Limnol. Oceanogr., 48(3), 2003, 1265–1276
© 2003, by the American Society of Limnology and Oceanography, Inc.

Seasonal dynamics of benthic O_2 uptake in a semienclosed bay: Importance of diffusion and faunal activity

Ronnie N. Glud
Marine Biological Laboratory, University of Copenhagen, Strandpromenaden 5, DK-3000 Helsingør, Denmark

Jens K. Gundersen
Unisense A/S, Science Park Aarhus, Gustav Wieds Vej 10, DK-8000 Aarhus, Denmark

Hans Røy and Bo Barker Jørgensen
Max Planck Institute for Marine Microbiology, Celsiusstr. 1, D-28359 Bremen, Germany

Abstract

The benthic O_2 uptake and the O_2 microdistribution in a coastal sediment of Aarhus Bay, Denmark, were investigated during a seasonal study. Measurements were performed in situ by a profiling lander and a flux chamber lander, as well as on recovered sediment cores. The O_2 penetration depth, the diffusive O_2 uptake, and the volume-specific O_2 consumption rate strongly depended on the seasonal changes in bottom water O_2 concentration and the sedimentation of organic carbon. The in situ O_2 penetration depth varied between 0.5 mm in summer and 4.5 mm in winter. The diffusive O_2 uptake varied between 8 and 30 mmol m^{-2} d^{-1}, whereas the volume-specific O_2 consumption rate varied by a factor of 13. The O_2 distribution was very sensitive to environmental controls, and microprofiles obtained in the laboratory tended to overestimate the in situ O_2 penetration depths and underestimate the in situ diffusive O_2 uptake. Three-dimensional O_2 flux calculations based on in situ microtopographic mapping showed that the actual diffusive exchange rate was ~10% higher than the simple one-dimensional, microprofile-derived diffusive O_2 exchange. The total O_2 uptake measured in the laboratory showed less distinct seasonal variation, but on the average, it was ~20% higher than the diffusive O_2 uptake. The difference reflected the microtopography of the sediment surface and the contribution from benthic macrofauna. In situ total O_2 uptake was generally twice as high as laboratory rates, reflecting a higher fauna-related O_2 consumption in the larger enclosures incubated in situ. Annually, the in situ three-dimensional diffusive O_2 consumption was 6.2 mol O_2 m^{-2}, whereas the additional benthos-mediated O_2 uptake was 3.9 mol O_2 m^{-2}. Thus, 40% of the total O_2 uptake was due to faunal activity and respiration. The present study demonstrates the importance of realistic faunal representation during sediment incubations in order to obtain correct benthic mineralization rates.

The oxygen uptake rate of the seafloor is the most widely used measure of benthic mineralization (e.g., Thamdrup and Canfield 2000). The total O_2 uptake (TOU) is usually quantified from the O_2 disappearance rate in sediment enclosures, and the TOU thereby represents an integrated measure of the diffusive, advective and fauna-mediated O_2 consumption. The enclosure technique, however, does not provide information on the O_2 penetration depth or the vertical distribution of O_2 consumption rate. The introduction of O_2 microelectrodes in aquatic biology in the early 1980s allowed the benthic O_2 dynamics to be studied in more detail (Revsbech et al. 1980).

Early microprofile measurements revealed that the oxic zone extends only a few millimeters into fine-grained coastal and shelf sediments (e.g., Revsbech et al. 1980). The oxic zone has proved to be very dynamic, with an intense heterotrophic and autotrophic O_2 consumption. Furthermore, detailed microsensor studies documented the existence of a 0.1–1.2-mm-thick diffusive boundary layer (DBL) (Jørgensen and Revsbech 1985; Archer et al. 1989; Gundersen and Jørgensen 1990; Jørgensen and Des Marais 1990). The main transport mode within the DBL is molecular diffusion, and the zone is characterized by linear O_2 concentration gradients (Jørgensen and Revsbech 1985). The diffusive solute transport through the DBL can limit biogeochemical reactions (Boudreau and Guinasso 1982) and benthic O_2 consumption of highly active sediments (Gundersen and Jørgensen 1990; Jørgensen and Des Marais 1990). The DBL blankets the complex three-dimensional (3D) microtopography of the sediment surface, and the DBL thickness is controlled by the flow velocity of the overlying water and by the sediment roughness (e.g., Jørgensen and Des Marais 1990).

The ability to resolve linear concentration gradients within the DBL allows the one-dimensional (1D) diffusive O_2 uptake (DOU) to be calculated (e.g., Jørgensen and Revsbech 1985). Alternatively, the diffusion-mediated O_2 consumption rate within the sediment can be modeled from the curvature of measured concentration profiles (e.g., Nielsen et al. 1990; Berg et al. 1998). This, however, requires knowledge on the

Acknowledgments

We thank ''Skipper-Hans'' for many joyful hours at sea, Fritz Hansen for skillful technical assistance, and Lars B. Pedersen and Anni Glud for producing the numerous electrodes used during this study. The study received financial support from the Danish Environmental Foundation and the Max Planck Society—the support is gratefully acknowledged. We thank Bent Sømod for providing the faunal data collected by the County of Aarhus, Denmark. Two anonymous reviewers are thanked for constructive criticism that helped improve the manuscript.

interstitial transport coefficients for O_2 (Iversen and Jørgensen 1993). The two relatively simple approaches assume that the DBL and the sediment–water interface is represented by infinite flat planes (Gundersen and Jørgensen 1990; Jørgensen and Des Marais 1990). On the scale of the DBL, however, the benthic interface is a topographically complex landscape, and consequently, simple 1D diffusion models might not adequately describe the 3D diffusion flux (Jørgensen and Des Marias 1990; Røy et al. 2002).

Faunal activity further complicates matters because irrigation enhances the ventilation of the sediment and introduces oxygenated water to deeper, otherwise anoxic, sediment layers (Kristensen 1988; Fenchel 1996; Aller 1998). Faunal activity can thereby strongly enhance the benthic exchange rates. In impermeable sediments without flow-induced advection, the additional fauna-mediated O_2 uptake (FOU) can be calculated as the difference between TOU and DOU (e.g., Archer and Devol 1992; Glud et al. 1994*a*). This parameter includes both the faunal respiration and the O_2 uptake in the surrounding sediment related to irrigation and other faunal activity.

In the present study, we compared three different measuring techniques for quantifying the benthic O_2 consumption rate. Measurements were performed in situ and in the laboratory during a seasonal study of a coastal marine sediment. The FOU was quantified, and its importance for the total benthic mineralization activity is discussed. Some of the data have been published previously in a report (Gundersen et al. 1995, in Danish) to the Danish Environmental Protection Agency.

Materials and methods

Study site—The semienclosed Aarhus Bay is situated in Kattegat on the Baltic Sea–North Sea transition, Denmark. The bay covers an area of 320 km^2 and has an average water depth of 15 m. The present study was carried out in the central part of the bay at Sta. 6 (56°9.1′N, 10°19.2′E) with a water depth of 16 m (Thamdrup et al. 1994). The presented data were mostly obtained during 1990–1992 as part of an intense field study focusing on coastal element cycling (Jørgensen 1996). The water column was stratified by a halocline during 75% of the study period (Rasmussen and Jørgensen 1992; Jørgensen 1996). The sediment consists of 20% fine sand, 22% silt, and 55% clay, and the site has a mean net deposition rate of 2.5 g m^{-2} d^{-1} (Pejrup et al. 1996). The upper 4 mm of the sediment has an average porosity of 0.87 ± 0.05 (v/v, $n = 34$) and an organic matter content of 9.9 ± 0.9% dry weight ($n = 34$) (Rasmussen and Jørgensen 1992).

Laboratory measurements—The study site was visited 24 times during 1990–1991 by a small research vessel, *Genetica II*. On each occasion, a series of sediment cores were recovered by a Haps corer (Kanneworff and Nicolaisen 1973). Six undisturbed subcores were taken by 25-cm-long Plexiglas tubes with an inner diameter of 5.4 cm. Water (~30 liters) was subsequently collected 20 cm above the seafloor by a pump positioned on a small tripod that was lowered from the ship. Temperature and O_2 concentration were determined in surface and bottom water on each occasion. Cores and water samples were transported back to the laboratory in insulated containers within 2 h after recovery. Upon return, six uncapped cores were submerged in an aquarium containing bottom water from the sampling site kept at in situ temperature. In order to maintain in situ O_2 concentration, the water was continuously flushed with an air/dinitrogen mixture regulated by a digital gas mixer. The rotation of Teflon-coated magnets attached to the inner wall of each core liner ensured a good exchange between the water phase of the cores and the exterior seawater (Rasmussen and Jørgensen 1992). Sediment cores were preincubated in darkness over night prior to measurements.

The next day, 2–12 (average of ~7) oxygen microprofiles were measured using Clark-type microelectrodes with an internal reference and a guard cathode (Revsbech 1989). The profiles were measured at a depth resolution of 50 μm and always in at least two different sediment cores. Profiles were generally measured in areas unaffected by faunal activity, and no significant difference was observed between profiles obtained in different cores on a given date. The microelectrodes had tip diameters of 3–20 μm, stirring effects <2%, and 90% response time of <2 s (Revsbech 1989; Glud et al. 2000). The sensors were positioned by a motorized micromanipulator, and the sensor current was measured by a picoamperemeter connected to an analog-to-digital converter, which transferred the signals to a computer (Revsbech and Jørgensen 1986). The microprofiles had two inherent calibration points: the reading in the overlying water with a known O_2 concentration and the constant low reading in the anoxic sediment.

After microprofiling, the sediment cores were capped, leaving an internal water height of 8–12 cm. A glass tube with an internal diameter of 5 mm penetrated each lid and allowed the subsequent insertion of an O_2 microelectrode in the overlying water phase. The glass tube was filled with paraffin oil to impede diffusive exchange between the enclosed water volume and the air (Rasmussen and Jørgensen 1992). During incubation, small magnets stirred the overlying water phase in each core. This ensured a DBL thickness during core incubations and microprofile measurements similar to the in situ DBL thickness.

O_2 in situ measurements—On each sampling occasion in 1990–1991, O_2 microprofiles were measured in situ using a profiling lander (Gundersen and Jørgensen 1990). The central part of the instrument consisted of a movable electronic cylinder equipped with microsensors. For the present study, six O_2 microelectrodes were used with similar measuring characteristics as outlined above. The cylinder was mounted on a tripod that was lowered by wire from the ship. After the instrument had stabilized on the seafloor for 1 h, the cylinder was moved downward in increments of 50 μm. At each depth horizon, data from all sensors were recorded and transferred via cable to an onboard computer. A video mounted on the tripod allowed visual inspection of the sediment during deployment.

During 1992, laboratory measurements and in situ microprofiles were obtained on a more irregular basis, whereas on 15 occasions, in situ TOU was measured by a benthic cham-

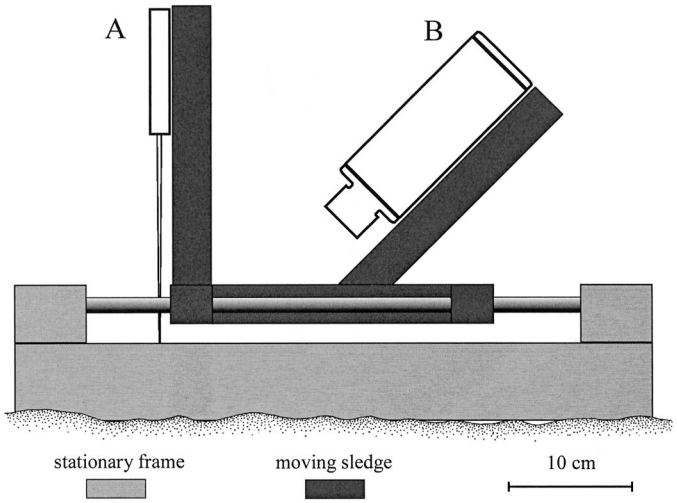

Fig. 1. Schematic presentation of the in situ instrument used for 3D topographic mapping of the seafloor. (A) The laser diode module. (B) The video camera.

ber lander (Glud et al. 1995). As the instrument was positioned on the seafloor, a central chamber of 896 cm^2 was inserted into the sediment. Video recordings demonstrated that the sediment surface was practically undisturbed during chamber insertion. After 1 h, the lid was closed, leaving an internal water height of approximately 10 cm. During incubation, a central impeller mixed the overlying water phase, and two minielectrodes with similar measuring characteristics as outlined above continuously recorded the O_2 concentration of the enclosed water volume. The stirring resulted in a DBL thickness of ~500 μm, which was similar to the DBL thickness in laboratory-incubated sediment cores and close to the average DBL thickness measured in situ (*see below*). During incubations, 10 spring-loaded syringes retrieved water samples at predefined time intervals for subsequent O_2 analysis and sensor calibration, along with an onboard reading in anoxic sediment. At the end of the incubation, a scoop closed the chamber from below, and after recovery, the exact water height of the water phase was determined. The enclosed sediment was sieved through a 1-mm mesh screen to collect the entire macrofaunal community. The fauna was identified and the dry weight was determined after 24 h at 70°C, whereas its organic matter content was determined as loss on ignition after 24 h at 550°C.

Microtopography mapping—The microtopography of the sediment surface at the study site was determined in December 2001 using an in situ version of the optical instrument described by Røy et al. (2002). A line-generating laser diode (Lasiris LAS 670 5 with LAS 20 line) was positioned on a moving sledge at ~15 cm distance to the seafloor. A digital video camera (SONY DX-1000 in Amphibico underwater house) was fixed on the sledge and recorded the movement of a vertically projected laser line from a 45° angle (Fig. 1). The position of the moving sledge relative to the stationary frame was recorded in the upper corner of the view field of the camera via a position sensor with an optical output. The

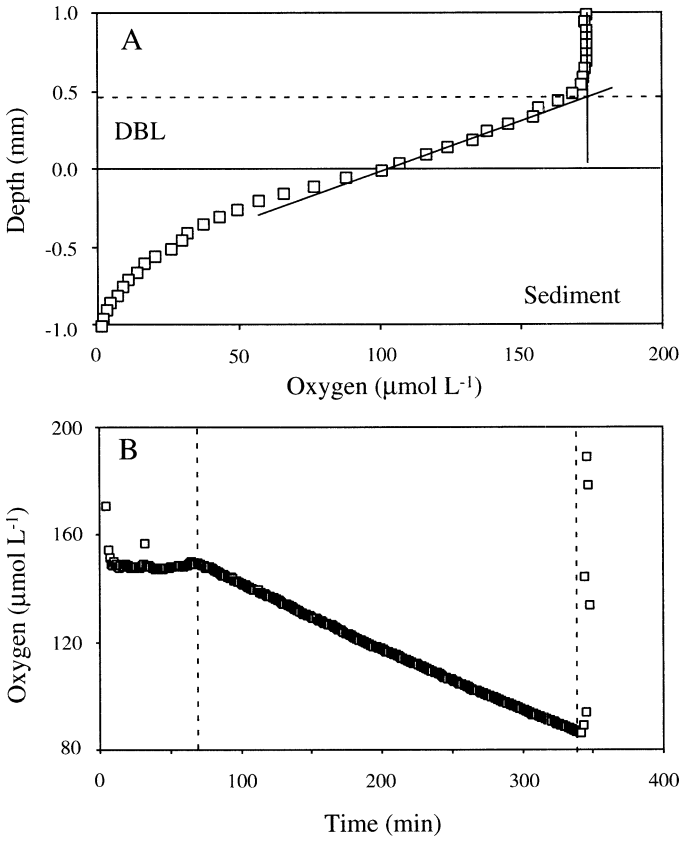

Fig. 2. (A) A typical O_2 microprofile measured in situ during late summer 1990. The solid horizontal line indicates the estimated position of the sediment surface, and the broken line indicates the estimated position of the upper DBL boundary. The slope of the concentration gradient within the DBL is shown. (B) The readings of an O_2 mini electrode during deployment of the benthic chamber lander in summer 1992. The time axis shows minutes after lander deployment. The left vertical broken line indicates the time when the chamber lid was closed, and the right line indicates the time of chamber recovery.

instrument was lowered by wire to the seafloor with the video camera continuously recording. After 1 min, the translation mechanism was activated, and the sledge translated a horizontal distance of 12–15 cm. Recorded images were extracted for every 0.1 mm of translation based on the state of the position sensor. Images of the projected line were used to determine the relative height of the sediment surface. Given the optical dimensions and the 0.1-mm distance between images, the microtopography was determined with 0.13- by 0.1-mm horizontal resolution, while vertical resolution was better than 20 μm (Røy et al. 2002). From 13 independent scans, 18 topographic maps were extracted, each covering ~40 cm^2.

Oxygen microprofile calculations—The upper DBL boundary of the measured microprofiles was determined as the intersection between the extrapolated linear O_2 gradient in the DBL and the constant O_2 value in the overlying water (Fig. 2A) (Jørgensen and Revsbech 1985). The thickness of the DBL was estimated from the intersection point and the

position of the sediment surface, which typically was identified from a distinct break in the concentration profile (Fig. 2A).

The DOU of the sediment was calculated from: DOU = $D_0(dC(z)/dz)$ where D_0 is the temperature-corrected molecular diffusion coefficient of O_2 and C is the O_2 concentration at a given depth, z, with the DBL (Fig. 2A) (Crank 1983). The D_0 was taken from Broecker and Peng (1974) and was temperature corrected as described by Li and Gregory (1974). The average volume-specific O_2 consumption rate was calculated by dividing the DOU by the O_2 penetration depth. For whole-core incubations, the TOU was calculated from the initial linear O_2 decrease in the enclosed water volume (Fig. 2B).

The volume-specific O_2 consumption rates were also quantified from the O_2 microprofiles measured within the sediment using a simple manual curve-fitting approach and assuming zero-order kinetics (Nielsen et al. 1990; Rasmussen and Jørgensen 1992). The measured profiles could always be fitted by one, two, or three two-degree polynomial. The depth-integrated O_2 consumption rate and the O_2 exchange at the sediment–water interface were subsequently calculated (Rasmussen and Jørgensen 1992). The DOU was thereby calculated from each microprofile by two independent approaches using either the concentration gradient measured in the DBL or the O_2 distribution measured in the interstitium. For the calculations based on the interstitial data, the sediment diffusion coefficient, D_s, of O_2 was estimated from the sediment porosity, ϕ, using the relationship $D_s = [1 + 3(1 - \phi)]^{-1}D_0$ (Iversen and Jørgensen 1993).

Results

The temperature of the bottom water varied throughout the year between 14.0°C in September and 1.5°C in February, whereas the temperature range of the surface water was from 16.2°C to 1.5°C. During autumn and winter, there was no temperature difference between surface and bottom water. In spring and early summer, the halocline was stabilized by a temperature difference between the two water masses (Fig. 3A). The pycnocline was mostly situated between 8 and 12 m water depth but varied considerably as a result of wind-induced seiching (Jørgensen 1996). The O_2 concentration in the surface water varied between 234 and 381 μmol L^{-1} but was always close to air saturation (90–110%). Light penetration was limited by the relatively high phytoplankton biomass, and we never observed net O_2 production at the seafloor. Consequently, periods with stratification resulted in O_2 depletion of the bottom water. Minimum O_2 concentration of 55–70 μmol L^{-1} (18–25% air saturation) were reached during summer and early autumn (Fig. 3B). Generally, the pattern in bottom water temperatures and O_2 concentrations from 1990 to 1991 were reproduced in 1992 (Fig. 3).

The laboratory and the in situ–determined O_2 penetration depths varied on a seasonal basis (Fig. 4). Both data sets revealed maximum penetration depths of ~4.5 mm during winter, whereas minimum values of ~0.8 mm were obtained in early autumn (Fig. 4). The approximate sixfold variation in O_2 penetration depth correlated well with the O_2 concentration of the bottom water (Figs. 3, 4). Oxygen depletion in the bottom water immediately resulted in a narrowing of the oxic zone. Thus, a decrease in O_2 bottom water concentration from 260 to 75 μmol L^{-1} in August 1990 was followed by a decrease in O_2 penetration from 2.2 to 0.8 mm (Figs. 3, 4). The few measurements of O_2 penetration performed in 1992 reproduced the data of 1990 with a single exception that coincided with a distinct depletion in bottom water O_2 concentration in the beginning of June 1992 (Figs. 3, 4).

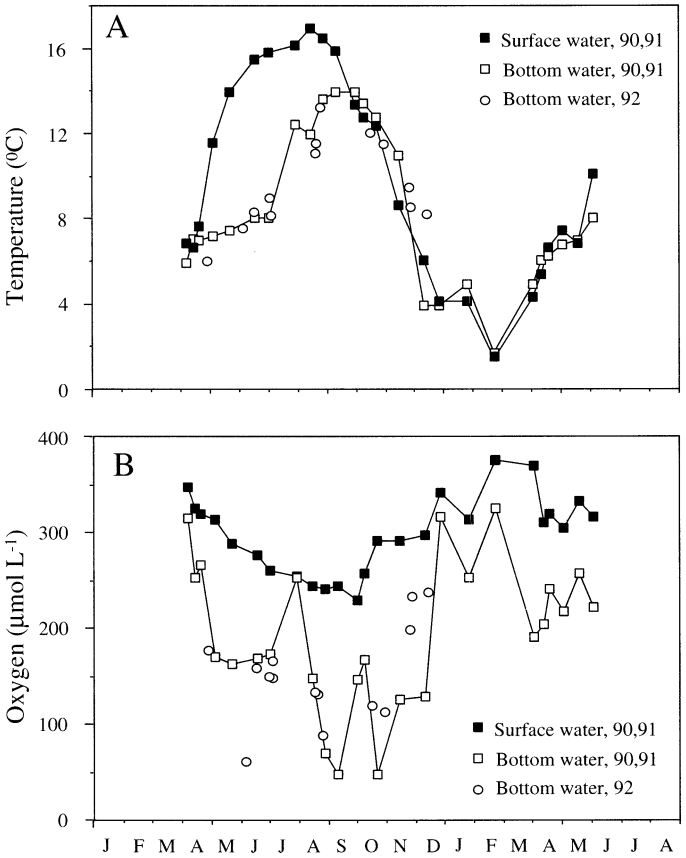

Fig. 3. (A) Temperature of surface water and bottom water during 1990–1991 and of bottom water in 1992. (B) O_2 concentration in the surface water and the bottom water during 1990–1991 and in the bottom water in 1992.

Along with the bottom water O_2, the input of organic carbon clearly affected the interfacial O_2 dynamics. In early September, the O_2 concentration of the bottom water was 53 μmol L^{-1} and the O_2 penetration depth was only 0.78 ± 0.04 mm. The major part of the volume-specific O_2 consumption as modeled from the curvature of the O_2 concentration profiles was associated with the oxic–anoxic interface, presumably because of intensified oxidation of reduced solutes diffusing up from the anaerobic degradation below (Fig. 5A). By mid-September, a bloom of dinoflagellates (*Ceratium* spp.) was deposited on the sediment surface, and shortly afterwards, wind-induced seiching resulted in elevated O_2 concentration in the bottom water. The two events led to an intensified O_2 consumption at the sediment–water interface, which was suddenly enriched with labile organic material and resulted in an increased O_2 penetration depth

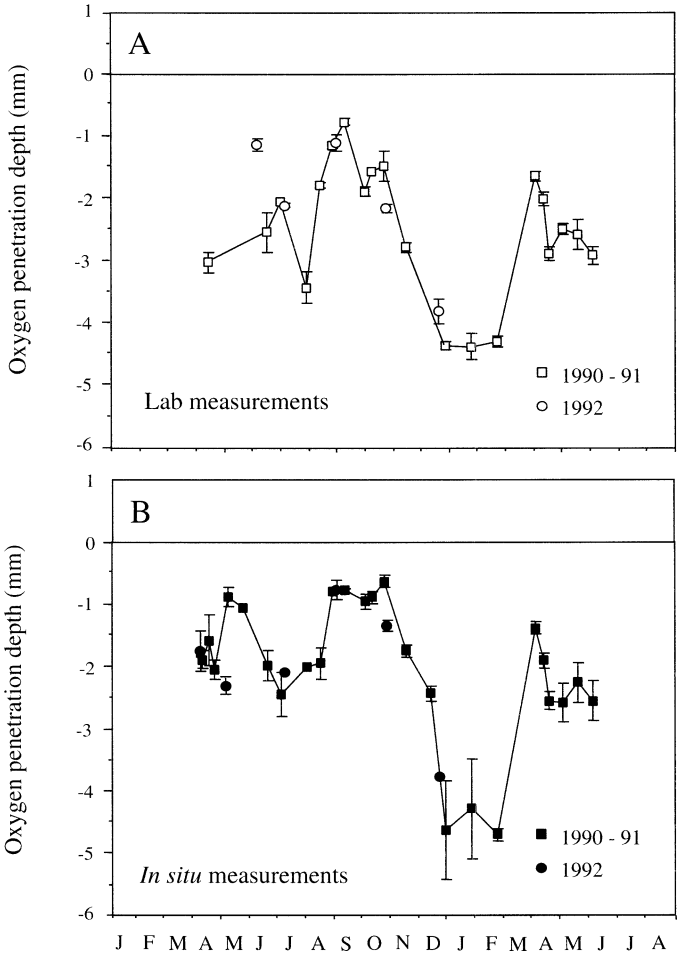

Fig. 4. (A) Oxygen penetration depths measured in the laboratory during 1990–1991 and 1992. (B) Oxygen penetration depth measurements in situ during 1990–1991 and 1992.

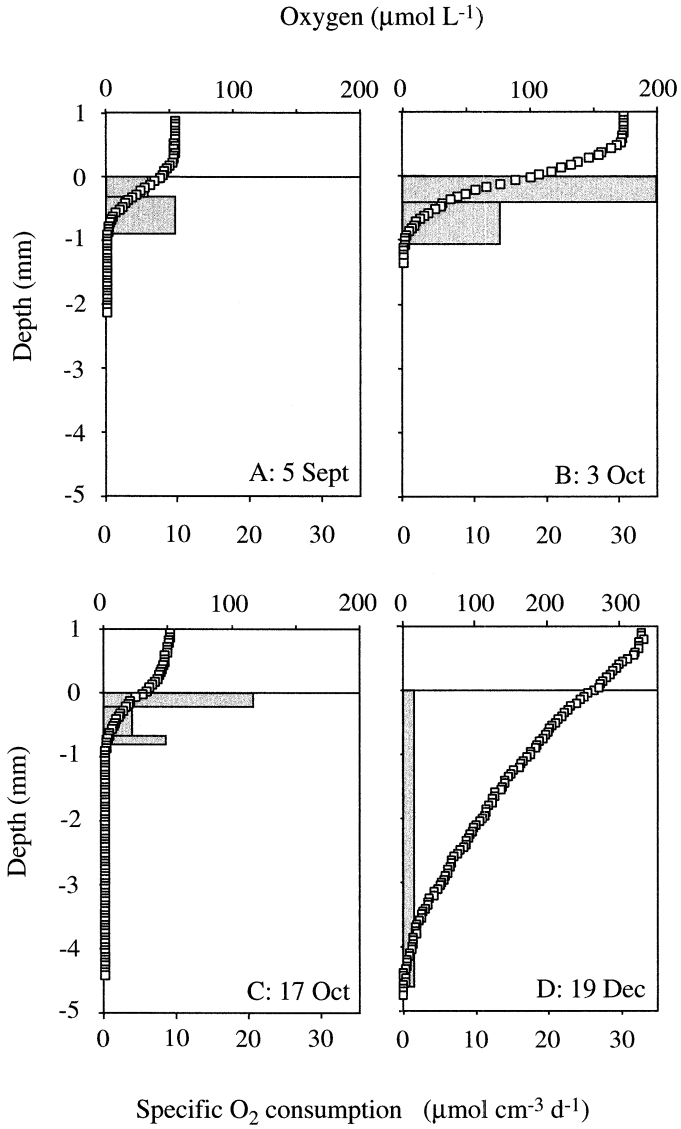

Fig. 5. Typical O_2 microprofiles measured in situ on four different occasions during 1990. The horizontal line indicates the estimated position of the sediment surface. Gray boxes represent the volume-specific O_2 consumption rates modeled from the curvature of the O_2 profiles.

(Fig. 5B). Subsequently, the ongoing mineralization resulted in declining O_2 concentration of the bottom water and a decrease in the O_2 penetration depth (Fig. 5C). The volume-specific O_2 consumption calculated from profiles measured on 17 October reflected intensified activity at the sediment surface and at the oxic–anoxic interface below. During winter, low sedimentation rates and high bottom water O_2 concentration resulted in a deep oxic zone with a low, depth-independent volume-specific O_2 consumption rate (Fig. 5D).

The diffusive O_2 uptake calculated from the in situ DBL profiles showed two seasonal maxima (Fig. 6A) coinciding with distinct sedimentation events in April and October 1990 (Valeur et al. 1995; Pejrup et al. 1996). The following spring bloom in April 1991 was less distinct but also caused an elevated DOU (Fig. 6A). The summer and winter were characterized by relatively low O_2 consumption rates, presumably because of limiting O_2 concentrations in summer and low organic sedimentation rates in winter. The seasonal pattern was recognized also in the DOU determined in recovered sediment cores, yet the temporal dynamics were less distinct (Fig. 6B). The O_2 consumption modeled from interstitial in situ O_2 microprofiles revealed a similar seasonal pattern as the in situ DBL measurements (Fig. 6C). On a yearly basis (from May 1990 to May 1991), the in situ DOU was 5.5 mol m^{-2} yr^{-1}, whereas the laboratory-determined DOU was 5.1 mol m^{-2}. The depth-integrated volume-specific O_2 consumption of the in situ microprofiles revealed a yearly O_2 consumption rate of only 4.2 mol m^{-2} yr^{-1}. Generally, data from 1992 followed the pattern of 1990 (Fig. 6).

The moderate seasonality in DOU actually covers much more intense dynamics in the aerobic benthic activity. The average volume-specific activity, as calculated from the ratio between the in situ DOU and O_2 penetration depth, varied by a factor of ~13 (Fig. 7). The previously resolved activity peaks become more distinct and reflect the availability of electron donors in the oxic zone, either as organic carbon or inorganic products of the anaerobic degradation.

By far, most microprofiles reflected a smoothly declining

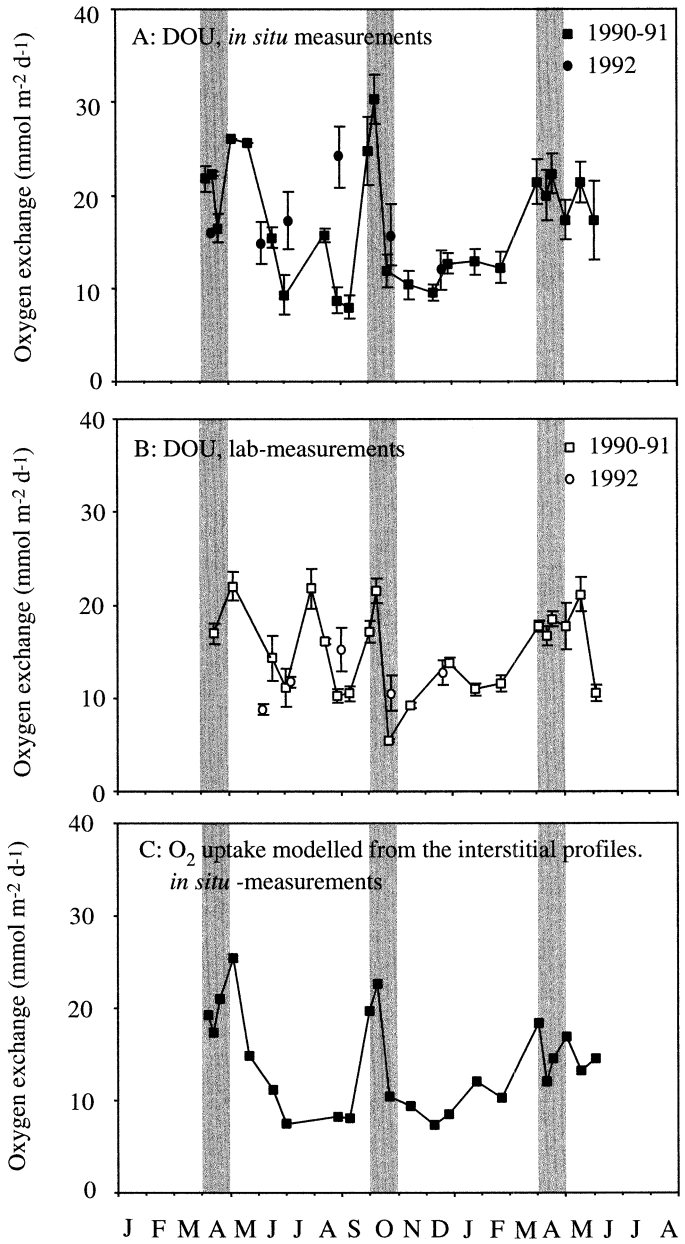

Fig. 6. (A) In situ DOU calculated from O_2 gradients measured within the DBL during 1990–1992. (B) Laboratory DOU calculated from O_2 gradients measured within the DBL during 1990–1992. (C) Area O_2 consumption rates modeled from the curvature of the average interstitial O_2 microprofiles measured in situ during 1990–1992. Circles of each panel represent measurements performed during 1992. The shaded areas represent periods of intensified sedimentation as deduced from Valeur et al. (1995).

O_2 concentration within the sediment (Fig. 5). However, on a few occasions measurements directly indicated that faunal activity was of importance for the benthic O_2 exchange. The in situ microprofile of Fig. 8 clearly reflects a rhythmic irrigation of a burrowed polychaete affecting the O_2 distribution at the sediment–water interface. Apparently, the microelectrode passed along the vertically oriented burrow in which the polychaete pumped O_2 down to otherwise anoxic sediment (Fig. 8).

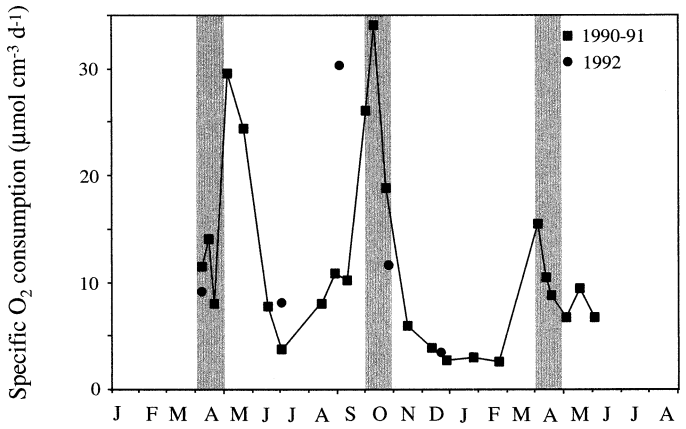

Fig. 7. Average volume-specific O_2 consumption rates within the oxic sediment calculated from the DOU and the O_2 penetration depth of in situ profiles during 1990–1991 (squares) and in 1992 (circles). The shaded areas represent periods of intensified sedimentation as deduced from Valeur et al. (1995).

The total O_2 uptake measured in recovered sediment cores was in general higher than the microelectrode-derived O_2 uptake rates (Fig. 9A). There was no distinct seasonal pattern in the laboratory-determined TOU, although the values tended to reach a minimum during winter (Fig. 9A). The average TOU for 1990–1991 was 18.7 mmol m^{-2} d^{-1}, and the integrated yearly TOU was 6.5 mol m^{-2} yr^{-1}. The corresponding values obtained the following year were 14.8 mmol m^{-2} d^{-1} and 5.1 mol m^{-2} yr^{-1}, respectively. The somewhat lower

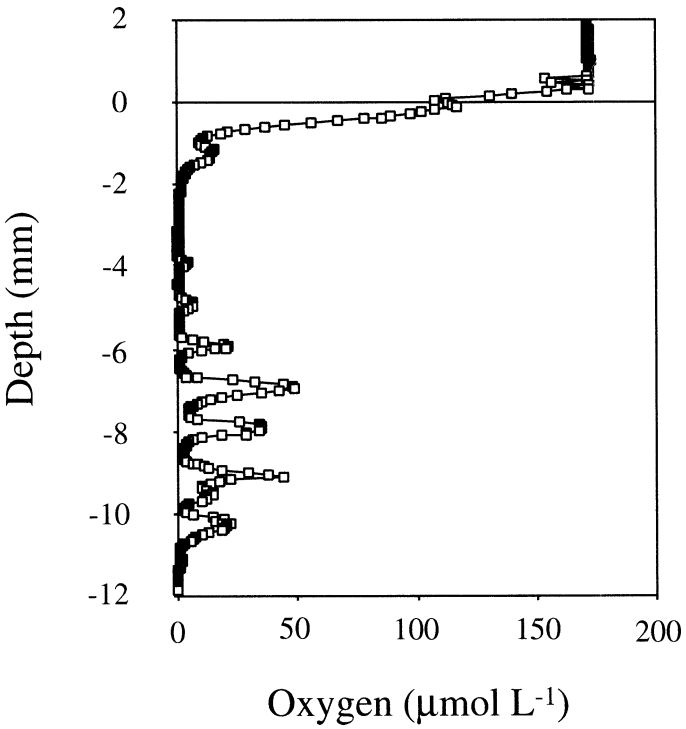

Fig. 8. An in situ O_2 microprofile measured in the vicinity of an actively ventilated polychaete burrow. The horizontal line indicates the estimated position of the sediment surface.

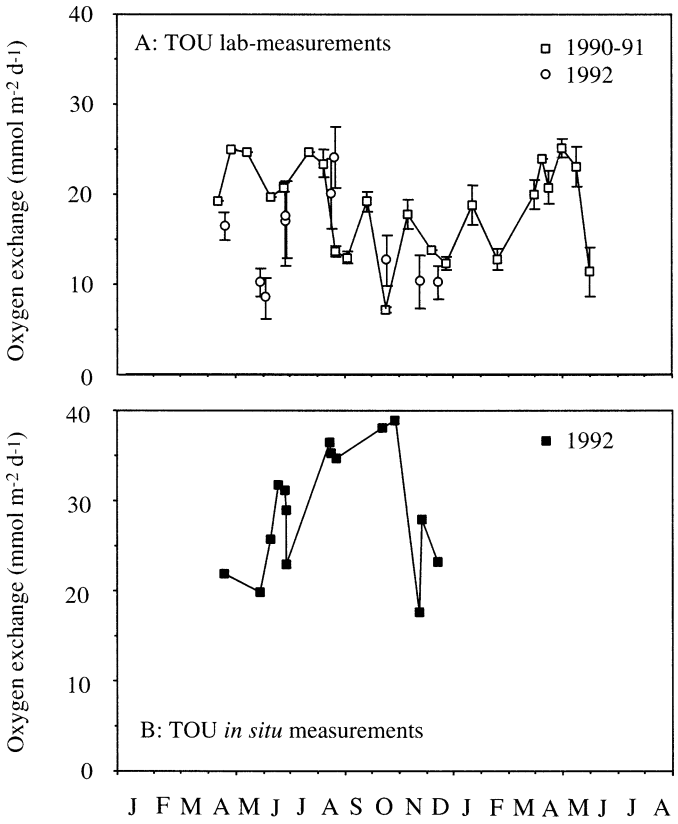

Fig. 9. (A) TOU measured in the laboratory in recovered sediment cores during 1990–1991 and 1992. (B) In situ TOU measured during 1992.

rates during 1992 were mainly caused by the O_2 depletion event in the beginning of June that presumably repressed the TOU (Fig. 9A). The in situ–determined TOU during 1992 also showed minimal values during winter (Fig. 9B), but the absolute rates were significantly higher than in laboratory incubations. On nine events, the TOU was measured simultaneously in situ and in the laboratory, and on average, the in situ rates were higher by a factor of 2.0. There was, however, no clear relationship between the recovered macrofaunal biomass and the in situ TOU (*see Web Appendix 1,* http://www.aslo.org/lo/pdf/vol_48/issue_3/1265al.pdf). The annual TOU as measured in situ was 10.1 mol m^{-2} yr^{-1}. The yearly benthic O_2 uptake determined by different techniques thereby varied between 4.2 and 10.1 mol m^{-2} yr^{-1} for the period of 1990–1992 (Table 1).

Two characteristic examples of the benthic microtopography at the investigated site are presented as shaded reliefs in Fig. 10. Most structures can be recognized as biogenic structures, such as fecal mounds and gastropod tracks (Fig. 10A,B). The typical vertical distance between maximal and minimal altitude in the scans was ~5 mm. The 3D sediment–water interface area, as estimated by matrix smoothing of the original scans (Røy et al. 2002), was on average 106 ± 1% of the horizontal plane area. Apart from the fact that the area across which diffusion takes place is larger than the plane horizontal area, the 3D topographic structure of the interface also means that a vertically aligned microelectrode

Table 1. Annual benthic oxygen uptake rates in Aarhus Bay, Denmark.

Measurement technique	O_2 uptake (mol m^{-2} yr^{-1})	
	May 90–May 91	Jan–Jun 92
DOU measured in the lab	5.1(5.7)	—
TOU measured in the lab	6.5	5.1
DOU measured in situ	5.5(6.2)	—
O_2 consumption modeled in situ	4.2	—
TOU measured in situ	—	10.1

Numbers in parentheses represent values accounting for a 3D diffusive interface (*see text*).

will approach the sediment surface at an angle (Jørgensen and Des Marais 1990). The average angle between the horizontal plane and the sediment surface was calculated by simple trigonometry to be 19.37° (cf. Jørgensen and Des Marais 1990). Because of the 3D structure of the sediment–water interface, the DOU calculated from the vertically obtained microprofiles will underestimate the actual diffusive O_2 uptake rate. The ratio between the 3D and the 1D diffusive O_2 uptake equals $(A'/A)(\delta'/\delta)$, where A'/A represents the ratio between the area of the slanted sediment surface and the area of the horizontal plane and (δ'/δ) is the ratio between the actual DBL thickness perpendicular to the slanted sediment surface and the measured DBL thickness (*for details see* Jørgensen and Des Marais 1990; Røy et al. 2002). Accounting for the average DBL thickness measured in situ (451 μm), the ratio between the 3D and 1D diffusive O_2 uptake varied between 1.0 and 1.9 for the two selected horizontal transects (Fig. 10E,F). The average difference between 3D and 1D DOU based on all the performed scans was a factor of 1.12 ± 0.01.

Discussion

In situ versus laboratory-determined O_2 uptake—Microprofile measurements performed at water depths >1,000 m have demonstrated that core recovery affects the interstitial O_2 distribution (Glud et al. 1994*a*, 1999; Sauter et al. 2001). Temperature- and pressure-induced artifacts lead to elevated DOU and underestimated O_2 penetration depths. For coastal environments with low O_2 penetration depth, transient temperature-induced disturbances are quickly reequilibrated when in situ conditions are reestablished in the laboratory, and in situ– and laboratory-obtained microprofiles generally show good agreement (Glud et al. 1998, 1999). There are, however, few comparative studies of in situ–determined microprofiles from coastal environments. In the present study, laboratory-determined DOU underestimated the in situ rates, whereas the O_2 penetration depth was generally overestimated (Fig. 11). The effect was most pronounced in highly active sediment with shallow O_2 penetration depths, where the interfacial O_2 dynamics were most sensitive to changes in the environmental controls (Fig. 11). Even though cores were taken to reestablish in situ conditions, in the laboratory, small differences in temperature or O_2 concentration cannot be excluded, and irreversible disturbances during core recovery could have affected the laboratory measurements.

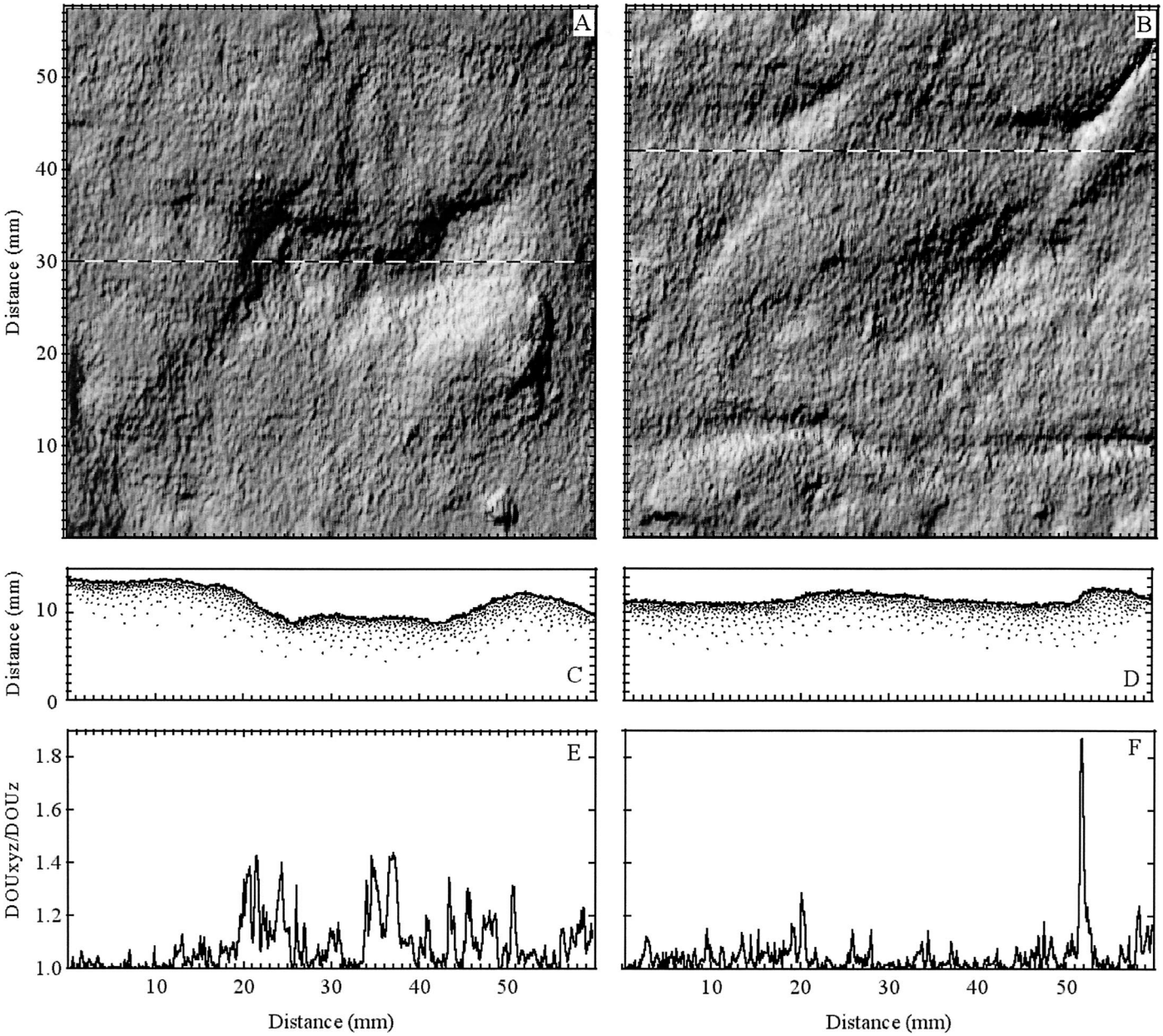

Fig. 10. (A, B) Examples of 30-cm^2 sediment topography presented as shaded reliefs. (C, D) Extracted topographic profiles. The lines in panels A and B represent the positions of the extracted profiles presented in panels C and D. (E, F) The relationship between the diffusive flux along the vertical axis as measured with microelectrodes and the true 3D diffusive flux, taking into account all spatial dimensions. The ratio has been calculated along the transects shown in panels A and C and in panels B and D.

Differences in DBL thickness can probably be neglected (*see below*). We have no general explanation for the observed difference. However, our data underline the importance of performing benthic exchange measurements under in situ conditions or, preferentially, in situ.

In situ and laboratory TOU measured in parallel clearly differed. On average, in situ rates were 2.0 ± 0.6 (n = 9) times higher than laboratory-determined rates. The discrepancy was due to an exclusion of larger faunal specimens in the relatively small sediment cores used for the laboratory incubations. By selecting undisturbed sediment cores, larger infauna tends to be excluded because animals and their burrows have been disturbed, destroyed, or blocked during core insertion. Furthermore, successfully recovered specimens might be inhibited in their pumping and respiration activity as a result of the mechanical disturbance associated with core recovery. In general, large sediment enclosures are to be preferred in order to obtain reliable total benthic exchange rates. The in situ–determined TOU represents only single deployments, and the statistical liability of the measurements cannot be directly assessed. However, in situ incubations performed on subsequent days resulted in similar TOU (and FOU) values (Fig. 9B), indicating that single deployments represent the fauna-related O_2 uptake well. A recent com-

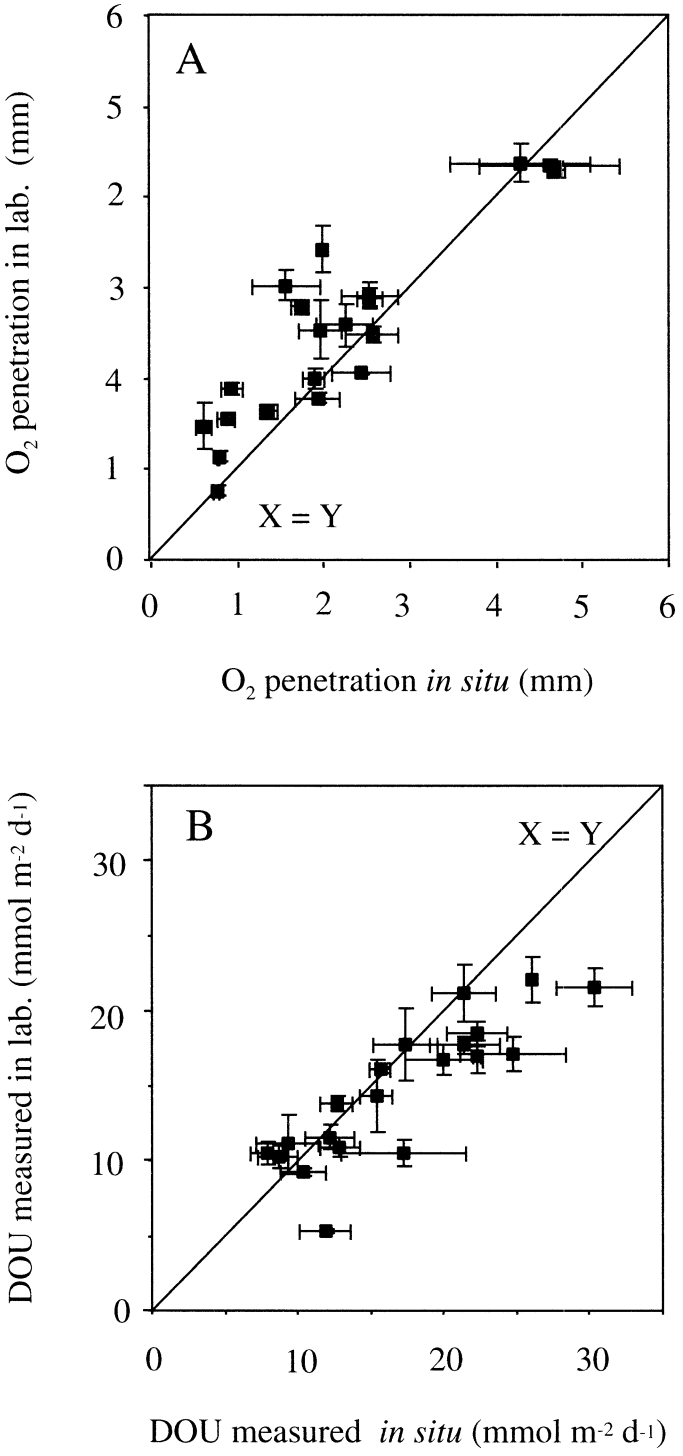

Fig. 11. (A) O_2 penetration depths measured in the laboratory compared to the corresponding values measured in situ. (B) DOU measured in the laboratory compared to the corresponding values measured in situ. The line $x = y$ is included in both panels.

puter study simulating multiple chamber insertions on a virtual seafloor inhabited by user-defined macrofaunal communities concluded that single deployments with the applied chamber would quantify the actual TOU of the macrofauna-inhabited sediment in Aarhus Bay during summer with a relative error of 9% (Glud and Blackburn 2002). This precision is in the same range as the standard deviations of our DOU measurements (Fig. 6). We therefore argue that the in situ TOU is the most correct measure of the actual benthic O_2 consumption rate in the present study.

Importance of the DBL for the DOU—The DBL thickness determined on the basis of in situ microprofiles varied between 299 and 706 μm, with an average value of 451 μm (n = 98). The corresponding range for the laboratory measurements was 313–590 μm, and the average was 457 μm (n = 138). The in situ DBL conditions were, thus, closely reproduced by the laboratory setup. The available data on in situ–determined DBL thicknesses are limited, but the present values are in the lower range of previously presented values derived from in situ microprofiles (Archer et al. 1989; Glud et al. 1994*a*, 1998; Jørgensen 2001; Wenzhöfer et al. 2001). Most of these values are, however, obtained at significantly deeper water depths, where a lower mean flow velocity can be expected. A microsensor-derived DBL thickness generally underestimated the actual DBL thickness, as microelectrodes have been shown to perturb the DBL, resulting in a 25–45% compression of the DBL thickness right below the sensor tip (Glud et al. 1994*b*). Therefore, the microprofile-derived DBL thickness should be regarded as a minimum value.

The mean diffusion time, t_{DBL}, for O_2 molecules to cross the DBL can be estimated as $t_{DBL} = \pi((\delta_{DBL})^2/4D_0)$, where δ_{DBL} is the DBL thickness and D_0 is the temperature-corrected molecular diffusion coefficient of O_2 (Sten-Knudsen 2002). Whether the transport time through the DBL limits the benthic O_2 consumption rate depends on the mean lifetime of an O_2 molecule within the sediment. During winter, the O_2 availability was high, the activity was low and, consequently, the oxic zone was relatively deep, as shown in Fig. 5D. The volume-specific O_2 consumption rate was depth independent, and only 16% of the decrease in benthic O_2 concentration occurred within the DBL. The amount of O_2 dissolved in the pore water could sustain the benthic O_2 consumption for 41 min, whereas the average transport time for an O_2 molecule across the 656-μm-thick DBL was 4.7 min. The O_2 flux was therefore mainly regulated by the consumption within the sediment, and changes in the DBL thickness would only affect the DOU marginally.

During early October, 45% of the O_2 decline occurred in the DBL (Fig. 5B); the entire interstitial O_2 pool would only sustain the O_2 consumption for 1.6 min; and the DBL passage for an O_2 molecule took, on average, 2.1 min. A reduction in the DBL thickness could therefore potentially have stimulated the O_2 uptake during this period. However, the volume-specific O_2 consumption was not depth independent (Fig. 5B), and a significant fraction of the O_2 consumption was probably related to the oxidation of solutes from anaerobic degradation (e.g., NH_4^+, Fe^{2+}), as indicated by the high activity at the oxic–anoxic interface. In this case, a more detailed modeling of the mobility of reduced constituents is required to quantitatively evaluate the importance of DBL impedance for DOU or for the O_2 penetration depth (Jørgensen and Boudreau 2001).

Microtopography and diffusive flux—Based on the microtopographic mapping, the difference between a 3D and a 1D DOU calculation was a factor of 1.12 ± 0.01. In other words, 10.7 ± 1.0% of the total diffusive flux was not accounted for by the simple 1D microprofile approach. The annual TOU measured in the laboratory was 22% higher than the corresponding DOU (Table 1). About half of this difference can now be ascribed to the simplified approach of performing a 1D calculation on a truly 3D interface.

A topographically structured oxic zone blankets the anoxic sediment, and vertical oxygen profiles penetrate this oxic skin at an angle and thereby overestimate the O_2 penetration depth. The average factor by which the actual O_2 penetration depth is overestimated by a vertical measurement can be calculated by simple trigonometry to be 1/cos(19.37) or 1.06 (Jørgensen and Des Marais 1992; Røy et al. 2002). The 6% overestimation by the vertical approach cannot fully explain the observed difference between the DOU and the depth-integrated O_2 consumption as derived from the interstitial microprofiles (Table 1). We used the average porosity of the upper 4 mm to access the tortuosity-corrected diffusive coefficient of interstitium (*see Materials and methods*). In reality, the porosity can be expected to decrease with sediment depth, and our simplification could have biased the calculated depth distribution of the volume-specific O_2 consumption rates. However, again, this cannot explain the observed discrepancy between the two independent measures of the diffusive mediated O_2 uptake. A number of studies have documented that interstitial meiofaunal activity can lead to enhanced dispersal and solute transport (Aller and Aller 1992; Glud and Fenchel 1999; Rysgaard et al. 2000). Such activity can increase the solute transport coefficients within the sediment, and for the given study, a 30% higher effective diffusion coefficient of the interstitium would lead to identical DOU and modeled depth-integrated O_2 consumption rates. We propose that this is the main cause for the observed difference between the two microprofile-based approaches for determination of the O_2 uptake.

Importance for fauna of the benthic O_2 uptake—The difference between TOU and DOU quantified in sediment cores during the present study ranged between 0.8 and 8.7 mmol m^{-2} d^{-1}, with an average value of 4.0 ± 3.1 mmol m^{-2} d^{-1}. Accounting for the topographic effect on the DOU, this only leaves an annual FOU of 0.79 mol m^{-2} yr^{-1} in the recovered sediment cores. The corresponding in situ value for FOU was, however, five times higher at 3.94 mol m^{-2} yr^{-1}, or ~40% of the measured TOU (Fig. 12). Recovered undisturbed sediment cores selected for laboratory incubation clearly undersampled the in situ density of macrofauna, especially for the larger specimens. The few cores that contained an active macrofauna specimen on a given day indeed revealed an elevated TOU. However, on a seasonal scale, there was no clear relationship between the biomass of the enclosed fauna during a given incubation and the measured TOU or calculated FOU (*see Web Appendix 1*, http://www.aslo.org/lo/pdf/vol_48/issue_3/1265al.pdf). The reason is presumably that faunal biomass poorly reflects the fauna-mediated O_2 uptake of a diverse benthic community undergoing seasonal changes in temperature and bottom water O_2 concentration. To what extent a given biomass stimulates the benthic O_2 consumption rate naturally depends on functional characteristics of the fauna (deposit feeding, filter feeding, irrigation patterns, etc.), but to what extent a given activity affects the benthic O_2 uptake also depends on the redox state of the sediment, the O_2 penetration depth, the O_2 concentration of the bottom water, and the temperature. The in situ TOU (or the FOU) quantified during a seasonal study does therefore not necessarily correlate well to enclosed biomass.

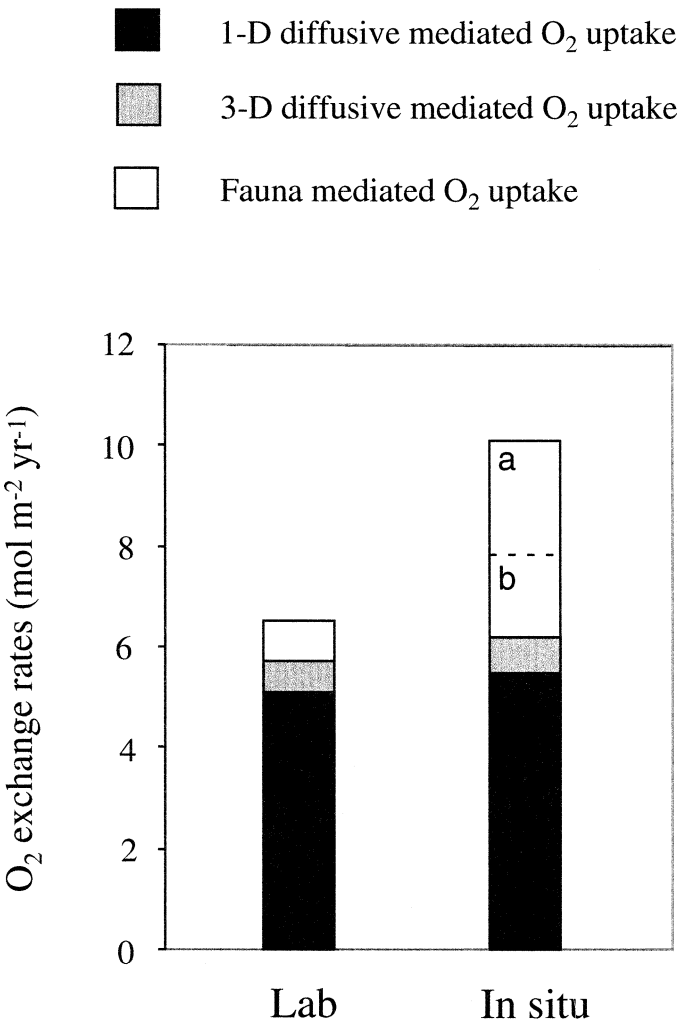

Fig. 12. The various components of the TOU measured in the laboratory and in situ. The broken line divides the in situ FOU into (a) the enhanced benthic O_2 consumption caused by animal activity (e.g., irrigation) and (b) the calculated maximum macrofaunal respiration.

The sediment recovered from the 15 in situ incubations with the chamber lander contained ~25 species of macrofauna, with an average density of 2,800 ± 700 m^{-2} and a dry weight of 89.5 ± 30.0 g m^{-2} (including shell weight). Both in abundance and biomass, small specimens of bivalves (*Abra alba*, *Mysella bidendata*, *Corbula gibba*, and *Macoma calcarea*) were dominant, while polychaetes (e.g., *Terrebellides stroemi*, *Nephtys* sp., and *Pectinaria* sp.) and echinoderms (e.g., *Ophiura albida* and *Echinocardium cordatum*) were encountered less frequently. These observations were

supported by survey data obtained by the local county that quantifies the abundance and biomass of each taxonomic group at the investigated site on a monthly basis (Technical Report 1998, County of Aarhus, www.aaa.dk). Using their values for the nine dominant species (accounting for ~80% of the total abundance) at the investigated site during 1996 and the empirical relationship between biomass and metabolic rate for marine invertebrates as established by Gerlach et al. (1985), the annual O_2 consumption of the benthic fauna was calculated to be ~1.64 mol m^{-2}. This estimate must be taken as a maximum since the applied relationship is based on a temperature of 20°C. There is no simple way to recalculate to the correct in situ temperature (Banse 1982; Gerlach et al. 1985). The calculated faunal respiration thus accounts for a maximum of ~40% of the annual FOU. The remainder is ascribed to stimulated microbial activity, especially along burrows and funnels of irrigating specimens. These calculations document that the fauna is indeed important for the benthic O_2 uptake in the studied sediment, but that the faunal respiration itself is the minor part of the total fauna-related O_2 consumption (Fig. 12). In environments rich in benthic fauna, in situ incubations by relatively large chambers are thus required in order to obtain realistic estimates of the benthic O_2 consumption rate.

Importance of benthic aerobic mineralization in Aarhus Bay—The annual net photosynthesis during 1991 in Aarhus Bay amounted to 21.8 mol C m^{-2} yr^{-1}, while the measured planktonic respiration was 14.8 mol C m^{-2} yr^{-1} (Jørgensen 1996). This leaves 7.0 mol C m^{-2} yr^{-1} for the entire benthic community, not accounting for lateral import or export. Sediment trap measurements performed during the same period concluded that the annual net deposition at the seafloor was somewhat higher, 9.9 mol C m^{-2} yr^{-1} (Valeur et al. 1995), whereas determination of the sediment accumulation rate showed that 2.1 mol C m^{-2} yr^{-1} was buried below the bioturbated horizon (Jørgensen 1996). The difference, 7.8 mol C m^{-2} yr^{-1}, should thus be available for the benthic community.

As argued above, the in situ TOU represents our best estimate of the integrated benthic activity, and by assuming a respiratory quotient (RQ) of 1.00, the annual benthic mineralization rate during 1992 was 10.1 mol C m^{-2} yr^{-1}. This is close to the net deposition rate and corresponds to ~46% of the net primary production in the area. Taken together with the distinct temporal pattern in sedimentation and DOU, this strongly indicates a tight pelagic–benthic coupling at the investigated site.

The anaerobic degradation in the sediment of Aarhus Bay is dominated by sulfate reduction. Accounting for the upper 16 cm of the sediment, the sulfate reduction during 1990–1991 was responsible for a carbon mineralization of 4.5 mol C yr^{-1}, whereas iron reduction accounted for 1.3 mol C yr^{-1} (Thamdrup et al. 1994). Manganese reduction was without quantitative importance (Thamdrup 2000), and denitrification amounted to 0.15 mol C yr^{-1} (Jørgensen 1996). Assuming a complete aerobic oxidation of the reduced sulfur and iron on an annual scale, the O_2 consumption required for H_2S and Fe(II) oxidation was equivalent to 5.8 mol yr^{-1}, or 57% of the total O_2 uptake. The aerobic degradation of organic carbon accounted for 4.2 mol C m^{-2} yr^{-1} (10.1 − [4.5 + 1.3 + 0.15]), or 42% of the total benthic mineralization. This is relatively high compared to previously presented studies on shelf and costal sediments, where the aerobic mineralization generally is estimated to be in the range of 5–25% of the total benthic mineralization (Thamdrup 2000). However, as shown in the present study, the FOU can be significant, and in many instances it might be poorly represented by traditional incubation techniques. Consequently, the relative contribution of the aerobic mineralization could be correspondingly underestimated.

References

ALLER, R. C. 1998. Benthic fauna and biogeochemical processes in marine sediments: The role of burrow structures, p. 301–338. *In* T. H. Blackburn and J. Sørensen [eds.], Nitrogen cycling in coastal waters. Wiley.

———, AND J. Y. ALLER. 1992. Meiofauna and solute transport in marine muds. Limnol. Oceanogr. **37:** 1018–1033.

ARCHER, D., AND A. DEVOL. 1992. Benthic oxygen fluxes on the Washington shelf and slope: A comparison of in situ microelectrode and chamber flux measurements. Limnol. Oceanogr. **37:** 614–629.

———, S. EMERSON, AND C. R. SMITH. 1989. Direct measurements of the diffusive sublayer at the deep seafloor using microelectrodes. Nature **340:** 623–626.

BANSE, K. 1982. Mass-scaled rates of respiration and intrinsic growth in very small invertebrates. Mar. Ecol. Prog. Ser. **9:** 281–297.

BERG, P., N. RISGAARD-PETERSEN, AND S. RYSGAARD. 1998. Interpretations of measured concentrations profiles in sediment porewater. Limnol. Oceanogr. **81:** 289–303.

BOUDREAU, B. P. AND N. L. GUINASSO, JR. 1982. The influence of a diffusive sublayer on accretion, dissolution, and diagenesis at the seafloor, p. 115–145. *In* K. A. Fanning and F. T. Manheim [eds.], The dynamic environment of the ocean seafloor. Lexington Books.

BROECKER, W. S., AND T. H. PENG. 1974. Gas exchange rates between air and sea. Tellus **26:** 21–35.

CRANK, J. 1983. The mathematics of diffusion. Clarendon Press.

FENCHEL, T. 1996. Worm burrows and oxic microniches in marine sediments. I. Spatial and temporal scales. Mar. Biol. **127:** 289–295.

GERLACH, S. A., A. HAHN, AND M. SCHRAGE. 1985. Size spectra of benthic biomass and metabolism. Mar. Ecol. Prog. Ser. **26:** 161–173.

GLUD, R. N., AND N. BLACKBURN. 2002. The effects of chamber size on in situ benthic oxygen uptake measurements: A simulation study. Ophelia **56:** 23–31.

———, AND T. FENCHEL. 1999. The importance of ciliates for interstitial solute transport in benthic communities. Mar. Ecol. Prog. Ser. **186:** 87–93.

———, J. K. GUNDERSEN, B. B. JØRGENSEN, N. P. REVSBECH, AND H. D. SCHULZ. 1994*a*. Diffusive and total oxygen uptake of deep-sea sediments in the eastern South Atlantic Ocean: In situ and laboratory measurements. Deep-Sea Res. **41:** 1767–1788.

———, ———, N. P. REVSBECH, AND B. B. JØRGENSEN. 1994*b*. Effects on the diffusive boundary layer imposed by microelectrodes. Limnol. Oceanogr. **39:** 462–467.

———, ———, ———, ———, AND M. HUETTEL. 1995. Calibration and performance of the stirred flux chamber from the benthic lander, Elinor. Deep-Sea Res. **42:** 1029–1042.

———, O. HOLBY, F. HOFFMAN, AND D. E. CANFIELD. 1998. Ben-

thic mineralization and exchange in Arctic sediments (Svalbard, Norway). Mar. Ecol. Prog. Ser. **173:** 237–251.

———, J. K. GUNDERSEN, AND O. HOLBY. 1999. Benthic in situ respiration in the upwelling area off central Chile. Mar. Ecol. Prog. Ser. **186:** 9–18.

———, ———, AND N. B. RAMSING. 2000. Electrochemical and optical oxygen microsensors for in situ measurements, p. 19–72. *In* J. Buffle and G. Horvai [eds.], In situ monitoring of aquatic systems: Chemical analysis and speciation. Wiley.

GUNDERSEN, J. K., AND B. B. JØRGENSEN. 1990. Microstructure of diffusive boundary layers and the oxygen uptake of the sea floor. Nature **345:** 604–607.

———, R. N. GLUD, AND B. B. JØGENSEN. 1995. Havbundens iltomsætning. Havforskning fra Miljøstyrelsen 57.

IVERSEN, N., AND B. B. JØRGENSEN. 1993. Diffusion coefficients of sulfate and methane in marine sediments: Influence of porosity. Geochim. Cosmochim. Acta **57:** 571–578.

JØRGENSEN, B. B. 1996. Case study—Aarhus Bay, p. 137–154. *In* B. B. Jørgensen and K. Richardson [eds.], Eutrophication in coastal marine ecosystems. American Geophysical Union.

———. 2001. Life in the diffusive boundary layer, p. 348–373. *In* B. P. Bodreau and B. B. Jørgensen [eds.]. The benthic boundary layer. Oxford Univ. Press.

———, AND B. P. BOUDREAU. 2001. Diagenesis and sediment–water exchange, p. 211–238. *In* B. P. Boudreau and B. B. Jørgensen [eds.]. The benthic boundary layer. Oxford Univ. Press.

———, AND D. J. DES MARAIS. 1990. The diffusive boundary layer of sediments: Oxygen microgradients over a microbial mat. Limnol. Oceanogr. **35:** 1343–1355.

———, AND N. P. REVSBECH. 1985. Diffusive boundary layers and the oxygen uptake of sediments and detritus. Limnol. Oceanogr. **30:** 111–122.

KANNEWORFF, E., AND W. NICOLAISEN. 1973. The Haps, a frame supported bottom corer. Ophelia **10:** 109–116.

KRISTENSEN, E. 1988. Benthic fauna and biogeochemical processes in marine sediments: Microbial activity and fluxes, p. 275–299. *In* T. H. Blackburn and J. Sørensen [eds.], Nitrogen cycling in coastal waters. Wiley.

LI, Y. H., AND S. GREGORY. 1974. Diffusion of ions in sea-water and in deep-sea sediments. Geochim. Cosmochim. Acta **38:** 703–714.

NIELSEN, L. P., P. C. CHRISTENSEN, N. P. REVSBECH, AND J. SØRENSEN. 1990. Denitrification and oxygen respiration in biofilms studied with a microsensor for nitrous oxide and oxygen. Microb. Ecol. **19:** 63–72.

PEJRUP, M., J. VALEUR, AND A. JENSEN. 1996. Vertical fluxes of particulate matter in Aarhus Bight, Denmark. Cont. Shelf Res. **16:** 1047–1064.

RASMUSSEN, H., AND B. B. JØRGENSEN. 1992. Microelectrode studies of seasonal oxygen uptake in a coastal sediment: Role of molecular diffusion. Mar. Ecol. Prog. Ser. **81:** 289–303.

REVSBECH, N. P. 1989. An oxygen microelectrode with a guard cathode. Limnol. Oceanogr. **34:** 474–478.

———, AND B. B. JØRGENSEN. 1986. Microelectrodes and their use in microbial ecology, p. 293–352. *In* K. C. Marshall [ed.], Advances in Microbial Ecology. Plenum Publ. Corp.

———, J. SØRENSEN, T. H. BLACKBURN, AND J. P. LOMHOLT. 1980. Distribution of oxygen in marine sediments measured with a microelectrode. Limnol. Ocenogr. **25:** 403–411.

RØY, H., M. HUETTEL, AND B. B. JØRGENSEN. 2002. The role of small-scale sediment topography for oxygen flux across the diffusive boundary layer. Limnol. Oceanogr. **47:** 837–847.

RYSGAARD, S. P., P. B. CHRISTENSEN, M. V. SØRENSEN. P. FUNCH, AND P. BERG. 2000. Marine meiofauna and nitrogen mineralization in sandy and soft sediments of Disko Bay, West Greenland. Aquat. Microb. Ecol. **21:** 59–71.

SAUTER, E. J., M. SCHLÜTER, AND E. SUESS. 2001. Organic carbon flux and remineralization in surface sediments from the northern North Atlantic derived from porewater oxygen microprofiles. Deep-Sea Res. **48:** 529–553.

STEN-KNUDSEN, O. 2002. Biological membranes: Theory of transport, potentials and electrical impulses. Cambridge Univ. Press.

THAMDRUP, B. 2000. Microbial manganese and iron reduction in aquatic sediments. Adv. Microb. Ecol. **16:** 41–84.

———, AND D. E. CANFIELD. 2000. Benthic respiration in aquatic sediments, p. 86–103. *In* O. E. R. Sala, R. B. Jackson, H. A. Mooney, and R. W. Horwarth [eds.], Methods in ecosystem science. Springer.

———, H. FOSSING, AND B. B. JØRGENSEN. 1994. Manganese, iron, and sulphur cycling in a coastal marine sediment, Aarhus Bay, Denmark. Geochim. Cosmochim. Acta **58:** 5115–5129.

VALEUR, J. R., A. JENSEN, AND M. PEJRUP. 1995. Turbidity, particle fluxes and mineralization of carbon and nitrogen in a shallow coastal area. Mar. Freshw. Res. **16:** 409–418.

WENZHÖFER, F., M. ADLER, O. KOHLS, C. HANSEN, B. STROTMANN, S. BOEHME, AND H. D. SCHULZ. 2001. Calcite dissolution driven by benthic mineralization in the deep-sea: In situ measurements of Ca^{2+}, pH, pCO_2. Geochim. Cosmochim. Acta **65:** 2677–2690.

Received: 23 October 2002
Accepted: 15 January 2003
Amended: 5 February 2003