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## Benthic carbon mineralization in the Atlantic: a synthesis based on in situ data from the last decade

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### Abstract

Benthic oxygen uptake rates quantified by the use of microsensors and flux chambers over a period of approx. 10 yr were compiled and used to assess the organic carbon mineralization in the central and South Atlantic (35°N–50°S). Measurements were performed in situ and in the laboratory on recovered sediment cores. In contrast to the laboratory data, both the in situ diffusive (DOU) and total oxygen uptake (TOU) decreased with increasing water depth. The data demonstrated that sediment recovery alter the O<sub>2</sub> microdistribution and affect the measured O<sub>2</sub> uptake rates. The ratio between TOU and DOU, a measure of the benthic fauna-mediated oxygen uptake, decreased from 3 to 4 in shallow and productive areas to around 1 at the deeper sites. The in situ oxygen uptake rates (both diffusive and total) also correlated with the oceanic primary production. Based on the compiled in situ measurements an empirical relation between the surface water primary production (PP, g C m<sup>-2</sup> yr<sup>-1</sup>), water depth ( $z, m$ ) and benthic mineralization deduced from the TOU and DOU was established (C-DOU =  $PP^{0.7358} z^{-0.3306}$  (g C m<sup>-2</sup> yr<sup>-1</sup>); C-TOU =  $PP^{1.0466} z^{-0.4922}$  (g C m<sup>-2</sup> yr<sup>-1</sup>)). These equations were extrapolated to the entire investigated area of the Atlantic. The mineralization mimicked the surface water primary production, with high consumption rates in the upwelling areas. For the entire area (water depth  $\geq 1000$  m) the benthic carbon mineralization was between  $134$  and  $168 \times 10^{12}$  g C yr<sup>-1</sup> (from C-DOU and C-TOU, respectively), which equals 1.7–2.1% of the surface water primary production. These rates are higher than previous estimates of benthic carbon mineralization in deep-sea sediments. Integrated for the investigated area of the Atlantic the benthic fauna-mediated carbon mineralization accounted for  $35 \times 10^{12}$  g C yr<sup>-1</sup> (or 21% of the total mineralization rate). Using our relations to calculate the organic carbon flux through the 1000 m depth horizon revealed that between  $212$  and  $333 \times 10^{12}$  g C yr<sup>-1</sup> sink below this depth horizon, of which 63% and 51% is remineralized in the sediments. Particulate organic carbon fluxes obtained from sediment trap data cannot support either the measured or extrapolated benthic mineralization. The areal distribution of the oxygen penetration depth (OPD) for the investigated area of the Atlantic was estimated from the relation between the in situ C-DOU and OPD measurements (OPD =  $114,6968 \text{ C-DOU}^{-0.7541}$  (mm)). © 2002 Elsevier Science Ltd. All rights reserved.

**Keywords:** Benthic mineralization; Oxygen; Landers; In situ measurements; Fauna-mediated transport; Atlantic

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## 1. Introduction

The open oceans (water depth  $\geq 1000$  m) cover a vast area of the global ocean, and 92% of the marine primary production is ascribed to these regions (Ryther, 1969; Antoine et al., 1996). While most of the produced organic material is recycled in the upper 1000 m of the water column (Suess, 1980; Martin et al., 1987; Deming and Baross, 1993; Lee et al., 1998), a significant fraction of the organic material also reaches the seafloor, where it is either remineralized or permanently buried in the sediment (Bernier, 1980; Canfield, 1993). On short time scales the benthic degradation of sedimentary organic matter regenerates inorganic carbon and nutrients for a continued water column production. On long time scales, however, sediments act as an important sink in the regional and global nutrient and carbon cycles (Mackenzie et al., 1993; Archer and Maier-Reimer, 1994).

The benthic carbon oxidation proceeds through a complex web of degradation pathways where the ultimate electron acceptors are  $O_2$ ,  $NO_3^-$ , Mn-oxides, Fe-oxides,  $SO_4^{2-}$  and  $CO_2$  (e.g. Jørgensen, 1977; Canfield et al., 1993; Thamdrup, 2000). The relative importance of the various pathways changes with sediment type and sedimentation rate, but generally  $O_2$  becomes more important with increasing water depth (Jørgensen, 1983; Canfield, 1993). The majority of the reduced counterparts from anaerobic oxidation are ultimately reoxidized by an equivalent amount of  $O_2$ , and consequently, the benthic  $O_2$  uptake is a commonly used measure for the total benthic mineralization rate (e.g. Smith and Hinga, 1983).

The benthic  $O_2$  uptake is either measured directly by incubation of enclosed sediment cores (e.g. Smith and Hinga, 1983) or calculated indirectly from the  $O_2$  concentration gradients measured across the benthic interface (Jørgensen and Revsbech, 1985; Reimers, 1987). For in situ determination of the benthic  $O_2$  uptake, landers performing measurements directly at the seafloor have been designed and optimized over the last few decades (for review see Tengberg et al., 1995; Reimers and Glud, 2000; Reimers et al., 2001).

The present study compiles the existing measurements on benthic  $O_2$  uptake rates from the central and South Atlantic, which previously has been regarded as an under-sampled area. The data set consists of benthic  $O_2$  uptake rates quantified from sediment incubations and  $O_2$  concentration profiles obtained both in the laboratory and in situ. The various measuring approaches are compared and discussed. The in situ measurements are used to construct an empirical relation between benthic mineralization, surface water primary production and water depth. The extrapolated maps for benthic mineralization of the investigated area of the Atlantic are discussed in the context of the few existing models assessing regional and global carbon mineralization of the deep-sea.

## 2. Data compilation and methods of measurements

During seven cruises between 1992 and 1999 a total of 63 stations in the South Atlantic and around the Canary Islands were visited by the research vessel "Meteor". The cruises were an integrated part of the German research projects SFB 261 and CANIGO. The stations were spread over an area between  $35^\circ N$  and  $50^\circ S$  (Fig. 1 and Table 1), which covers the central and South Atlantic, but for simplification in the following we use the term Atlantic. In situ oxygen uptake rates were measured at 35 stations, and ex situ flux measurements were performed in sediment cores recovered from 56 stations (Table 1). Measurements were concentrated along the coastlines of West Africa and eastern South America at water depths ranging from 400 to 5055 m (Fig. 1; Table 1). Some data have previously been presented elsewhere, however, here they are compiled along with the other existing in situ measurements of the central and South Atlantic (see Table 1). The data from Hales and Emerson (1997) were in the vicinity of our measurements in front of the Amazon fan, and the data from Jahnke et al. (1989, 1994) close the gap in our data set in the western South Atlantic between  $0^\circ$  and  $30^\circ N$  (Canary Island). The entire data set consists of 43 ( $\sim 139$  microprofiles) and 21 ( $\sim 25$  chamber

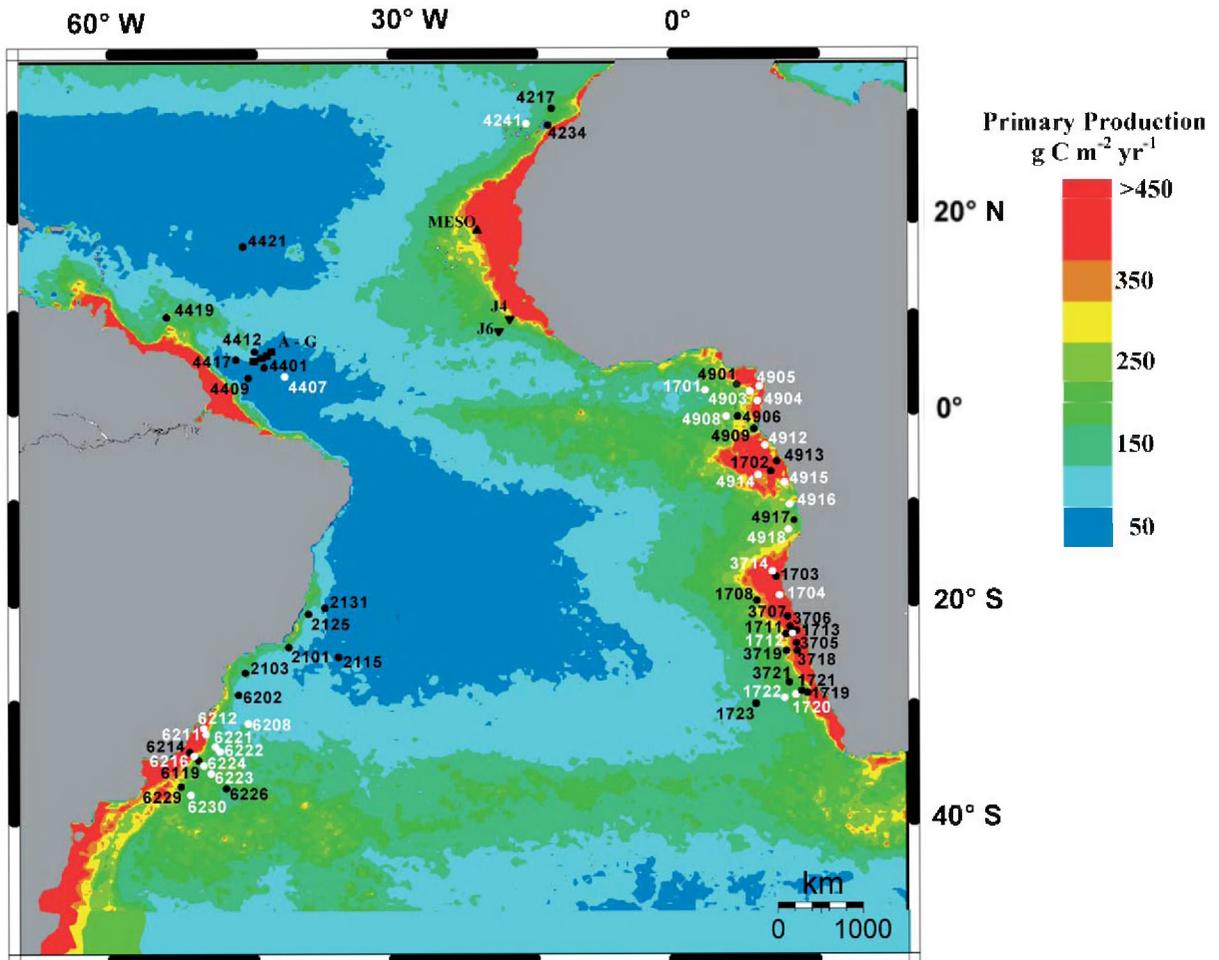


Fig. 1. Locations of the stations and surface water primary production (after Behrenfeld and Falkowski, 1997) of the investigated area. Shown are sites with in situ flux measurements (●) and sites with laboratory flux measurements (○); for detailed information see also Table 1. Additional in situ flux data from Hales and Emerson (1997) (■) and Jahnke et al. (1994) (▲) and 1989 (▼) were included.

incubations) determinations of in situ diffusive oxygen uptake (DOU) and total oxygen uptake (TOU), respectively. While 50 and 19 determinations of ex situ DOU and TOU are included (Table 1). Measurements were obtained over a period of ~10 yr but always during the months of November to March.

### 2.1. Oxygen uptake measurements

In situ oxygen fluxes were measured with autonomously working landers carrying either

profiling units for DOU measurements or benthic chambers for TOU measurements (Gundersen and Jørgensen, 1990; Glud et al., 1994; Wenzhöfer et al., 2001a, b). The profiling units were equipped with an array of oxygen sensors. For high-resolution microprofiles Clark-type oxygen microelectrodes with an internal reference and a guard cathode were used (Revsbech, 1989). The sensors had an outer tip diameter of 10–30 μm, a response time of <2 s and a stirring sensitivity of <2% (Revsbech, 1989; Glud et al., 2000a). For coarser profiles or very oxygenated sediments, rugged

Table 1

Geographical position and characteristics of the stations. BW-O<sub>2</sub> is the bottom water oxygen concentration, DOU is the diffusive oxygen uptake, OPD is the oxygen penetration depth and TOU is the total oxygen uptake. Values in parentheses indicate the number of replicates

Station	Position	Water depth (m)	BW-O <sub>2</sub> (μM)	In situ			Laboratory			Reference <sup>a</sup>
				DOU (mmol m <sup>-2</sup> d <sup>-1</sup> )	OPD (mm)	TOU (mmol m <sup>-2</sup> d <sup>-1</sup> )	DOU (mmol m <sup>-2</sup> d <sup>-1</sup> )	OPD (mm)	TOU (mmol m <sup>-2</sup> d <sup>-1</sup> )	
1701	01°57.0'N 03°33.0'E	4162	214	—	—	—	3.6±0.2	16±2	—	[1]
1702	06°33.2'S 10°19.0'E	3107	214	1.6±0.2(3)	33±2	1.8	2.6±0.3(4)	27±2	3.5±0.2(2)	[1]
1703	17°26.8'S 11°00.8'E	1747	210	4.8±1.1(3)	10±1	15.5	7.2±1.3(16)	9±1	12.9±0.5(2)	[1]
1704	19°24.4'S 11°36.7'E	399	64	—	—	—	1.9±0.3(5)	5.8±0.3	2.4±0.2(2)	[1]
1708	20°05.8'S 08°58.0'E	2321	214	1.9±0.4(2)	25±2	—	3.7±0.5(5)	9±1	3.9±0.3(2)	[1]
1711	23°20.4'S 12°22.9'E	1947	215	2.4±0.4(4)	22±3	3.0	4.4±1.1(4)	9±1	4.7±0.5(2)	[1]
1712	23°15.2'S 12°48.3'E	992	160	—	—	—	5.3±0.4(5)	6.9±0.2	5.6±0.2(2)	[1]
1713	23°14.3'S 13°00.8'E	604	96	3.8±0.8(3)	5.6±0.9	9.2	4±0.7(4)	5.9±0.8	5.5	[1]
1719	28°57.1'S 14°10.5'E	1015	180	2.7±0.5(2)	13±1	11.3	3.8±0.6(6)	11.5±0.5	5.6±0.6(2)	[1]
1720	28°59.9'S 13°50.4'E	2005	225	—	—	—	4.1±0.5(6)	8.5±0.4	6	[1]
1721	29°11.6'S 13°05.4'E	3095	237	2.1±0.5(4)	55±2	4.2	3.4±0.2(5)	41±2	4.8±0.2(2)	[1]
1722	29°27.1'S 11°45.0'E	3978	233	—	—	—	3.3±0.2(6)	25±3	3.9±0.5(2)	[1]
1723	29°53.1'S 08°39.9'E	4986	228	0.5±0.2(4)	200±10	—	1.8±0.3(5)	50±4	2.9±0.3(2)	[1]
2101	23°59.7'S 41°12.5'W	1809	216	0.48±0.01(2)	38±1.5	0.53	1.91±0.3(4)	—	1.37	[2]
2103	27°10.5'S 46°27.8'W	1047	218	1.46±0.2(4)	26±1	2.33	2.38±0.2(6)	—	1.95	[2],[3]
2115	25°30.0'S 36°00.0'W	4100	205	—	—	—	—	—	0.69±0.13(2)	[2],[3]
2125	20°49.7'S 39°50.6'W	1500	186	0.87±0.1(3)	—	—	1.79±0.3(6)	—	2.67±0.3(2)	[2],[3]
2131	20°39.0'S 37°18.6'W	1400	185	—	—	2.07	—	—	—	[2],[3]

3705	24°18.7'S 12°59.9'E	1305	194	2.9±0.44(5)	13±3	—	—	—	—	[3]
3706	22°43.5'S 12°36.3'E	1323	195	2.3±0.37(6)	16±2.5	—	—	—	—	[3]
3707	21°37.8'S 12°11.8'E	1355	193	2.5±0.24(6)	11.6±2	—	—	—	—	[3]
3714	17°09.9'S 10°59.8'E	2060	190	—	—	—	—	—	3.1±1.2(3)	[3]
3718	24°53.9'S 13°10.0'E	1310	195	2.7±0.32(4)	9.7±1.1	—	—	—	2.8±0.3(3)	[3]
3719	24°59.9'S 12°52.0'E	1995	236	2.3±0.41(5)	19.8±0.3	—	—	—	—	[3]
3721	28°08.8'S 12°24.2'E	3017	248	1.8±0.42(6)	22.8±3.9	2.3	—	—	2.5±0(2)	[3]
4217	30°26.0'N 12°53.7'W	2504	220	0.3±0.05(2)	—	—	0.85	30.5	—	[4]
4234	28°53.3'N 13°13.5'W	1362	213	0.6±0.08(4)	75±9.5	—	2.34	26	—	[4]
4241	29°10.0'N 15°27.2'W	3610	247	—	—	—	0.46	28.7	—	[4]
4401	04°45.6'N 43°45.5'W	3350	263	0.9	80	—	—	—	—	[5]
4407	03°49.4'N 41°37.3'W	3305	254	—	—	—	1.75±0.2(5)	—	—	[6]
4409	03°38.5'N 45°14.4'W	3850	273	0.6±0.06(2)	90	—	—	—	—	[6]
4412	05°42.3'N 44°22.4'W	3770	273	0.47	—	—	2.4±0.3(2)	—	—	[6]
4417	05°08.7'N 46°33.6'W	3510	278	0.66±0.03(2)	120±0	—	0.56±0.06(3)	5.7±0.3	—	[5]
4419	09°40.2'N 54°15.5'W	4486	265	0.72±0.02(2)	110±7	—	9±0.2(6)	2.9±0.3	—	[5]
4421	16°59.1'N 46°00.9'W	3180	257	0.1±0.01(2)	260±0	—	1.31±0.1	—	—	[5]
4901	02°40.8'N 06°43.8'E	2185	233	0.3±0(3)	90±5	1.2	1.14	10	—	[3],[7]
4903	01°55.0'N 08°10.2'E	2385	230	—	—	—	1.73±0.28(2)	20±0.7	—	[8]
4904	00°57.0'N 08°52.8'E	1340	208	—	—	—	1.65±0.07(2)	22.5±6	—	[8]
4905	02°30.1'N 09°23.5'E	1328	200	—	—	—	2.58±0.15(2)	21±1.8	—	[8]
4906	00°41.2'S 08°22.9'E	1275	184	2±0.08(4)	15.5±2.6	2.0	1.76±0.34(2)	25±0.35	—	[3],[7]

Table 1 (continued)

Station	Position	Water depth (m)	BW-O <sub>2</sub> (μM)	In situ			Laboratory			Reference <sup>a</sup>
				DOU (mmol m <sup>-2</sup> d <sup>-1</sup> )	OPD (mm)	TOU (mmol m <sup>-2</sup> d <sup>-1</sup> )	DOU (mmol m <sup>-2</sup> d <sup>-1</sup> )	OPD (mm)	TOU (mmol m <sup>-2</sup> d <sup>-1</sup> )	
4908	00°42.7'S 06°50.3'E	3028	208	—	—	—	1.02	26	—	[3],[7]
4909	02°04.4'S 08°37.6'E	1310	184	1±0.05(3)	25±2.5	2.96	—	—	—	[3],[7]
4912	03°43.9'S 09°47.1'E	1300	212	—	—	—	2.08±0.2(3)	24±0.7	—	[8]
4913	05°30.0'S 11°04.4'E	1300	194	2.9±0.12(4)	15±0.8	3.2	1.83±0.09(5)	21±2	—	[3],[7]
4914	06°56.0'S 09°00.0'E	3975	210	—	—	—	1.63±0.45(4)	26±2.7	—	[8]
4915	07°45.0'S 11°52.4'E	1305	208	—	—	—	1.65±0.7(2)	25±1.4	—	[8]
4916	10°10.4'S 12°41.2'E	1300	208	—	—	—	1.6±0.51(3)	17.4±1.8	—	[8]
4917	11°54.4'S 13°04.3'E	1300	190	3±0.15(4)	14±1.1	5.1	1.2±0.24(2)	18.5±8.5	—	[3],[7]
4918	12°50.4'S 12°41.8'E	1340	180	—	—	—	1.2±0.5(2)	9±5	—	[8]
6202	29°05.1'S 47°09.7'W	1496	183	0.66±0.16(4)	—	—	—	—	—	[3]
6208	31°48.5'S 45°39.9'W	3693	192	—	—	—	0.85±0.15(2)	—	—	[3]
6211	32°30.5'S 50°14.6'W	654	91/184	—	—	—	0.8±0.16(4)	—	—	[3]
6212	32°41.2'S 50°06.6'W	1010	216	—	—	—	0.7±0.11(2)	—	—	[3]
6214	34°31.2'S 51°26.3'W	1566	185	1.24±0.62(3)	28±9.5	2.2	1.5±0.12(3)	—	—	[3]
6216	34°37.0'S 51°14.0'W	2033	208	—	—	—	0.3	—	—	[3]
6219	35°11.1'S 50°33.9'W	3550	201	0.87±0.15(4)	55.5±0.9	—	1.4±0.37(4)	25.5±0.7	—	[3]
6221	33°33.0'S 49°13.3'W	3038	205	—	—	—	0.6	—	—	[3]
6222	34°04.9'S 48°36.9'W	3450	194	—	—	—	0.75±0.2(4)	—	—	[3]
6223	35°44.4'S 49°40.9'W	4280	212	—	—	—	1.08±0.21(6)	—	—	[3]

6224	35°24.0'S 50°13.4'W	3787	185	—	—	—	1.4±0.27(2)	—	—	[3]
6226	37°09.3'S 47°53.5'W	5055	211	0.77±0.04(4)	—	—	0.86±0.05(3)	—	—	[3]
6229	37°12.8'S 52°39.1'W	3442	199	1.45±0.36(4)	33.5±4.2	3.0	2.72±0.6(2)	26.5±13	—	[3]
6230	37°53.7'S 51°41.4'W	4380	202	—	—	—	2.3	—	—	[3]
J4	09°14.0'N 16°59.7'W	1007	~130	1.2	20	—	—	—	—	[9]
J6	08°23.0'N 17°36.3'W	4470	~240	0.8	—	—	—	—	—	[9]
MESO	19°27.8'N 21°01.5'W	3110	245 µmol kg <sup>-1</sup>	—	—	2.6±0.38	—	—	—	[10]
A	05°17.0'N 43°34.0'W	4000	258 µmol kg <sup>-1</sup>	0.7	80	0.7±0.25	—	—	—	[11]
B1	05°16.0'N 43°34.0'W	3280	255 µmol kg <sup>-1</sup>	0.3–0.55	—	—	—	—	—	[11]
B2	05°16.0'N 43°34.0'W	3290	255 µmol kg <sup>-1</sup>	0.4–1.0	—	0.5±0.2	—	—	—	[11]
B3	05°16.0'N 43°34.0'W	3270	255 µmol kg <sup>-1</sup>	0.35–0.7	—	—	—	—	—	[11]
C	05°00.0'N 45°00.0'W	4120	254 µmol kg <sup>-1</sup>	0.3	—	—	—	—	—	[11]
G	06°10.0'N 42°53.0'W	4685	233 µmol kg <sup>-1</sup>	0.3–0.4	—	0.5±0.16	—	—	—	[11]

<sup>a</sup>[1] Glud et al., 1994; [2] Glud, Holby and Gundersen, unpublished data; [3] Wenzhöfer, Boehme Boetius, Ferdelman, Glud, Gundersen, Hensen, Holby, Pfeifer, Riess, Steinmetz, Strotmann, in progress; [4] Wenzhöfer and Riess, unpublished data; [5] Wenzhöfer et al., 2001a; [6] Wenzhöfer and Holby, unpublished results; [7] Wenzhöfer et al., 2001b, [8] Wenzhöfer and Boehme, unpublished results; [9] Jahnke et al., 1989; [10] Jahnke et al., 1994; [11] Hales and Emerson, 1997.

mini-optodes were used simultaneously with the microelectrodes (Glud et al., 1999a; Wenzhöfer et al., 2001a). The mini-optodes had an outside tip diameter of 1 mm, a response time of < 2 min and no stirring sensitivity (Wenzhöfer et al., 2001a). Standing at the seafloor, the array of sensors was lowered in increments of 100  $\mu\text{m}$  to 5 mm depending on the type of sediment. The concentration profiles had two inherent calibration points, the constant readings in the bottom water and the anoxic sediment strata. The  $\text{O}_2$  concentration of the bottom water was determined by Winkler titration (Grasshoff, 1983) on a lander-recovered water samples (Glud et al., 1994). DOU ( $\text{mmol m}^{-2} \text{d}^{-1}$ ) was calculated from the measured microprofiles and Fick's first law of diffusion

$$\text{DOU} = D_0 \text{d}C/\text{d}z, \quad (1)$$

where  $D_0$  ( $\text{cm}^{-2} \text{s}^{-1}$ ) is the molecular diffusion coefficient in water,  $C$  ( $\mu\text{M}$ ) is the solute concentration, and  $z$  (cm) is the depth within the DBL (Jørgensen and Revsbech, 1985; Glud et al., 1994). The temperature and salinity corrected  $D_0$  values for oxygen were derived from Broecker and Peng (1974) and Li and Gregory (1974).

Upon landing on the seafloor the benthic chamber enclosed an 896  $\text{cm}^2$  sediment area. Lid closure isolated the sediment along with a 6–12 cm water column. During incubations the water was gently mixed by a central stirrer (8–12 rpm), which created an average DBL thickness of approx. 500  $\mu\text{m}$ , depending on the water height and the sediment roughness (Glud et al., 1995). The  $\text{O}_2$  concentration of the enclosed water volume was followed continuously by two Clark-type mini-electrodes mounted in the lid of the chamber (Glud et al., 1995). The sensors had a reinforced outer casing (tip diameter 1–3 mm) but the same measuring characteristics as outlined above (Glud et al., 2000a). The electrodes were calibrated from an onboard zero reading at in situ temperature and the constant reading in the bottom water. Occasionally, the  $\text{O}_2$  concentration was determined on water samples recovered at the end of the in situ incubation, and included in the calibration routine. The TOU ( $\text{mmol m}^{-2} \text{d}^{-1}$ ) was calculated from the linear regression of the concentration

versus time

$$\text{TOU} = ((\text{d}C/\text{d}t)V_{\text{BW}}/A_{\text{ch}}), \quad (2)$$

where  $\text{d}C/\text{d}t$  ( $\mu\text{M h}^{-1}$ ) is the concentration change over incubation time,  $V_{\text{BW}}$  ( $\text{cm}^3$ ) is the volume of overlying water in the enclosed chamber, and  $A_{\text{ch}}$  ( $\text{cm}^2$ ) is the area of sediment enclosed by the chamber.

Laboratory measurements of TOU and DOU were performed in sediment cores recovered by a multiple corer (Barnett et al., 1984). Sediment cores appeared undisturbed, with a clear overlying water phase and intact microstructures at the sediment surface. Cores were placed in an incubation bath kept at in situ temperature and  $\text{O}_2$  tension (Glud et al., 1994). Small rotating magnets attached to the inner core wall ensured well-mixed overlying waters and a DBL thickness close to the in situ conditions (Rasmussen and Jørgensen, 1992; Glud et al., 1994). Laboratory microprofiles were measured with  $\text{O}_2$  microelectrodes having the same measuring characteristics as outlined above and mounted on a motor driven micromanipulator. Sensor signals were transferred to a strip chart recorder and via an AC/DC converter to a PC (Revsbech and Jørgensen, 1986). Laboratory TOU was determined after the cores were closed with a gas tight lid leaving an internal water height of 6–10 cm, which was continuously stirred during the incubation. In a given time interval  $\text{O}_2$  samples were recovered from the enclosed water and the sampling volume was replaced by water from the incubation tank (the dilution was later corrected for). The oxygen concentration was determined by Winkler titration. Occasionally electrodes mounted in the lid were used to monitor the  $\text{O}_2$  decrease.

## 2.2. Primary production and bathymetry

Annual primary production (Fig. 1) was derived from the oceanic primary production maps of Behrenfeld and Falkowski (1997). They constructed an empirical correlation from the concentration of remotely sensed photosynthetic pigments (especially chlorophyll *a*), sea surface temperature, incident solar irradiance and depth of the mixed layer. The primary production

distribution was calculated with the vertically generalized production model (VGPM; Behrenfeld and Falkowski, 1997) on monthly climatologically averaged physical data computed over a 3-yr period. Different recently developed models using remotely sensed data for oceanic primary production estimates resulted in similar values (Sathyendranath et al., 1995; Longhurst et al., 1995; Antoine et al., 1996; Behrenfeld and Falkowski, 1997), with rates generally higher than a previous often-used compilation (Berger, 1989). Primary production in the surface waters of the Atlantic generally ranged from  $\sim 50 \text{ g C m}^{-2} \text{ yr}^{-1}$  in the oligotrophic areas to around  $450 \text{ g C m}^{-2} \text{ yr}^{-1}$  in the eutrophic waters (Fig. 1), with maximum values of  $\sim 1000 \text{ g C m}^{-2} \text{ yr}^{-1}$  in the central upwelling area off southwest Africa. Because of the complex hydrodynamics of shallow coastal regions, resulting in a considerable spatial and temporal variability in primary production and sedimentation rate, and because of the relatively few benthic measurements performed at shallow depths, only data from locations with water depth  $\geq 1000 \text{ m}$  are considered in this study. The topography of the Atlantic seafloor was taken from the ETOPO5 global topography data set (Data Announcement 88-MGG-02, Digital relief of the Surface of the Earth. NOAA, National Geophysical Data, Boulder, CO, 1988), which provides a 5-min grid of the water depths. The grid was adapted and aligned to the grid of primary production.

### 3. Benthic oxygen consumption

#### 3.1. Benthic $\text{O}_2$ uptake versus water depth and regional variability

In situ DOU measured in the Atlantic exhibited an exponential decrease with increasing water depth (Fig. 2A). There was, however, a distinct separation between the western and eastern areas, with  $\sim 2.5$  times higher  $\text{O}_2$  uptake in the eastern upwelling area at a similar depth. This pattern mirrors the difference in primary production of the two areas (Fig. 1). The few outliers are typically at stations with relatively low surface primary production in the northeast Atlantic (e.g. 4217,

4234 Canary Islands and the literature data in the equatorial eastern Atlantic; Figs. 1 and 2). The TOU reflected a similar trend as the DOU, but with much higher absolute values in the shallow and highly productive area off southwest Africa. Consequently, the TOU of the compiled data set showed much stronger depth attenuation as compared to the DOU (Fig. 2B). The oxygen penetration depth (OPD) increased with water depth and reached maximum values around 200 mm at 5000 m water depth (Fig. 2C). The geographic separation between the east and west was, however, less clear than for the DOU data (Fig. 2). This is the result of a nonlinear relation between OPD and DOU with relatively constant OPD in the DOU range of  $1\text{--}4 \text{ mmol m}^{-2} \text{ d}^{-1}$ , representing most of our data both in the east and west (Fig. 3) (Cai and Sayles, 1996). In contrast, low activity areas ( $< 1 \text{ mmol m}^{-2} \text{ d}^{-1}$ ) are characterized by a steep decrease in OPD with increasing activity (Fig. 3). The good correlation between water depth (and primary production, see later), benthic oxygen uptake (DOU and TOU) and OPD confirm that the flux of organic matter reaching the seafloor is the key factor regulating the benthic mineralization rate.

The compiled data set gave the possibility to follow the oxygen uptake rate on a north–south transect along the 1300-m isobath (except J4, 1719 at 1000 m and 1703 at 1900 m) off the West African coast. All measurements were performed in winter months but in four different years and mimicked the spatial distribution of the surface annual primary production. DOU was enhanced in the upwelling region (Figs. 1 and 4), with station 1703 in the central upwelling area exhibiting the highest oxygen uptake. The DOU showed an abrupt decrease at station 4909, potentially due to a lower surface primary productivity between the two high-productive areas off the Zaire and Niger rivers. TOU reflected the same pattern but with elevated rates, especially in the highly productive area.

#### 3.2. TOU versus DOU

The ratio between simultaneously obtained TOU and DOU at various stations was nearly

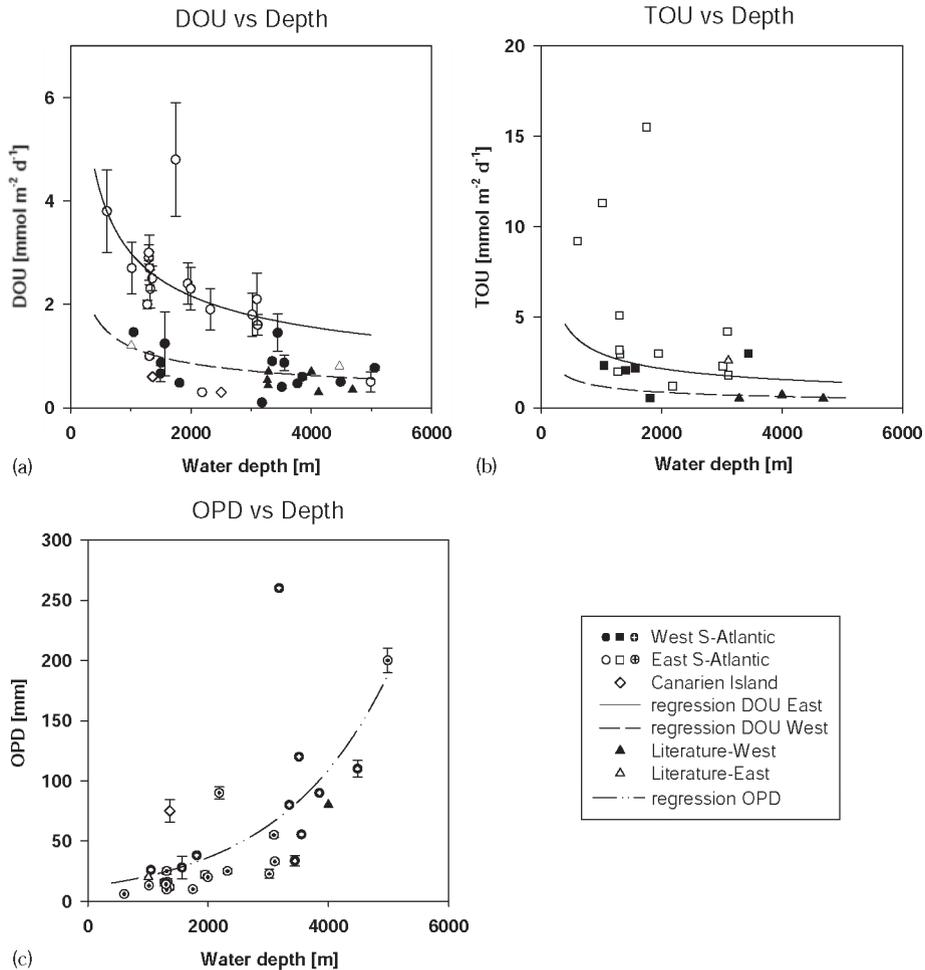


Fig. 2. In situ diffusive oxygen uptake (DOU; A), total oxygen uptake (TOU; B) and oxygen penetration depth (OPD; C) as a function of water depth. The compiled diffusive oxygen fluxes were fitted by two exponential regressions describing the DOU of the eastern ( $\text{DOU} = 76.714z^{-0.4695}$ ;  $r^2 = 0.9$ ) and western ( $\text{DOU} = 28.0385z^{-0.459}$ ;  $r^2 = 0.2$ ) Atlantic as a function of water depth (A). The two regressions from the DOU data are also plotted in the TOU graph (B). The compiled OPD data was fitted by an exponential regression (C:  $\text{OPD} = 12,0946e^{(0.0005z)}$ ;  $r^2 = 0.5$ ).

always  $> 1$  (Figs. 4 and 5). Despite the scatter and the limited amount of data, there was a trend to high ratios of up to 3–4 in the shallow and productive areas. At less productive and deeper sites the ratio was close to one (Fig. 5). It has been shown that the difference between in situ TOU and DOU correlates with the biomass of benthic fauna, and the difference has been used as a measure of the non-diffusive fauna-mediated  $\text{O}_2$  uptake of shelf and coastal sediments (Archer and

Devol, 1992; Glud et al., 1994, 1998, 1999a). In reduced sediments the major fraction of the fauna-mediated  $\text{O}_2$  uptake is related to irrigation of excavates and burrows combined with local resuspension events rather than the respiration of metazoans (Pelegri et al., 1994; Kristensen, 1988; Glud et al., 2000b; Aller, 2001). It may be argued that even if the fraction of organic carbon metabolized by fauna is depth independent the relative importance of irrigation for benthic  $\text{O}_2$

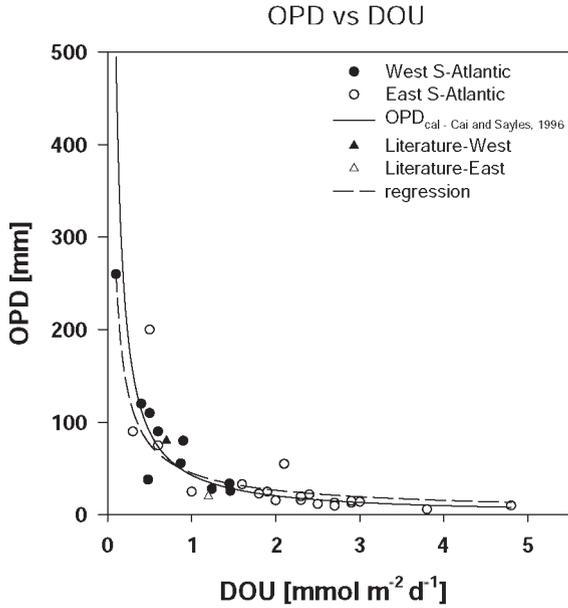


Fig. 3. Oxygen penetration depth (OPD) versus the diffusive oxygen uptake (DOU). The line represents the OPD calculated after the empirical equation found by Cai and Sayles (1996).

uptake decreases with increasing OPD. Partly because of relatively more deposit feeding fauna, and partly because of less steep  $O_2$  concentration gradients. This, however, remains to be tested. Our observation is in accordance with measurements from the abyssal Pacific, where it was shown that the diffusive oxygen uptake accounted for the majority of the total oxygen exchange (Jahnke et al., 1990; Reimers et al., 1992; Glud et al., 1999a). In situ tracer studies of solute transport across the sediment-water interface at a deep-sea site in the North Atlantic also revealed that non-diffusive transport accounted only for <25% of the total transport (Sayles and Martin, 1995). A previous comparison between the total oxygen flux and the ratio of the total flux to the diffusive flux also showed a trend of increasing ratios with greater oxygen fluxes (Jahnke, 2001). Therefore, Jahnke (2001) concluded that macrobenthic activity can have a major influence on the oxygen uptake of sediments in specific regions with high carbon input, such as continental upwelling

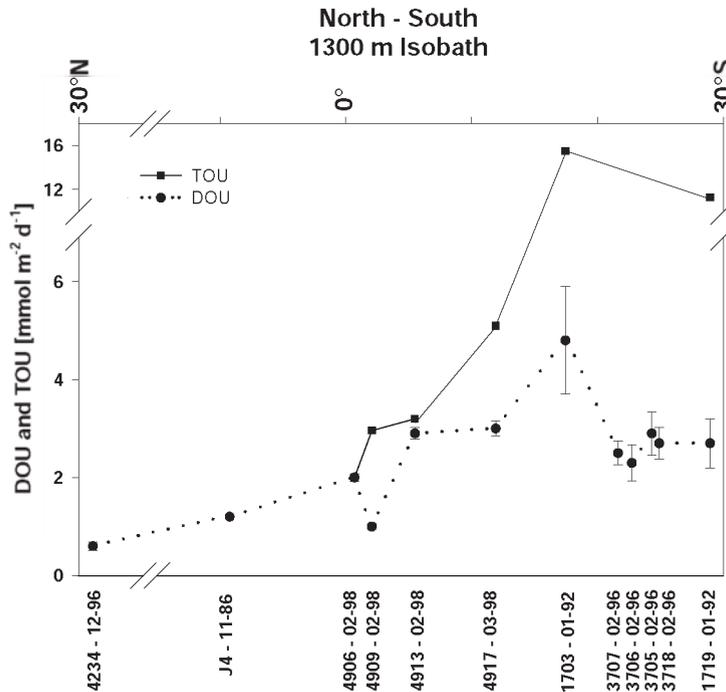


Fig. 4. Diffusive (DOU) and total (TOU) oxygen uptake along a north–south transect at the 1300-m isobath (except station J4, 1719 at 1000 m and 1703 at 1900 m).

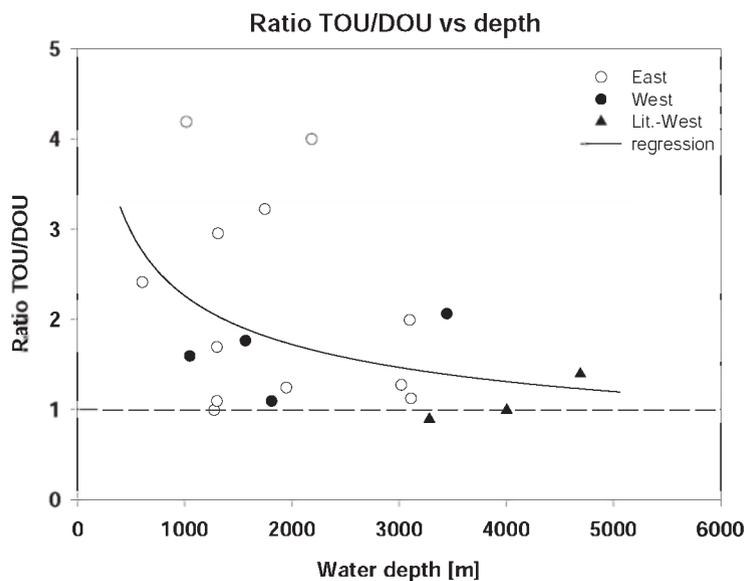


Fig. 5. Ratio of the total oxygen flux (TOU) to the diffusive oxygen flux (DOU) versus the water depth. Dashed line represent the ratio where TOU and DOU are equal ( $\gamma = 1$ ).

(eastern Atlantic, Glud et al., 1994; eastern South Pacific, Glud et al., 1999b) and upper continental slope and shelf areas (eastern North Pacific, Archer and Devol, 1992).

### 3.3. *In situ versus laboratory measurements*

In contrast to the in situ data, the laboratory measurements ( $\text{DOU}_{\text{lab}}$ ,  $\text{TOU}_{\text{lab}}$  and  $\text{OPD}_{\text{lab}}$ ) showed no clear correlation to water depth (Fig. 6). The reason for this has previously been ascribed to two factors: (I) stimulated microbial activity in the laboratory and (II) under-representation or inactivation of macrofauna in recovered sediment cores (Glud et al., 1994, 1999a; Aller et al., 1998; Sauter et al., 2001). The DOU obtained in the laboratory generally exceeded rates obtained by the in situ measurements, and the OPD in the laboratory was much lower than the in situ values (Fig. 7A and C). Transient heating during core recovery may stimulate the microbial activity, which in combination with an increased availability of labile carbon released during lysis of barophilic or psychrophilic microbiota enhances the benthic  $\text{O}_2$  consumption. This would result in a steeper oxygen gradient with

higher DOU and lower OPD of shipboard investigations. For TOU there appeared to be a separation between sediments with low and high total  $\text{O}_2$  uptake rates representing sites with low and high abundance of fauna, respectively. For low TOU rates the laboratory measurements exceeded the in situ rates, as was the case for DOU. In contrast at sites with high TOU rates laboratory incubations were significantly lower than the in situ rates (Fig. 7B). The latter effect is most likely a result of poor representation and inactivation of the macrofauna in the relatively small sediment cores recovered from the very productive and fauna-rich stations (Devol and Christensen, 1993; Glud et al., 1994, 1998). Thus TOU measured in the laboratory may be affected by two sources of systematic errors: (1) transient heating during core recovery which increases the oxygen uptake, and (2) exclusion and inactivation of fauna which decreases the oxygen uptake.

### 3.4. *Small-scale spatial variability in benthic flux measurements*

Benthic exchange rates quantified by chamber incubations are dependent on correct representation

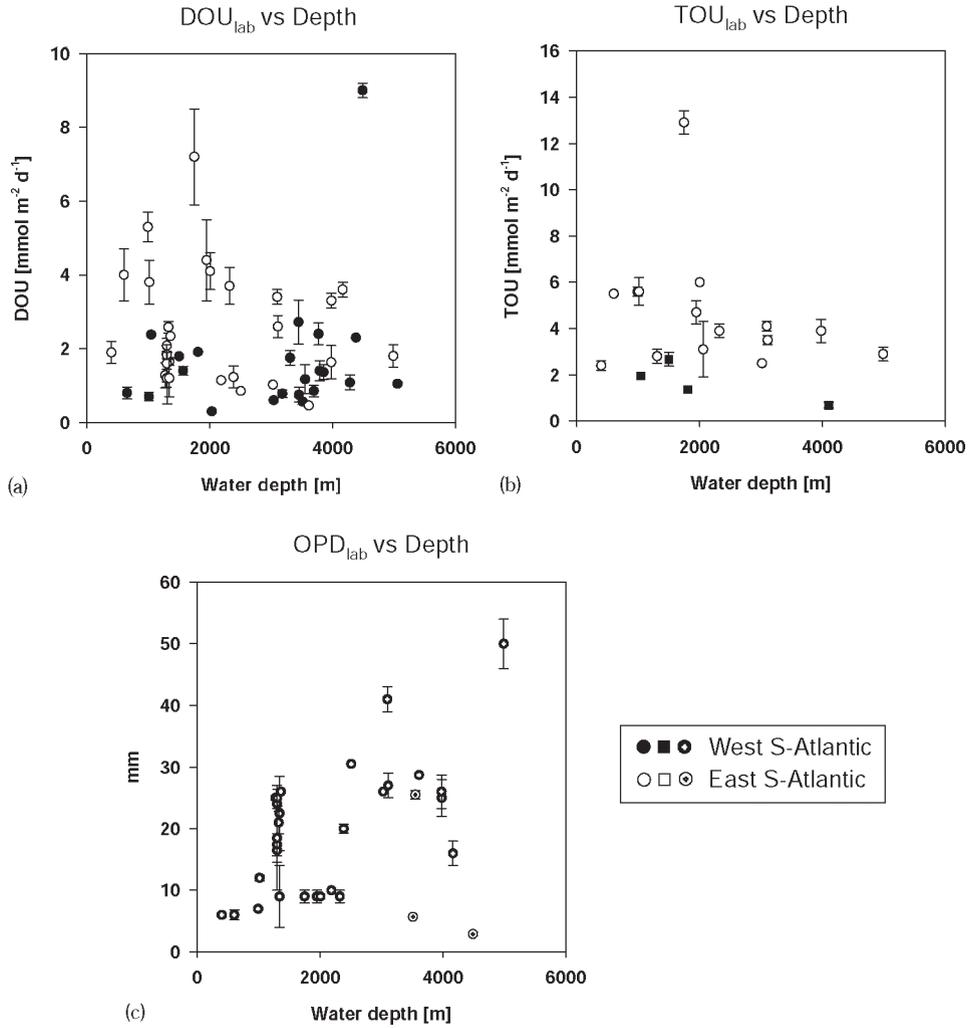


Fig. 6. Laboratory measured diffusive oxygen uptake (DOU<sub>lab</sub>; A), total oxygen uptake (TOU<sub>lab</sub>; B) and oxygen penetration depth (OPD<sub>lab</sub>; C) as a function of water depth.

of the faunal activity. Enclosures containing an anomalously large population of irrigating fauna may result in an overestimate of the average benthic exchange rate. Our benthic lander carries only one chamber, consequently single deployments do not allow any quantitative assessment of the small-scale variability. This is a compromise between enclosing one large sediment area or several small areas (Tengberg et al., 1995). Landers carrying more chambers typically resolve variabilities in the range of 5–20% between parallel incubations performed in the deep-sea or in shelf

sediments (Berelson et al., 1990; Archer and Devol, 1992; Pfannkuche, 1993; Witte and Pfannkuche, 2000; Smith et al., 1994, 2001). It is reasonable to assume that our TOU is determined with at least the same accuracy for a larger sediment area (Glud and Blackburn, 2002). It cannot be excluded, however, that single outliers are caused by incorrect representation of the average faunal density. DOU only represents point measurements, and abnormal/irregular profiles, such as microprofiles penetrating through or along an animal burrow suggesting fauna activity

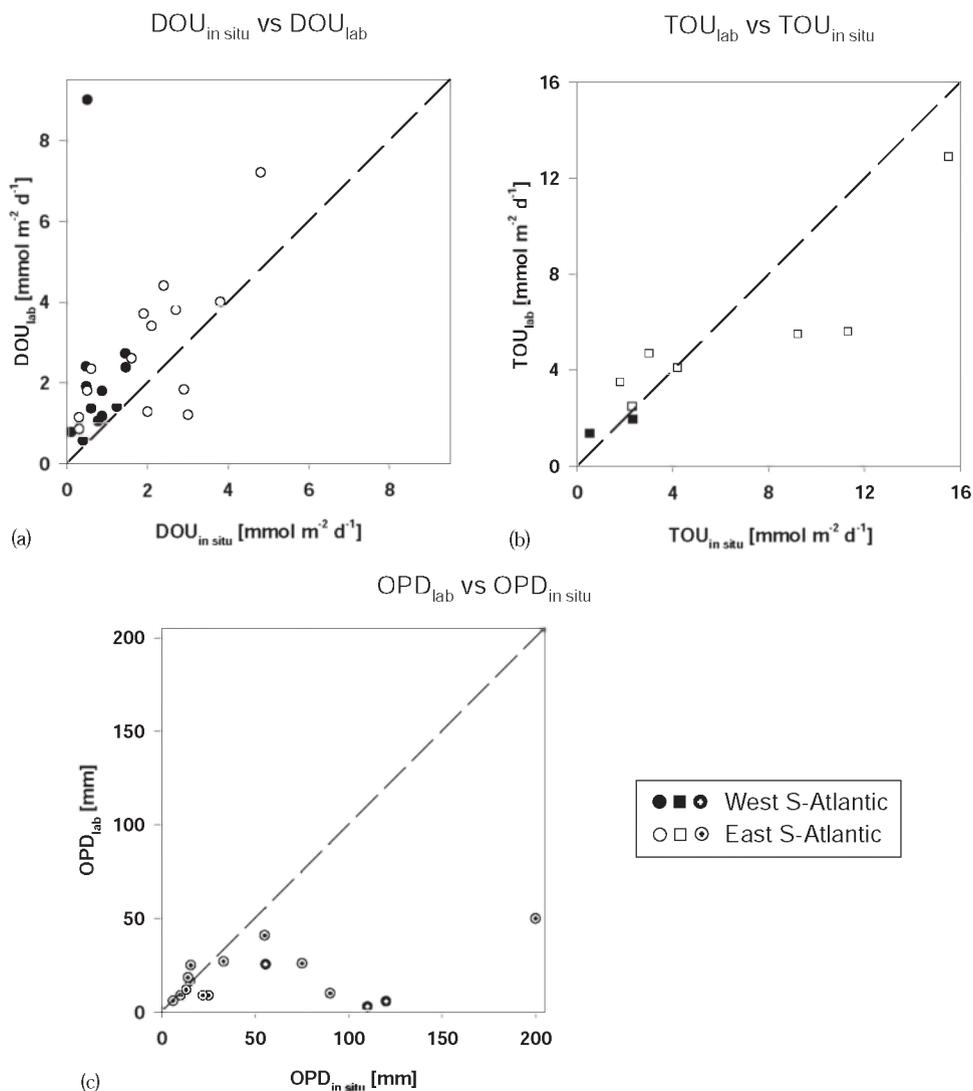


Fig. 7. Comparison of in situ and laboratory determined diffusive oxygen uptake (DOU; A), total oxygen uptake (TOU; B) and oxygen penetration depth (OPD; C). Lines symbolize the 1:1 case.

(Glud et al., 1994; Jørgensen and Boudreau, 2001), are rarely encountered for shelf and deep-sea sediments. Consequently it is difficult to resolve spatial variability associated with fauna from microprofiles. In order to better resolve both spatial and temporal variability of shelf and deep-sea benthic mineralization the adaptation of chambers, profiling units and cameras to rovers seems to be the optimal solution for the future

(Smith et al., 1997). Planar sensors resolving 2D-images of the interstitial O<sub>2</sub> distribution may also be an important tool in this context (Glud et al., 2001).

### 3.5. Inter-annual variability and seasonality

The O<sub>2</sub> uptake rates presented here were measured during a 10-yr period. All measurements

were for logistic reasons measured from November to March. Comparing the data obtained at stations close to each other during different cruises indicate an insignificant inter-annual variation. For instance, two stations in the equatorial western Atlantic (4412—A and 4401—B, visited in March 1994 and 1997, respectively) and two stations in the upwelling area off Namibia (1711–3706 and 1721–3721, visited in January 1992 and February 1996, respectively) revealed similar values on the two occasions (Table 1). An insignificant inter-annual variability was also concluded from a time series of in situ TOU measurements performed in the northeast Pacific (Smith et al., 2001) and from measurements performed on revisited abyssal stations (Pfannkuche, 1993; Sayles et al., 1994). Long-time sediment trap studies in the Atlantic also revealed that the inter-annual variability of the particulate organic carbon (POC) was low in the eastern South Atlantic (Walvis Ridge, 20°S) and the oligotrophic subtropical gyres, but the upwelling area at Cape Blanc (20°N) showed higher inter-annual variability, depending on the strength of the horizontal upwelling in this area (Fischer et al., 2000).

Despite a generally insignificant inter-annual variability in benthic mineralization rates, evidence for a seasonal response in the benthic O<sub>2</sub> uptake of abyssal sediments is accumulating (e.g. Smith et al., 2001). Our compiled data set could be biased by the fact that measurements always were performed from November to March. Sediment trap data from the South Atlantic indeed revealed a seasonal pattern of the POC flux for the upwelling areas with elevated rates in spring (February and March) and summer (August), but the oligotrophic regions showed an almost time independent POC flux (Fischer et al., 2000). However, comparing POC flux data and the time for benthic oxygen uptake measurements showed that our measurements generally were performed during periods of relatively low POC fluxes (except station MESO) (Fischer et al., 2000). This indicates that our measurements do not represent maximal benthic mineralization values obtained during high deposition events. The effect of seasonality in primary production on the benthic

oxygen uptake from the Atlantic region still remains to be clarified.

#### 4. Primary production and organic carbon sedimentation

Given the fact that the laboratory data poorly represent in situ conditions, we have decided to use only the in situ data for relating the benthic mineralization to primary production and sedimentation. Also, given that the TOU and DOU give different rates at shallow or productive stations, we have chosen to separate the two data sets. The benthic oxygen fluxes were converted to carbon equivalents (C-DOU and C-TOU) by applying the Redfield ratio (C:O=106:138; Redfield et al., 1963) in order to compare them to the carbon fixed by primary production. Using the modified Redfield ratio of Takahashi et al. (1985) and Anderson and Sarmiento (1994) would result only in minor changes of <10% in the benthic C-flux.

The annual primary production as derived from Fig. 1 correlated positively with the C-DOU and C-TOU (Fig. 8A and C). Various empirical correlations have been constructed to assess the fraction of the primary production that actually reaches the seafloor (Suess, 1980; Betzer et al., 1984; Berger et al., 1987). The most commonly applied equation is given by Berger et al. (1987):

$$J_{\text{Corg}} = 9\text{PP}/z + 0.7\text{PP}/z^{0.5}, \quad (3)$$

where  $J_{\text{Corg}}$  (g C m<sup>-2</sup> yr<sup>-1</sup>) is the sedimentary flux of organic carbon, PP (g C m<sup>-2</sup> yr<sup>-1</sup>) is the primary production, and  $z$  (m) is the water depth. The estimated annual input of organic carbon to the seafloor (using PP of Fig. 1) correlated well with the C-DOU, but the correlation to C-TOU was less pronounced (Fig. 8B and D). However, as can be seen from the 1:1 line in Fig. 8C and D the estimated sedimentation or organic carbon flux from the water column could not always support the benthic mineralization as quantified from C-DOU or C-TOU. This was especially true for water depths >1500 m, where on average, 125% of the estimated sedimenting

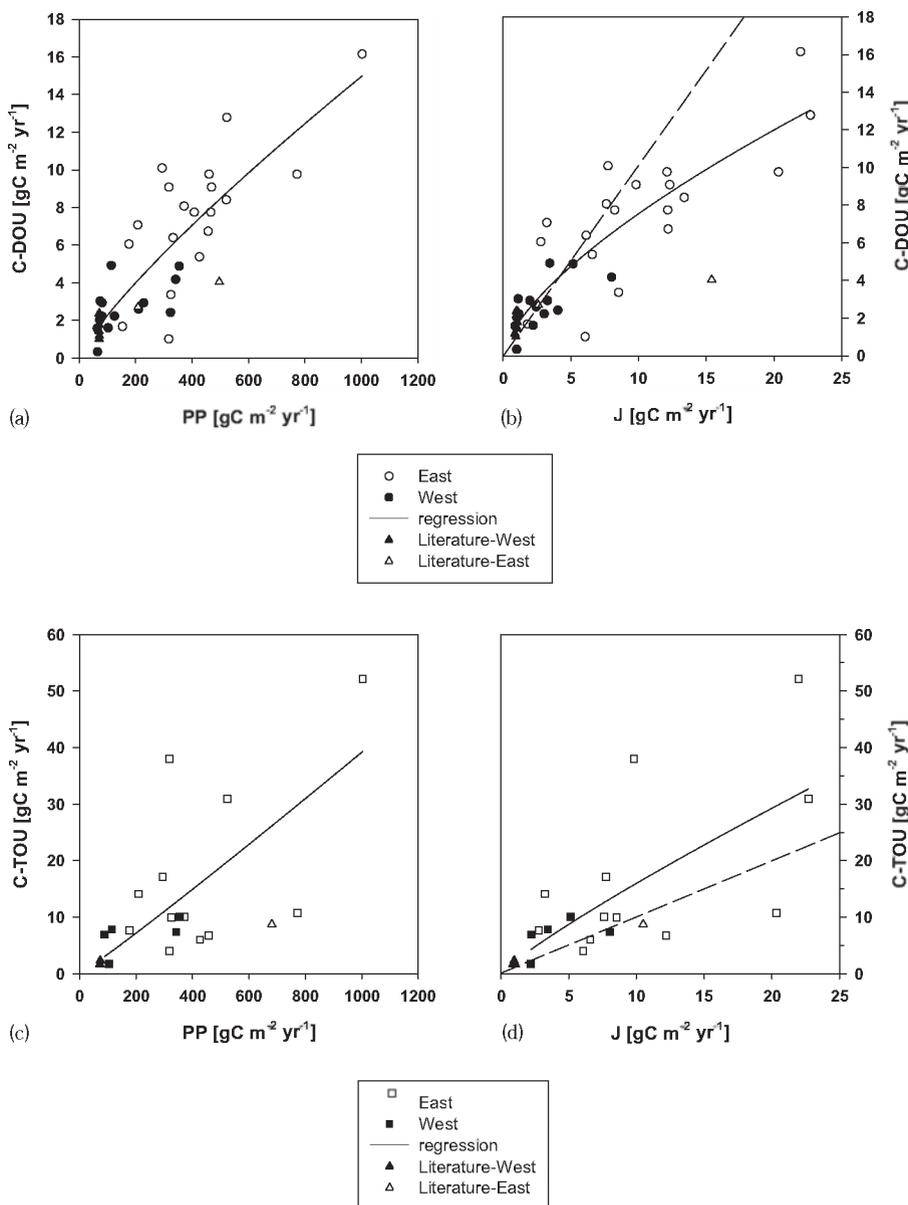


Fig. 8. Carbon flux, estimated from in situ diffusive oxygen flux measurements (C-DOU) and in situ total oxygen flux measurements (C-TOU) as a function of surface water primary production (A,  $r^2 = 0.67$  and C,  $r^2 = 0.62$ ) and as a function of the sedimentary organic carbon ( $J$ ; derived from Eq. (3), Berger et al., 1987) (B,  $r^2 = 0.75$  and D,  $r^2 = 0.43$ ; broken lines represent 1:1 case).

organic carbon was mineralized as inferred from C-DOU and the equivalent number for C-TOU was 216%.

Sediment trap studies from the Atlantic revealed high (1.75–2% PP) and “moderately high”

(0.8–1.1% PP) organic carbon export fluxes for coastal and equatorial upwelling areas, respectively, but the subtropical oligotrophic gyres yielded low (0.6% PP) organic export fluxes (Fischer et al., 2000). Particulate organic carbon

(POC) fluxes (from sediment traps 500 m above the seafloor) in the vicinity of our in situ sites in the eastern South Atlantic (station 1708 at Walvis Ridge and 1721 in the Namibia upwelling) were 2.3–6.3 and 1.6 g C m<sup>-2</sup> yr<sup>-1</sup>, respectively (Fischer et al., 2000). However, comparing these POC fluxes with our in situ benthic carbon mineralization rates (POC:C-DOU and C-TOU) results in ratios of 0.4–1.0 and 0.3–0.5, respectively. The export of organic carbon as inferred from sediment trap data can often not account for the estimated or measured requirement of benthic communities (e.g. Smith, 1987; Smith and Kaufmann, 1999; Glud et al., 1999a; Witte and Pfannkuche, 2000; Smith et al., 2001). The reason is most likely related to under-sampling of the particulate matter by sediment traps or lateral advection of organic material within the benthic boundary layer (Smith et al., 2001).

Despite the uncertainty in the correlation between organic matter supply and benthic mineralization, the sediment organic carbon content is a key factor for the benthic activity. A quantitative correlation between the core top organic carbon content, bottom water oxygen concentration and benthic oxygen consumption was found in the northeast Pacific, which was also applicable to data from the North Atlantic (Cai and Reimers, 1995). This empirical relation match our DOU rates fairly well, but underestimated our TOU by a factor 2–4.

**5. Modeling benthic oxygen uptake with primary production and water depth**

As an alternative to sedimentation rates we used the compiled in situ data, estimated primary production (Fig. 1), and water depth to construct an empirical relation. Accounting for the exponential decrease of benthic O<sub>2</sub> uptake with increasing water depth and decreasing primary production (Figs. 2 and 8) a multiple regression of the in situ carbon mineralization was made

$$C-DOU = PP^{0.7358} z^{-0.3306} \quad (\text{g C m}^{-2} \text{ yr}^{-1}) \quad (4)$$

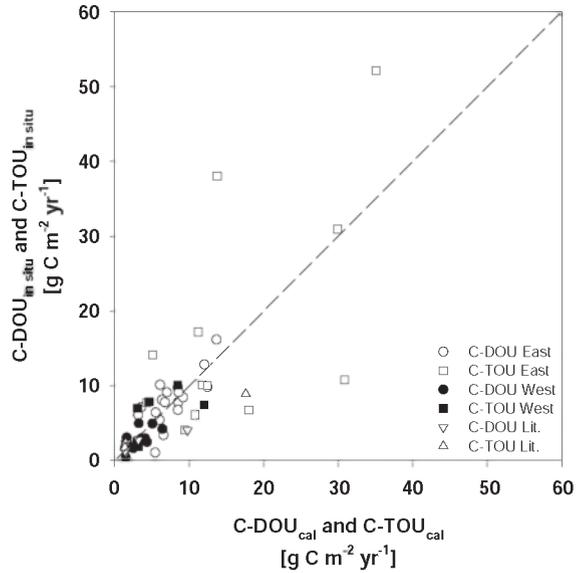


Fig. 9. Comparison of the in situ measured diffusive and total oxygen uptake rates and calculated fluxes from the two fitted regressions (Eqs. (4) and (5)).

and

$$C-TOU = PP^{1.0466} z^{-0.4922} \quad (\text{g C m}^{-2} \text{ yr}^{-1}), \quad (5)$$

where PP (g C m<sup>-2</sup> yr<sup>-1</sup>) represent the average annual primary production, and z (m) the water depth. The resulting regression of both equations was significant (C-DOU: *r* = 0.86, *r*<sup>2</sup> = 0.75, *p* = 0.06; C-TOU: *r* = 0.66, *r*<sup>2</sup> = 0.44, *p* = 0.08) and the standard error of the coefficient for PP was ±0.0745 and ±0.266 and for z was ±0.063 and ±0.2367, respectively. The validity of our modeled oxygen uptake rates was checked by comparing the in situ measurements with values calculated by the two equations (Eqs. (4) and (5)). Generally the overall magnitudes of the calculated fluxes match the in situ measurements and the values were evenly distributed around the 1:1 line (Fig. 9). However, three outliers of C-TOU in the eastern South Atlantic were apparent. At two sites (1703 and 1719) the in situ flux was higher, and one station (4913) had a smaller oxygen uptake than expected. The high rates measured at station 1703 and 1719 coincided with an extremely high biomass found at these sites (101.5 and

33.0 g m<sup>-2</sup>, respectively; Glud et al., 1994), and could indicate a lateral transport of organic carbon at these sites. This was partly supported by the simultaneously measured C-DOU, which was 20% and 30% higher than the calculated rates.

## 6. Ocean basin benthic carbon mineralization and global comparisons

By applying the empirical correlations between annual primary production, water depth and benthic carbon mineralization (Eqs. (4) and (5)) we extrapolated our findings to the entire investigated area of the Atlantic (Fig. 10). The pattern of C-DOU (which can be regarded as a minimum value, not including faunal contribution) and C-TOU are very similar (Fig. 10A and B). High fluxes with values around 7 and 14 g C m<sup>-2</sup> yr<sup>-1</sup> for C-DOU and C-TOU derived data, respectively, were apparent along the coastline of West Africa. Identical, but considerably lower fluxes of 1.5–2 g C m<sup>-2</sup> yr<sup>-1</sup> were derived from both approaches for the deep gyre region. Subtracting the two images reveal areas where a significant contribution of benthic faunal activity to the overall benthic mineralization can be expected (Fig. 11A). In highly productive areas the difference between C-TOU and C-DOU is on average  $\geq 50\%$  with maximum values of 68% (equals a TOU-DOU ratio of  $>3$ ). This is consistent with the in situ measurements and underlines the importance of fauna for the benthic oxygen uptake. The difference in the oligotrophic open ocean areas is of the same order as the accuracy of the applied methods. For the entire investigated area of the Atlantic the fauna-mediated mineralization was on the order of  $35 \times 10^{12}$  g C yr<sup>-1</sup>, or 21% of the total benthic mineralization (Table 2). It is important to realize that this value represent the sum of the respiration of the fauna itself and stimulated microbial activity in the vicinity of the animals.

Using the distribution of C-DOU for the Atlantic (Fig. 10A) and the correlation between DOU and OPD (Fig. 3) provides an estimation of

the OPD for the investigated area (Fig. 11B). The relation between C-DOU and OPD was described by

$$\text{OPD} = 114.6968 \text{ C-DOU}^{-0.7541} \text{ (mm)} \quad (6)$$

Since the C-DOU is a function of primary production and water depth (Eq. (4)), combining Eqs. (6) and (4) describes the oxygen penetration as a function of the organic matter synthesized in surface waters and water depth, which are easy accessible parameters

$$\text{OPD} = 114.6968 \text{ PP}^{-0.555} z^{0.249} \text{ (mm)} \quad (7)$$

The given correlations for OPD (Eqs. (6) and (7)) are, however, based on a data set of highly uniform bottom water oxygen concentrations. Recently, Cai and Reimers (1995) and Cai and Sayles (1996) showed that the bottom water oxygen concentration (BW<sub>O<sub>2</sub></sub>) could be a regulating factor for the diffusive oxygen uptake. Taking this into account a multiple regression of OPD (mm), C-DOU (g C m<sup>-2</sup> yr<sup>-1</sup>) and BW<sub>O<sub>2</sub></sub> (μM), and PP (g C m<sup>-2</sup> yr<sup>-1</sup>) and z (m) was made

$$\text{OPD} = \text{BW}_{\text{O}_2}^{0.8619} \text{ C-DOU}^{-0.7341} \text{ (g C m}^{-2} \text{ yr}^{-1}) \quad (8)$$

and

$$\text{OPD} = \text{BW}_{\text{O}_2}^{0.8619} \text{ PP}^{-0.54} z^{0.243} \text{ (g C m}^{-2} \text{ yr}^{-1}). \quad (9)$$

The regression coefficient ( $r^2$ ) for both the empirical relationships Eqs. (6)/(7) and Eqs. (8)/(9) was 0.77 and 0.73, respectively. All the given equations calculating OPD (Eqs. (6)–(9)) revealed similar penetration depths and showed a good correspondence with the compiled in situ measurements (data not shown). However, because of the fact that the relationship between DOU or C-DOU and OPD is very sensitive in low activity areas (Fig. 3), accurate OPD estimates can be made only to a penetration of 100 mm (Fig. 11B). Single oxygen sensor measurements, however, revealed penetration depths in the range 120–260 mm for the oligotrophic area of the western equatorial Atlantic (Table 1; Wenzhöfer et al., 2001a). These oligotrophic deep-sea areas, with their extremely low oxygen uptake rates and high oxygen penetration, are

included in our compilation but are still under-sampled.

A previous compilation and extrapolation of in situ benthic mineralization performed by Jahnke (1996) pointed to extremely low oxygen fluxes in the central gyre of the Atlantic. The global flux distribution was built on an empirical relation

between the burial of organic carbon (corrected for calcium carbonate accumulation) and benthic oxygen uptake rates. The low mineralization rates for the central South Atlantic ( $< 1 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) was ascribed to extremely low sedimentary organic carbon content and high  $\text{CaCO}_3$  values, combined with under-sampling of the area. Benthic carbon

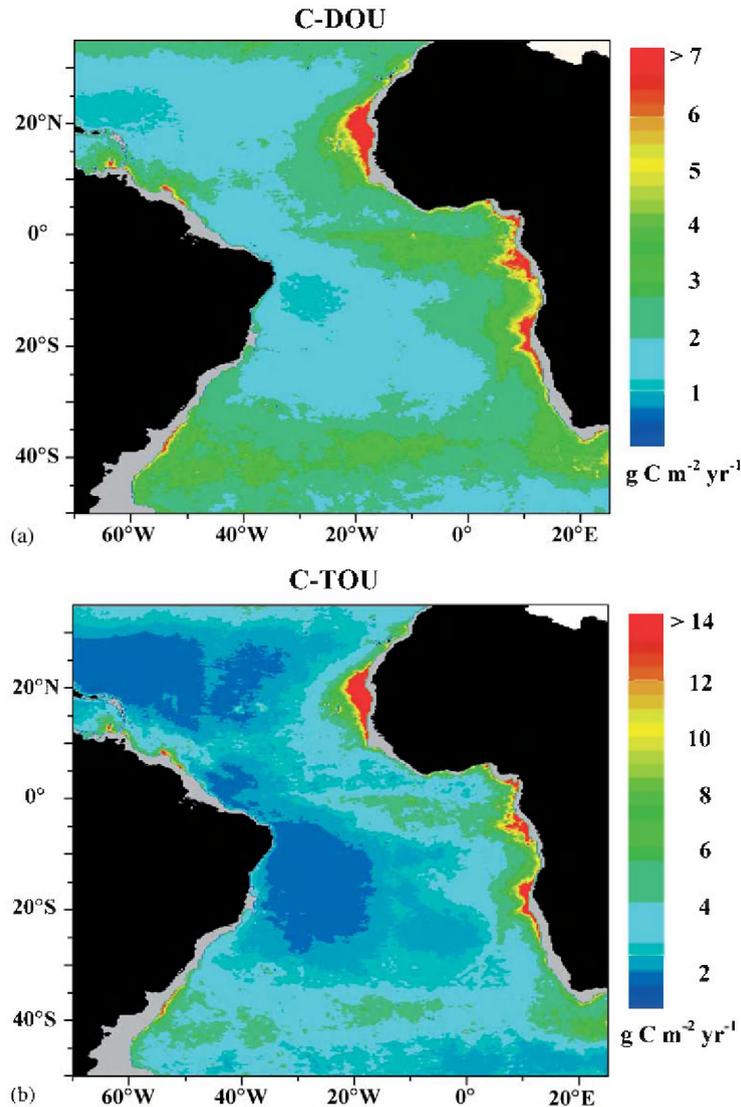


Fig. 10. Modeled organic carbon fluxes at the seafloor in the Atlantic (water depth  $\geq 1000$  m). (A) Carbon consumption as a function of the diffusive oxygen uptake (C-DOU), primary production, and water depth after Eq. (4); (B) Carbon consumption as a function of the total oxygen uptake (C-TOU), primary production, and water depth after Eq. (5).

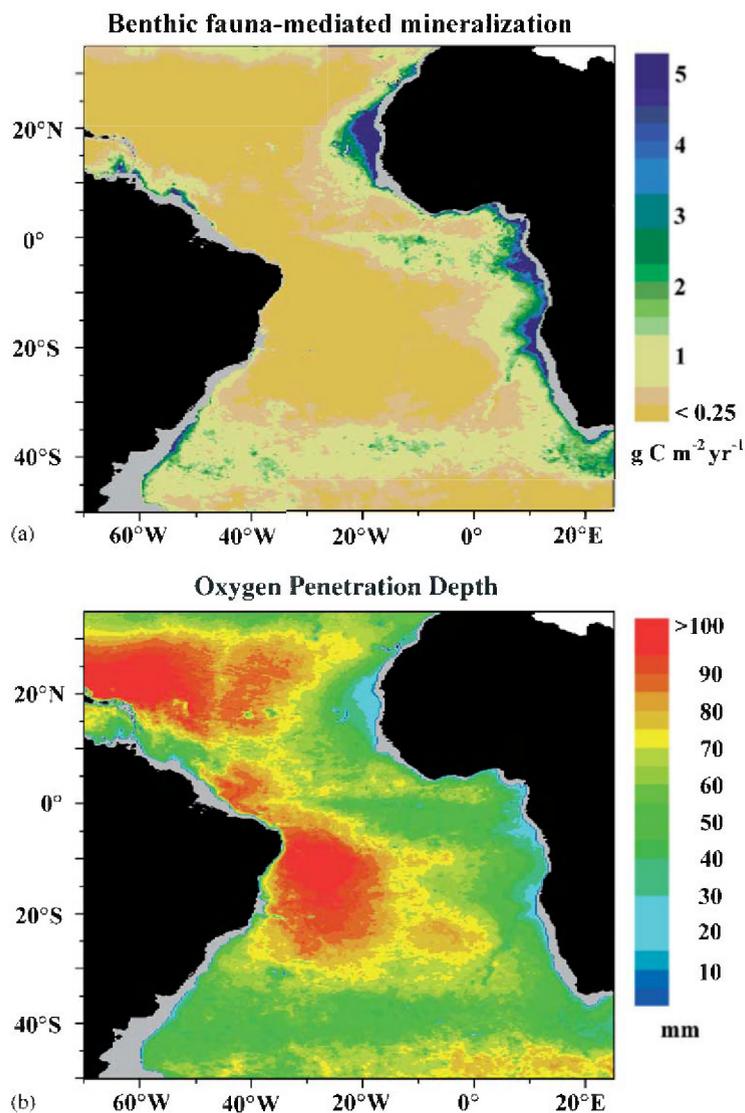


Fig. 11. (A) Benthic fauna-mediated mineralization in the Atlantic (water depth  $\geq 1000$  m) determined by subtracting the solely diffusive supported carbon mineralization (C-DOU, Fig. 10A) from the total carbon mineralization (C-TOU, Fig. 10B). (B) Estimated oxygen penetration depth (OPD) in the Atlantic. Values were calculated with Eq. (6) and the C-DOU data from Fig. 10A.

mineralization rates derived from our equations yielded benthic mineralization rates that were up to 2 times higher for the same areas (C-DOU:  $1.9 \text{ g C m}^{-2} \text{yr}^{-1}$  and C-TOU:  $2.0 \text{ g C m}^{-2} \text{yr}^{-1}$ ), thus indicating that the slowly accumulating oligotrophic deep-sea sediments have higher carbon mineralization rates than previously thought.

However, this area admittedly is still under-sampled. For the shelf areas the values from Jahnke (1996) match with our C-DOU rates, but our C-TOU rates were significantly higher (African shelf: 1.8 times higher and South American shelf: 1.6 times higher). The empirical relation between benthic oxygen demand (in situ and

Table 2

Benthic carbon flux, C-flux at 1000 m water depth and primary production for the investigated area of the Atlantic (35°N–50°S) and the entire Atlantic Ocean

	PP $10^{12}$ g C yr <sup>-1</sup>	Benthic flux $10^{12}$ g C yr <sup>-1</sup>	% PP
<i>Investigated area Atlantic (35°N to 50°S)<sup>a</sup></i>			
Primary production	7875		
Benthic carbon consumption			
C-DOU		133.5	1.7
C-TOU		168.1	2.1
C-Flux 1000 m			
C-DOU		212.4	2.7
C-TOU		332.8	4.2
<i>Extrapolation to the Atlantic Ocean<sup>b</sup></i>			
C-DOU Atlantic Ocean (present study)		174	
C-TOU Atlantic Ocean (present study)		219	
C-flux Atlantic Ocean (Jahnke, 1996)		136	
C-flux Atlantic Ocean (Christensen, 2000)		204	

<sup>a</sup>Estimated area of the investigated Atlantic (35°N–50°S):  $56.8 \times 10^6$  km<sup>2</sup>.

<sup>b</sup>Estimated area entire Atlantic Ocean (60°N–60°S):  $74 \times 10^6$  km<sup>2</sup>.

laboratory measurements), primary production and water depth recently suggested by Christensen (2000) tended to slightly underestimate DOU and TOU compared to our measurements for water depths > 3000 m and primary productivity < 200 g C m<sup>-2</sup> yr<sup>-1</sup> by 5–20%. However, for the shallow, highly productive areas the relationship overestimated fluxes by factors of 2.5 and 1.3 as compared to our DOU and TOU measurements, respectively.

Integrating the values for the investigated area (35°N–50°S), the amount of benthic carbon mineralization equaled 133.5 and  $168.1 \times 10^{12}$  g C yr<sup>-1</sup>, respectively, depending on the chosen oxygen uptake measurement (DOU or TOU; Table 2). This amounts to 1.7–2.1% of the annual primary production for the Atlantic. Normalizing the benthic oxygen fluxes of the investigated area to a water depth of 1000 m according to Jahnke (1996) revealed that 2.7–4.2% of the annual primary production reached a water depth of 1000 m, and consequently 51% and 63% of the total carbon consumption below 1000 m occurs in the deep-sea sediments. This is similar to a value of 59% estimated for the northern North Atlantic by Schlüter et al. (2000). The values are somewhat

higher than estimates for the global deep ocean as taken from Jahnke (1996), which was on the order of 45%, but they are almost 2 times higher than the estimates from Christensen (2000), who estimated that only 32% of the organic material sinking through 1000 m is consumed in the sediments. However, whereas the extrapolations by Jahnke (1996) and Christensen (2000) were made on a global scale, the present compilation and the work of Schlüter et al. (2000) are based solely on regional data sets from the Atlantic and the northern North Atlantic, respectively.

Assuming that our relation for the investigated area of the Atlantic is representative for the entire Atlantic Ocean further extrapolations can be performed and compared to the two other benthic mineralization estimates for the Atlantic Ocean based on oxygen uptake measurements (Table 2). Our estimates for the benthic carbon mineralization for the entire Atlantic Ocean yielded values of 174 and  $219 \times 10^{12}$  g C yr<sup>-1</sup> (equals 18.9 and  $23.8 \times 10^{12}$  mol O<sub>2</sub> yr<sup>-1</sup>), respectively, and were in the same range as values reported by Christensen (2000), but are 1.3–1.6 times higher than the estimate made by Jahnke (1996). It remains to be

shown if the Atlantic is representative for the global oceans.

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