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Benthic *in situ* respiration in the upwelling area off central Chile

Ronnie Nøhr Glud*, Jens Kristian Gundersen, Ola Holby*****

Max Planck Institute for Marine Microbiology, Microsensor Research Group, Celsiusstraße 1, 28359 Bremen, Germany

ABSTRACT: Benthic O_2 uptake rates and O_2 microprofiles were measured in the upwelling area off central Chile. Measurements were performed both *in situ* and in the laboratory on recovered sediment cores. Comparison between the 2 data sets confirmed retrieval and handling artifacts inferred from previous studies. Onboard measurements indicated that the effects were mainly associated with core warming during recovery. Fauna mediated O_2 uptake was significant even at abyssal depths and generally *in situ* O_2 uptake rates were higher and showed stronger attenuation with water depth than previous measurements performed in the NE Pacific. However, O_2 uptake rates and O_2 penetration depths were very similar to measurements performed in the SE Atlantic, and the compiled data sets were approximated by simple exponential equations relating the measurements to water depth. By comparing our total O_2 *in situ* uptake rates to simultaneous measurements of primary production (PP) and new production (NP) of the overlying water column, it was calculated that the benthic mineralization accounted for 13 to 66% of the PP and for 28 to 92% of the NP at water depths shallower than 1000 m. At water depths from 1000 to 4000 m, the benthic mineralization equaled 2 to 11% of the PP and 22 to 38% of the NP. The benthic mineralization thereby accounted for a significant turnover of organic material even at the abyssal stations. The presented data add to the limited number of *in situ* deep sea mineralization measurements from the southern hemisphere.

KEY WORDS: Benthic mineralization · Oxygen · Landers · *In situ* · Microsensors

INTRODUCTION

Organic carbon that settles to the sea floor is mineralized through a complex web of fermentative and respiratory processes, mainly mediated by different populations of microorganisms. Eventually mineralization ceases, and the remaining organic material is buried in the sediment (Berner 1980). Benthic mineralization thereby plays an important role in limiting the burial of carbon in the marine environment. The oxidation of organic carbon to CO_2 is balanced by the reduction of available electron acceptors O_2, NO_3^-, Mn-oxides, Fe-oxides and SO_4^-. Although O_2 generally may play a minor role in the direct heterotrophic degradation of organic carbon, reduced solutes released during anaerobic degradation are ultimately reoxidized by an equivalent amount of oxygen (Canfield et al. 1993). Therefore common techniques to quantify total benthic mineralization have been the measurements of the total O_2 uptake rate (TOU) of the sea floor (e.g. Smith & Hinga 1983), or alternatively the measurement of the total benthic release of dissolved inorganic carbon (DIC), the ultimate product from organic carbon mineralization (e.g. Anderson et al. 1986).

The region off central Chile is characterized by intense wind-driven upwelling during summer (September–April), which gives rise to some of the highest primary production in the ocean (Fossing et al. 1995). During non-upwelling periods primary production rates are more moderate, but the area is still among the most productive marine environments in the world (Berger et al. 1987) and supports a bountiful fishery. Despite a general interest in the area and numerous investigations in relation to 'El Niño', very few mea-

Present addresses:
*Marine Biological Laboratory, University of Copenhagen, Strandpromenaden 5, 3000 Helsingør, Denmark. E-mail: mblrg@mail.centrum.dk
**National Environmental Research Institute, Vejlsøvej 25, 8600 Silkeborg, Denmark
***Högskolan Dalarna, Röda Vägen 3, 78188 Borlänge, Sweden

surements of the benthic carbon oxidation have been performed in this area (Thamdrup & Canfield 1996). We here present the first *in situ* study on benthic exchange and mineralization rates from the upwelling area off Chile. Data are compared to measurements made in the laboratory and to similar studies performed in other regions. The importance of benthic carbon mineralization is discussed in relation to estimates of export production (C_{org}), primary production (PP) and new production (NP) for the area.

MATERIALS AND METHODS

Logistics. During 2 cruises, a total of 10 stations were investigated. Stns C6 and C18 were visited between 12 and 17 March 1994 during the 'Thioploca cruise 1994' with the RV 'Vidal Gomaz' (Fossing et al. 1995). The second cruise took place during the period 11 to 31 May 1995. Here a total of 8 stations were visited. Locations of the individual stations are indicated in Fig. 1 and are listed with station characteristics in Table 1. Sediment cores were recovered for laboratory measurements at all oxic stations, and a profiling lander (Profilur) (Gundersen & Jørgensen 1990) and a benthic chamber lander (Elinor) (Glud et al. 1994) were successfully deployed at 7 and 9 stations, respectively (see Table 1).

Laboratory measurements. At each station, 4 to 6 sediment cores with a diameter of 9.6 cm and an approximate length of 30 cm were recovered by a multiple corer (Barnett 1984). The sediment surface was undisturbed to the extent that small surface structures appeared intact. Immediately after recovery, samples from the overlying water phase were recovered for O_2 and DIC determination. Oxygen concentrations were determined by Winkler titration (Strickland & Parsons 1972), while samples for DIC were stored in 7 ml gastight exetainers (Labco, High Wycombe, UK) spiked with 200 µl saturated $HgCl_2$. The DIC concentrations were later determined by coulometric titration (VIC, CM 5012) (Johnson et al. 1987) .

The sediment cores were submerged in an incubation tank without caps. When cores were from shallow stations (<100 m), the tank was filled with bottom water prior to the incubations, whereas surface water was used with cores at the deeper stations.

The O_2 consumption of surface water was marginal as compared to the sediment O_2 consumption rats (not shown). The temperature of the incubation tank was at all stations maintained at the *in situ* value by a thermostated cooler, while the *in situ* O_2 concentration of the overlying water was ensured through continuous flushing with an air/N_2 mixture, regulated from a digital gasmixer (Brooks Instruments). The cores were preincubated for 6 to 12 h before any measurements were made. Small Teflon-coated magnets were attached to the inner wall of each tube, and their rotation, which was driven by an external magnet, ensured a well-mixed overlying water (Rasmussen & Jørgensen 1992). The stirring rate gave rise to a diffusive boundary layer (DBL) thickness of approximately 600 µm (data not shown).

At each station 3 to 9 O_2 microprofiles were measured in 3 different sediment cores. The applied O_2 sensors were Clark type microelectrodes equipped with a guard cathode and an internal reference (Revsbech 1989). The microelectrodes had outside tip diameters between 10 and 25 µm, stirring effects <1%, and a 90% response time <1 s (Revsbech 1989). The position of each microelectrode was controlled by a motor driven micromanipulator, and the sensor signal was recorded by a picoammeter connected to a strip-chart recorder and an A/D-converter which transferred the signals to a PC (Revsbech & Jørgensen 1986). During profiling, the O_2 concentration was recorded at a depth interval of 100 µm.

The remaining cores were used for whole core incubation. These cores were closed by a butyl-rubber stopper with 2 penetrating glass tubes leaving an internal water height above the sediment interface of 6 to 10 cm. The cores were kept in the incubator throughout the whole sampling program. Samples for O_2 determinations (10 ml) were drawn from the enclosed water phase through one tube while the sampling vol-

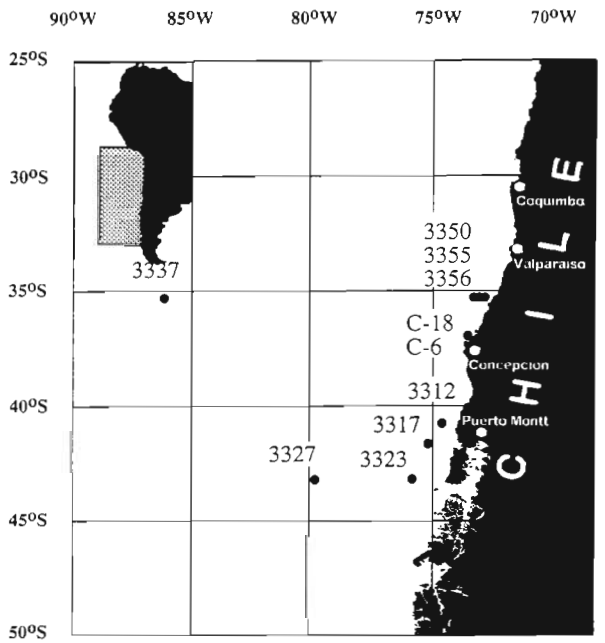

Fig. 1. Study site indicating the positions of the investigated stations

Table 1 Characteristics of each sampling site. L = laboratory measurements, E = Elinor successfully deployed, P = Profilur successfully deployed

Station	Latitude	Longitude	Water depth (m)	Bottom water O_2 (µM)	Bottom water temp. (°C)	Cast
C6	36° 37.3' S	73° 00.6' W	34	0	11.4	EP
C18	36° 31.4' S	73° 08.2' W	87	0	11.7	EP
GeoB 3312	40° 59.5' S	74° 20.1' W	606	209	5.5	LE
GeoB 3317	42° 01.9' S	75° 18.1' W	3012	147	1.8	LE
GeoB 3323	43° 13.0' S	76° 00.0' W	3459	161	1.8	LEP
GeoB 3327	43° 14.0' S	79° 87.0' W	3533	170	1.7	LE
GeoB 3337	35° 15.0' S	86° 00.0' W	4079	182	1.7	LP
GeoB 3350	35° 15.3' S	73° 25.2' W	2470	153	1.8	LEP
GeoB 3355	35° 13.0' S	73° 06.7' W	1445	136	2.7	LEP
GeoB 3356	35° 13.1' S	73° 12.2' W	580	176	5.6	LEP

ume was replaced by water from the incubation tank through the second tube (the dilution was later corrected for). The samples were recovered in gastight glass syringes and Winkler reagents were added directly to the syringes. Six samples were recovered from each core at an evenly spaced time interval. The O_2 concentrations were never allowed to decrease by more than 35% of the initial concentration during the 3 to 75 h long incubations before the incubation was ended. The O_2 concentrations of the samples were later determined by titration.

***In situ* measurement.** The 2 benthic landers, Profilur and Elinor, were deployed in order to measure O_2 microprofiles and benthic exchange rates *in situ*. Both landers worked as independent vehicles and after deployment they sank towards the seafloor at a speed of approximately 35 m min^{-1}. The Profilur was equipped with 4 to 7 O_2 microelectrodes with the same characteristics as the sensors applied in the laboratory. One hour after landing at the sea floor, the Profilur lowered the sensor array in increments of 100 µm and at each depth the signals of all sensors were recorded and stored (Gundersen & Jørgensen 1990). After a total traveling distance of 20 cm, the sensors were retracted and a bottom water sample was collected for sensor calibration. The obtained microprofiles contained 2 inherent calibration points, the constant reading in the bottom water and the constant low reading in the anoxic sediment.

The benthic chamber lander, Elinor, implanted a central respiration chamber during landing and after a resting period of 1 h; incubation was initiated by lid-closure (Glud et al. 1994). The water phase was stirred by a central impeller which gave rise to an average DBL thickness of approximately 520 µm (Glud et al. 1995a). The O_2 concentration was measured continuously by minielectrodes (Glud et al. 1995a). During the incubation, 5 to 10 water samples of 50 ml were retracted from the overlying water phase at predefined time intervals. The water was replaced by water from outside the chamber and the dilution was later corrected for. Ten ml of each sample were stored in gastight glass ampoules for later O_2 determination while the rest was stored in 50 ml plastic syringes. At the end of the incubation a scoop closed beneath the chamber and the incubated sediment was recovered together with the lander. On deck the water samples for O_2 and DIC were treated as described above. The O_2 determination was used for subsequent sensor calibration. Exchange rates of DIC were only measured during incubations with a presumed high activity or when logistics allowed long deployments. The lander recovered sediment was sieved through a mesh screen of 1 mm; the macrofauna was collected, stored in 70% ethanol and later sorted into taxa. The dry weight and the weight loss following ignition at 560°C for 24 h was determined for each group of macrofauna.

It has been shown that central stirring of benthic chambers creates radial pressure gradients, which can initiate an advective porewater transport in permeable sediments (Huettel & Gust 1992a, Glud et al. 1996). However, the sediments we investigated were fine grained and highly impermeable. Enhanced flushing of empty burrows caused by the stirring cannot be completely excluded. However, the maximal pressure gradients in the chamber at the applied stirring rate was 0.048 Pa cm^{-1} (Glud et al. 1995a), which only marginally can affect flushing of U-shaped burrows (Huettel & Gust 1992b).

Calculations. From the obtained microprofiles it was possible to determine the upper boundary of the DBL as the intersection point between the extrapolated linear O_2 gradient in the DBL and the constant O_2 value in the overlying water (see Fig. 3 ['Results'], Jørgensen & Revsbech 1985). Since the position of the sediment surface typically was indicated by a distinct break in the profile (Glud et al. 1995b), the DBL thickness could be determined. The diffusive O_2 uptake (DOU) was calcu-

lated from measured microprofiles by applying Fick's first law of diffusion: $-DOU = D_0(\delta C/\delta z)$, where D_0 is the diffusion coefficient in water and C is the solute concentration at a given depth (z) within the DBL. The temperature corrected D_0 values for O_2 were derived from Broecker & Peng (1974) and Li & Gregory (1974). Fig. 3D demonstrates how the DBL, the position of the sediment surface and the concentration slope within the DBL were defined. The average specific O_2 consumption was calculated by dividing the DOU with the thickness of the oxic zone. Total fluxes of DIC and O_2 (TOU) were calculated by linear regression of solute concentrations as a function of incubation time accounting for the enclosed water volume.

RESULTS

The O_2 concentration of the bottom water varied among the investigated stations. At the 2 shallowest stations the bottom water (BW) was fully anoxic, while the O_2 concentration varied between 136 and 209 µM at the remaining stations (Table 1). Values obtained by Winkler titration on water recovered by the landers or the 'multiple corer' never deviated by more than 5% from data recorded by a CTD (data not shown). Measurements performed during the 'SCORPIO'-cruises at stations in immediate vicinity of some of the deeper stations investigated in this study (GeoB-3323, 3327, 3350, 3355, 3356) resulted in BW O_2 concentrations which differed by no more than 7% from our measurements (Reid 1973, Warren 1973).

At each of the 2 anoxic stations the chamber lander was deployed twice. At Stn C6 the measured DIC release rates were 210 and 116 mmol m^{-2} d^{-1}, while the rates were 31.4 and 25.0 mmol m^{-2} d^{-1} at Stn C-18 (Table 2). The variability in exchange rate at each site reflects the sediment heterogeneity. Massive, but heterogeneous, occurrence of the colorless sulfur bacteria *Thioploca* spp. and *Beggiatoa* spp. was apparent at both stations, and the total bacterial biomass was found to be 700 and 1200 g m^{-2} (wet weight) at sites close to C6 and C18, respectively (Fossing et al. 1995, Schulz et al. 1996). However, despite sediment variability the *in situ* DIC release rates, matched depth integrated carbon oxidation rates determined by bag incubations techniques within a factor of 2 at those same stations (Thamdrup & Canfield 1996).

At each of the remaining stations the chamber lander was deployed once. The *in situ* TOU varied from −15.7 mmol m^{-2} d^{-1} at Stn GeoB 3312 to a minimum value of −1.4 mmol m^{-2} d^{-1} at Stn GeoB 3327 (Table 2). The *in situ* DIC release rate co-varied with TOU, and the (DIC release/TOU)-ratio varied between 1.0 and 1.5 at the investigated stations (Table 2). This demonstrates that the TOU and the DIC release rates resulted in comparable benthic mineralisation rates. Both TOU measured in the laboratory and *in situ* correlated with water depth (Table 2), but generally the laboratory values overestimated the *in situ* values at the deepest stations, while they were lower at the more shallow stations (Table 2). Fig. 2 presents examples of incubation measurements obtained *in situ*.

The profiling lander was deployed once per station. In general *in situ* and laboratory microprofiles were similar, and only at the deepest station (where both measurements were successfully performed) did the profiles differ significantly (Table 2, Fig 3). Here the O_2 penetration in the laboratory only accounted for 30% of the *in situ* value, while the laboratory DOU was approximately 3 times higher than the corresponding *in situ* value (Table 2).

The *in situ* O_2 uptake rates and O_2 penetration depths were comparable to similar measurements performed in the SE Atlantic (Glud et al. 1994). In both data sets the difference between TOU and DOU was

Table 2. Total exchange of oxygen (TOU) and dissolved inorganic carbon (DIC); diffusive oxygen uptake (DOU) and oxygen penetration (O_2 pen.) depth measured *in situ* and in the laboratory. Standard deviations are included. Values in parentheses show the number of replicates

Station	TOU—*in situ* (mmol m^{-2} d^{-1})	DIC—*in situ* (mmol m^{-2} d^{-1})	DOU—*in situ* (mmol m^{-2} d^{-1})	O_2 pen.—*in situ* (mm)	TOU—in lab (mmol m^{-2} d^{-1})	DOU—in lab (mmol m^{-2} d^{-1})	O_2 pen.—in lab (mm)
C-6	0.0 ± 0.0 (2)	163 ± 47 (2)	0.0 ± 0.0 (6)	0.0 ± 0.0 (6)	–	–	–
C-18	0.0 ± 0.0 (2)	28.2 ± 3.2 (2)	0.0 ± 0.0 (6)	0.0 ± 0.0 (6)	–	–	–
GeoB 3312	−15.7	18.3	–	–	−10.9 ± 1.8 (3)	−12.3 ± 1.9 (7)	1.0 ± 0.4 (7)
GeoB 3317	−3.9	–	–	–	−2.1 ± 0.5 (3)	−2.6 ± 0.7 (9)	7.8 ± 1.1 (9)
GeoB 3323	−2.8	–	−0.9 ± 0.3 (6)	37.8 ± 2.9 (6)	−4.0 ± 1.0 (3)	−2.9 ± 0.8 (11)	11.4 ± 1.8 (11)
GeoB 3327	−1.4	–	–	–	−2.6 ± 0.3 (3)	–	–
GeoB 3337	–	–	−0.3 ± 0.1 (5)	129.7 ± 10.2 (5)	−1.9 ± 0.5 (3)	–	–
GeoB 3350	−2.8	4.1	−2.4 ± 1.0 (5)	12.6 ± 1.6 (5)	−3.7 ± 0.6 (3)	−2.6 ± 0.2 (5)	7.1 ± 2.1 (5)
GeoB 3355	−3.6	3.7	−2.8 ± 0.7 (5)	11.1 ± 3.4 (5)	−4.5 ± 0.8 (3)	−2.4 ± 0.5 (3)	7.5 ± 1.5 (3)
GeoB 3356	−9.7	10.6	−4.9 ± 0.9 (6)	6.5 ± 1.4 (6)	−7.7 ± 0.7 (3)	−4.6 ± 0.1 (3)	6.6 ± 0.1 (3)

significant at the shallow fauna-rich stations, but converged at the deeper stations (Fig. 4A). The compiled data set was fitted by 2 simple exponential equations expressing TOU and DOU as a function of water depth (z); TOU = $2.76e^{-0.57\times10^{-3}z}$ (r^2 = 0.65) and DOU = $1.93e^{-0.55\times10^{-3}z}$ (r^2 = 0.88) (Fig. 4A). The O_2 penetration depth in both studies increased exponentially with water depth as the average specific O_2 consumption rate decreased by almost 3 orders of magnitude at water depths from 500 to 5000 m (Fig. 4B,C). The strong correlations between water depth and (1) benthic O_2 uptake rates, (2) O_2 penetration depth and (3) the specific O_2 consumption rate indicate that the sedimentation of organic carbon to the seafloor was the key variable regulating the benthic O_2 uptake in both regions. Data did not correlate well with bottom water O_2 concentration (not shown).

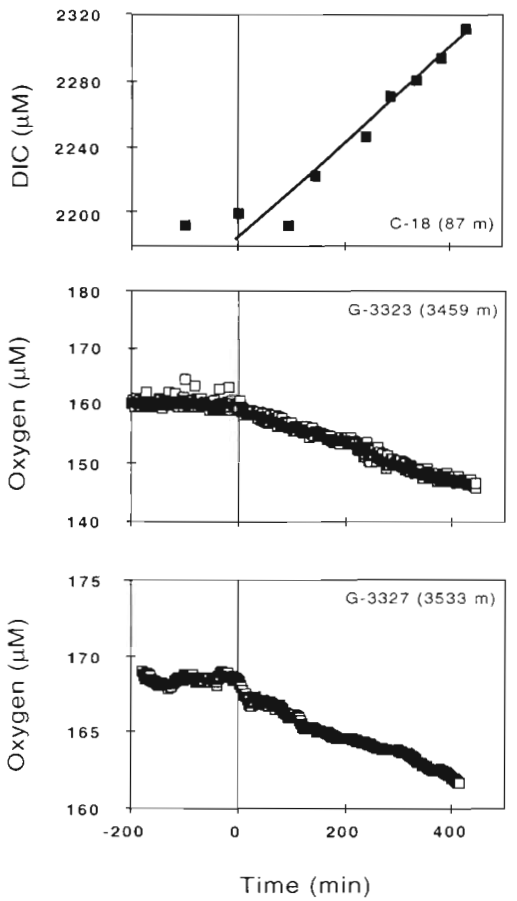

Fig. 2. Concentration of DIC and O_2 as measured during 3 separate deployments of the benthic chamber lander. The selected data represent a very shallow station, the deepest station, and the deepest station where both landers were successfully deployed. Data collected during descent are omitted and the vertical line (time 0) indicates lid closure. The water column heights in the chamber during the 3 incubations were 7.4, 6.2 and 12.1 cm, respectively

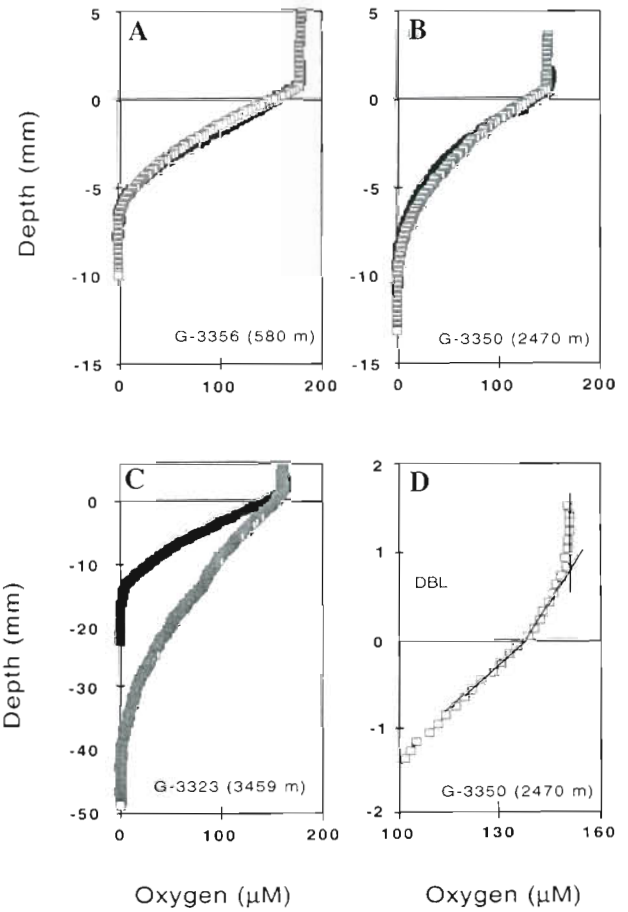

Fig. 3. (A–C) Individual oxygen microprofiles measured *in situ* (gray squares) and in the laboratory (black squares). (D) Expanded view of the measuring points at the interface of the *in situ* profile shown in (B). Horizontal line indicates the position of sediment surface (depth 0). DBL: diffusive boundary layer

DISCUSSION

O_2 uptake measured by the various techniques

This study's comparison between *in situ* and laboratory data confirm that retrieval and handling artifacts also inferred in previous studies (Devol & Christensen 1993, Glud et al. 1994, Aller et al. 1998). At shallow stations, laboratory and *in situ* microprofiles were similar, while they differed at the deepest investigated station (Table 2, Fig. 3). In a previous study it was demonstrated that at water depths >2000 m *in situ* microprofiles exhibited significantly deeper O_2 penetration and lower DOU values as compared to microprofiles measured in recovered sediment cores (Glud et al. 1994). The effect was a function of water depth and the maximum difference was observed at approximately 5000 m water depth where the O_2 penetration in the

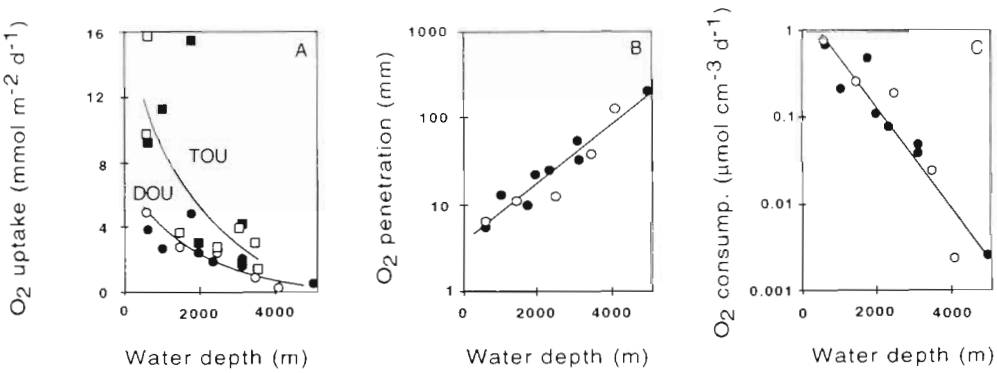

Fig. 4. Total O_2 uptake squares (TOU, squares) and the diffusive O_2 uptake (DOU, circles) as a function of the water depth. Filled symbols represent data measured in the Benguela upwelling area of the SE Atlantic (Glud et al. 1994), while open symbols represent data from the present study. The compiled data set was fitted to 2 exponential equations describing the DOU and TOU as a function of water depth. (B) and (C) represent the O_2 penetration depth (OP) and the average specific O_2 consumption (O_2 consump.) calculated from microprofiles obtained in the present study (○) and by Glud et al. (1994) (●). The compiled data set was fitted by $OP = 1.32e^{0.77\times10^{-3}z}$ ($r^2 = 0.91$) and $O_2\ con = 0.62e^{1.33\times10^{-3}z}$ ($r^2 = 0.89$), respectively

laboratory only accounted for 25% of the *in situ* value while the laboratory DOU value was 3.5 times higher than the corresponding *in situ* value (Glud et al. 1994). These findings are confirmed by the present study (Table 2, Fig. 3).

The recovery of sediment cores from 3500 m water depth to the warmer surface waters combined with the onboard handling prior to preincubation caused the temperature in the center of the core to increase from 1.7 to 7.1°C (data not shown). Consecutive microprofile measurements in such a sediment core placed at *in situ* temperature in the incubation chamber reflected elevated DOU values which gradually approached the *in situ* rate (Fig. 5). A parallel core which initially was allowed to reach a temperature of 20°C (reached after 45 min at room temperature) prior to placement in the incubation tank at *in situ* temperatures showed a stronger but similar response. The data demonstrate that for abyssal sediments, a transient rise in temperature during recovery alters the oxygen consumption rate in recovered sediment cores and that in such cases long preincubation periods at in situ temperature (>60 h) are required in order to reestablish *in situ* O_2 conditions.

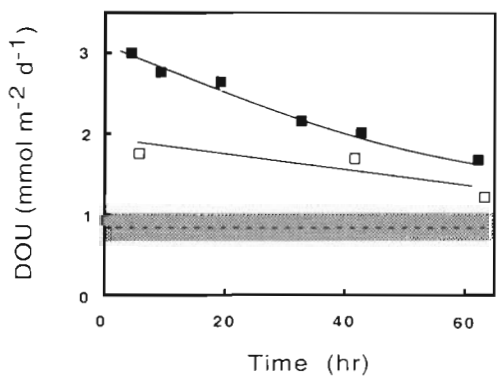

Fig. 5. Temporal development of the diffusive O_2 uptake (DOU) in 2 recovered sediment cores. The cores were recovered at time 0 min. Broken horizontal line indicates the average DOU measured *in situ*, and the shaded bar the SD of the measurement. Lines following the data points were handdrawn (the data are partly redrawn from a Danish report, Gundersen et al. 1995)

We speculate that heating, potentially in combination with release of labile organic carbon from lysed psychro- or barophilic microbiota, stimulates the microbial activity of recovered sediment cores. Placed at *in situ* temperature the activity decreases; however, the diffusive supply of O_2 towards the deeper sediment layers which have been depleted in O_2 during the transient heating require a preincubation period. For shallow water depths, higher *in situ* temperature and lower O_2 penetration depth shortens the required preincubation period, and for stations at water depths <2000 m 6 to 12 h was sufficient in the present study (Table 2). Such a recovery effect also explains the relatively high TOU rates measured in sediments recovered from the abyssal stations (Table 2). At the shallow fauna-rich stations the laboratory determined TOU, however, generally underestimated the *in situ* values (Table 2). As previously suggested, we ascribe this to inactivation of recovered fauna and more representative inclusion of larger infauna species in the larger *in situ* incubation chamber (896 cm^2) as compared to the smaller sediment cores applied in the laboratory (68 cm^2) (Devol & Christensen 1993, Glud et al. 1994, 1998). Thereby laboratory determined TOU rates are affected by 2 opposing effects: temporary heating which increases the O_2 uptake and exclusion or inactivation of

Table 3. Amount of benthic fauna and fauna mediated oxygen uptake (TOU-DOU), porosity and organic carbon values for the upper 5 mm in the investigated sediments. LOI = loss on ignition. nm = not measured

Station	Water depth (m)	Fauna LOI (g m^{-2})	TOU-DOU (mmol m^{-2} d^{-1})	Porosity (vol/vol)	Organic C (%)
C6	34	5.1	nm	0.88	6.31
C18	87	3.0	nm	0.93	4.43
GeoB 3312	606	9.4	3.4 ± 1.9[a]	0.87	nm
GeoB 3317	3012	4.1	1.3 ± 0.7[a]	0.91	1.50
GeoB 3323	3459	2.4	1.9 ± 0.3	0.83	nm
GeoB 3327	3533	1.9	nm	0.86	nm
GeoB 3337	4079	–	nm	0.84	0.63
GeoB 3350	2470	2.2	0.4 ± 1.0	0.90	2.73
GeoB 3355	1445	8.2	0.8 ± 0.7	0.86	3.04
GeoB 3356	580	16.2	4.8 ± 0.9	0.89	nm

[a]DOU determined in the laboratory

macrofauna which decreases the O_2 uptake. In relation to water depth the *in situ* TOU was more scattered than the DOU (Fig. 4A); this is most likely caused by patchy distribution of benthic fauna.

Simultaneous *in situ* measurements of DOU and TOU were only successfully performed at 4 stations. The difference between TOU and DOU, which is a measure of the fauna-mediated O_2 uptake (Archer & Devol 1992), varied from 0.4 to 4.8 mmol m^{-2} d^{-1} at the investigated stations. The values generally correlated to the amount of fauna recovered by the Elinor chamber (Table 3). The macrofauna was at all stations dominated by polychaetes, both in numbers and weight, and the benthos mediated O_2 uptake was probably caused largely by burrow irrigation, exposing otherwise anoxic sediment to O_2. The fauna-mediated O_2 uptake was higher than that deduced from comparable measurements performed off central California (Jahnke et al. 1990) but generally comparable to measurements performed off Namibia (Glud et al. 1994). These observations suggest that macrofaunal activity may indeed be significant and consequently of importance for regional C cycling in deep sea sediments located in regions of continental upwelling.

High O_2 uptake of the southern upwelling areas

Our *in situ* O_2 uptake rates for the SE Pacific are higher than previous *in situ* measurements taken at comparable water depths in the North and NE Pacific (Smith & Baldwin 1984, Jahnke & Jackson 1987, Jahnke et al. 1990, Archer & Devol 1992, Reimers et al. 1992, Smith et al. 1994, 1997). To our knowledge no *in situ* measurements from the South Pacific have previously been published. The presented data match measurements taken in the Benguela upwelling area (Fig. 6), and both data sets show stronger attenuation with water depth compared to measurements in upwelling areas of the Northern Pacific and Atlantic (Fig. 6, Glud et al. 1994). Data extracted from a recently constructed global map of estimated benthic O_2 consumption rates at water depths less than 1000 m (Jahnke 1996) underestimated our measurements in both upwelling areas especially at shallow depths as did a predictive equa-

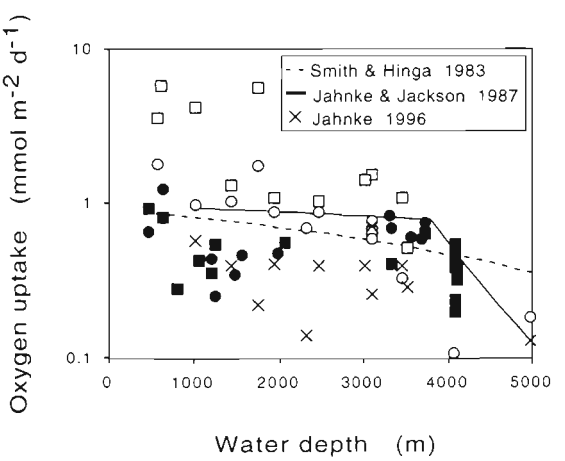

Fig. 6. O_2 uptake rates as a function of water depth from a number of different studies and predictive equations. Open symbols represent measurements made in the SE Atlantic (Glud et al. 1994) and the SE Pacific (TOU = squares, DOU = circles), while closed symbols represent data obtained in the NE Pacific in 3 other studies (Jahnke et al. 1990, Archer & Devol 1992, Smith et al. 1994). Data points within an extremely strong O_2 minimum zone and at water depth <500 m are omitted. Two predictive equations from the NE Pacific relating the TOU to water depth are included together with values for all investigated stations as extracted from Jahnke (1996). For the predictive equation of Smith & Hinga (1983) we applied the regional yearly primary production as accumulated by Berger et al. (1987)

Table 4. Benthic mineralisation (BM) in percent of (1) the yearly export production from the photic zone (Exp P) (derived from Hebbeln et al. in press), (2) primary production (PP) and (3) new production (NP) at the investigated stations (data supplied by O. Ulloa unpubl.). The latter 2 parameters were measured during the same period and at the same locations as those at which the BM measurements were obtained. nm = not measured

Station	Water depth (m)	BM % of Exp P	BM % of PP	BM % of NP
C6	34	–	66.4	91.5
C18	87	–	18.9	28.1
GeoB 3312	606	–	41.0	nm
GeoB 3317	3012	41	11.1	24.1
GeoB 3323	3459	29	8.8	24.5
GeoB 3327	3533	15	10.5	38.2
GeoB 3337	4079	3[a]	1.7[a]	22.4[a]
GeoB 3350	2470	29	nm	nm
GeoB 3355	1445	38	4.4	nm
GeoB 3356	580	–	13.4	45.0

[a]Number calculated on the basis of *in situ* DOU

tion for the Pacific proposed by Smith & Hinga (1983) (Fig. 6). A predictive equation of Jahnke & Jackson (1987), which was generated for water depth >1000 m for the NE Pacific, gave a reasonable fit to our data, but still tended to underestimate the measurements at water depth <3000 m (Fig. 6). Another model, based on data from the North Pacific, expresses the O_2 flux as a function of the bottom water O_2 concentration and the organic carbon percentage of the surficial sediment (Cai & Reimers 1995) and also underestimated our compiled data set (not shown). (Surface organic carbon was only obtained at 6 stations off Chile [Table 3], but at all stations off Namibia.)

Our observations confirm that eastern upwelling areas of the Atlantic and the Pacific have substantially higher O_2 uptake than the central or western non-upwelling regions (Jahnke & Jackson 1987, Jahnke 1996) and suggest that the southern upwelling areas are characterized by higher O_2 consumption rates as compared to investigated northern upwelling regions. However, comparison of O_2 uptake rates obtained in various regions is complicated by local, seasonal and interannual variation.

A 2 yr sediment trap study in the SE Pacific (30° 00' S, 73°11' W) in the vicinity of our research area estimated the annual organic carbon export from the photic zone (C_{org}) to be 3.5 mol C m^{-2} The export rate varied seasonally with maximum values of about 29 mmol C m^{-2} d^{-1} in September 1993 and minimum values around 1.7 mmol C m^{-2} d^{-1} in May–June the following year (Hebbeln et al. in press). Our rates for the deeper sites were obtained in May 1995, and the C_{org} export estimated in the same seasonal period in 1994 by Hebbeln et al. (in press) (between 1.5 and 2 mmol C m^{-2} d^{-1}) could not account for the benthic mineralization we measured (see Table 2). Potential reasons for the gap between the 2 data sets are (1) the site investigated by Hebbeln et al. (in press) is not representative for our stations (2) interannual variation, or (3) temporal displacement between water column production and benthic mineralization. *In situ* measurements have demonstrated that benthic O_2 uptake responds to the seasonal input of organic carbon even at abyssal depths but that the response is significantly dampened (e.g. as the export of C_{org} varied by a factor of 10 to 15, the benthic O_2 uptake varied by less than a factor of 2.5) (Smith et al. 1994, 1997). In more oligotrophic waters *in situ* measurements have demonstrated seasonally invariable TOU rates despite the fact that the export of C_{org} fluctuated by a factor of 4 (Sayles et al. 1994). If we assume that our *in situ* TOU measurements represent the yearly average benthic mineralization rate, then 3 to 41% of the annual exported C_{org} estimated by Hebbeln et al. (in press) is mineralized in the sediment (stations >1000 m water depth), leaving 97 to 59% for water column respiration and permanent burial (Table 4).

During the 2 cruises reported here PP and NP of organic carbon were determined at the same locations and at the same time as we performed our measurements (O. Ulloa unpubl.). The measurements were performed by carbon isotope incubation and estimated from the nitrogen requirement during a 24 h cycle (O. Ulloa unpubl.). The fraction of the PP mineralized in the sediment generally inversely correlated with water depth and reached a maximum value of 66% at 34 m water depth while a minimum value of 2% was obtained at the deepest site of 4079 m (Table 4). For most stations the measured NP rates were higher than the export of production measured during the same seasonal period in 1994 at the site investigated by Hebbeln et al. (in press). For the abyssal stations 25 to 38% of the new production of organic carbon was min-

eralized in the sediment, while a maximum of 92% of NP was mineralized in the sediment at the 34 m station (Table 4). These measurements represent the conditions in May 1995, and it is difficult to evaluate to what extent our measurements resolve the temporal fluctuations in the coupling between NP and TOU. Nevertheless, our calculations strongly indicate that the benthic mineralization in the upwelling areas of the SE Pacific, even at abyssal depths, is responsible for recycling a significant fraction of the organic carbon leaving the photic zone.

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