s study station, in the western Mediterranean, characterized by fine mud sediments and 2300 m depth, showed an increase in the rate of carbon remineralization from $1.12 \times 10^{-6}$ to $1.62 \times 10^{-6} \mu$mol cm$^{-2}$ s$^{-1}$, with increasing amounts of organic matter, as manipulated through laboratory enrichments. A decrease in the depth of oxygen penetration from 5 to 1 cm was also observed. The rate of carbon remineralization exhibited at station BI fell between the two values defined by Gehlen et al. (1997), while the values for stations 4 and 5 were an order of magnitude lower. When compared to the results of Gehlen et al. (1997), the results of this study showed deeper oxygen penetration depths, which changed less than carbon remineralization rates relative to surface-water primary production. On the west side of Isla Isabela, the greater penetration implies overall remineralization was greater than observed in the Mediterranean by Gehlen et al. (1997).

One factor contributing to the difference in rates on the west and east sides of the island may have been the phytoplankton composition. Surface waters to the west of Isla Isabela were dominated by large diatoms, which can sink relatively fast. In contrast, small phytoplankton were dominant on the east side. When compared to larger phytoplankton, smaller phytoplankton sink out of the surface waters more slowly and may be more susceptible to grazing, resulting in less material reaching the seafloor (Martin et al. 2000). For this reason, the sedimentary processes analyzed appear to be more representative of surface-water primary production on the western side of the island (station BI) than on the eastern side (stations 4 and 5).

The rates of carbon remineralization did not generally increase with increasing water depth. A greater rate of carbon remineralization implies that a smaller percentage of delivered carbon is being stored in the sediments. The high rate of carbon remineralization exhibited at
station BI compared to the other stations does not necessarily mean that lower amounts of carbon exist there, however. The greater primary productivity at station BI, and the dominance of diatoms there, could instead translate to greater amounts of organic carbon in the surface water overlying station BI, likely greater amounts of carbon transferred to the seafloor, and possibly higher amounts of carbon in the sediments despite the larger remineralization rates. Depth of the water column also plays an important role in this situation, however, because with increasing depth comes decreasing carbon rain rate. Therefore, little can be inferred from these data about sediment organic carbon concentrations; future work could measure these directly.

As previously mentioned, a great deal of time was spent searching for sediments to sample, with the conclusion being that sediments were patchy in most vicinities around the islands. Although some carbon is likely being stored in Galapagos sediments, it is unlikely that the region is a major sink for atmospheric CO$_2$ because of this lack of sediments available for deep-sea sequestration, as well as the high rates of carbon remineralization on the west side.

**Conclusions**

Due to the similarity in grain size, color, amount of biological organisms and the lack of evidence for bioturbation, stations BI and 5 offered a reliable comparison between sediments underlying regions of high and low productivity. Although these two stations showed visual evidence of biological activity (worms, shell fragments, etc.), the oxygen concentration profiles did not show evidence of disturbance. On the other hand, sediments at station 4 offered visual and numerical evidence of biological activity, with both the presence of worms and an oxygen profile that was likely disturbed by bioturbation. This comparison suggested that greater rates of primary production in the surface waters were associated with shallower oxygen penetration
depths and greater rates of carbon remineralization in the sediments. Thus, sedimentary carbon remineralization in the area reflects regional variability in surface-water processes. The sparseness of sediments around the Galapagos Islands and the interpreted high rates of carbon remineralization, especially on the west side of Isla Isabela, suggest that the region is not a major sink for atmospheric CO$_2$. 
References


## Tables

Table 1. Station locations and depths for sediment samples obtained from 20-28 January 2006 research. Also see Fig. 1 for station locations.

<table>
<thead>
<tr>
<th>Station</th>
<th>Latitude (South)</th>
<th>Longitude (West)</th>
<th>Depth (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0° 32.80'</td>
<td>91° 22.91'</td>
<td>1089</td>
</tr>
<tr>
<td>2</td>
<td>0° 33.34'</td>
<td>91° 22.39'</td>
<td>1072</td>
</tr>
<tr>
<td>3</td>
<td>0° 33.90'</td>
<td>91° 22.20'</td>
<td>1083</td>
</tr>
<tr>
<td>4</td>
<td>0° 5.91'</td>
<td>91° 7.18'</td>
<td>2257</td>
</tr>
<tr>
<td>5</td>
<td>0° 21.40'</td>
<td>90° 48.77'</td>
<td>640</td>
</tr>
</tbody>
</table>
Table 2. Oxygen consumption, carbon remineralization rate and oxygen penetration depth in sediments in relation to chlorophyll *a* concentrations and rates of primary production in overlying surface waters at each sample station. The standard error reported for station BI indicates the variability seen at stations 1-3; the error reported for stations 4 and 5 is the standard error of the quadruplicate subcores at each respective station.

<table>
<thead>
<tr>
<th>Station</th>
<th>O₂ Consumption (nmol cm⁻² s⁻¹)</th>
<th>C Remineralization Rate (µmol cm⁻² s⁻¹)</th>
<th>O₂ Penetration Depth (mm)</th>
<th>Chlorophyll a (ug L⁻¹)</th>
<th>Primary Production (µmol C L⁻¹ d⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>BI</td>
<td>1.8 x 10⁻³ ± 0.66 x 10⁻⁴</td>
<td>1.4 x 10⁻⁶ ± 5.1 x 10⁻⁸</td>
<td>7.2 ± 0.6</td>
<td>0.6</td>
<td>13.6</td>
</tr>
<tr>
<td>4</td>
<td>1.0 x 10⁻³ ± 3.2 x 10⁻⁴</td>
<td>0.77 x 10⁻⁶ ± 25 x 10⁻⁸</td>
<td>10.4 ± 0.3</td>
<td>0.3</td>
<td>6.5</td>
</tr>
<tr>
<td>5</td>
<td>0.81 x 10⁻³ ± 0.71 x 10⁻⁴</td>
<td>0.62 x 10⁻⁶ ± 2.0 x 10⁻⁸</td>
<td>12.1 ± 2.0</td>
<td>0.5</td>
<td>9.4</td>
</tr>
</tbody>
</table>

A. Inferred from CTD fluorometry calibrated to extracted chlorophyll *a* values of Snow (2006).

B. Measured in surface water at each station at 100% light level by Gilmore (2006).

C. Sub-core 1 (Fig. 4A) was not used in calculations of O₂ consumption, C remineralization and O₂ penetration depth; see text for details.
Figure Legends

Figure 1. Map of the western Galapagos Islands showing station locations for the five box cores obtained during cruise TN-189 of R/V Thomas G. Thompson in January 2006, with respect to South America. Station details are given in Table 1. Stations 1-3 are in an area of high primary production due to upwelling of the Equatorial Undercurrent, and are collectively referred to, in the text, as station BI. Stations 4 and 5 are in areas of lower productivity. Map of the Galapagos Islands adapted from Kurz et al. (2001); map of South America adapted from Surtrek Tour Operator (unpubl.).

Figure 2. Typical distribution of oxygen in (A) undisturbed sediments and (B) sediments disturbed by burrowing organisms. The effect of burrowing (bioturbation) is to increase the permeability of the upper sediment layers, thereby permitting deeper penetration of oxygen-rich waters through sediments. Figure adapted from Sayles, F.L. and Goudreau, J. (unpubl.).

Figure 3. Sedimentary oxygen concentration profiles for all sub-samples from stations 1, 2 and 3 (A), (B) and (C), respectively, which form a collective station BI. Stations 1-3 are characterized by overlying regions of relatively high surface-water primary productivity and chlorophyll a levels. Oxygen concentrations are shown with respect to depth, relative to the sediment-water interface. See Fig. 1 and Table 1 for station locations.

Figure 4. Sedimentary oxygen concentration profiles for all sub-samples from stations 4 and 5, (A) and (B), respectively. Stations 4 and 5 are characterized by overlying regions of relatively low surface-water primary production and chlorophyll a levels. Oxygen concentrations are shown with respect to depth, relative to the sediment-water interface. See Fig. 1 and Table 1 for station locations.
Figure 5. Representative sedimentary oxygen concentration profiles for stations BI (relatively high productivity) and 4 and 5 (relatively low productivity). For estimates of standard error, see Table 2.
Figures

Figure 1.
Figure 2.
Figure 3.
Figure 4.
Figure 5.