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In situ benthic oxygen fluxes in a nearshore coastal marine system: a new approach to quantify the effect of wave action

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ABSTRACT: A simple benthic chamber, with a flexible membrane to allow for wave-induced interstitial water flow, is described. The membrane has a low permeability to oxygen, compared to other materials previously employed in chamber studies. Polyethylene and latex rubber (condoms) are highly permeable to oxygen and clearly unsuitable for oxygen-related studies. Glass syringes tested for oxygen permeability were far superior to plastic syringes, the latter being completely inappropriate even in short-term studies. A study at Kings Beach, South Africa, using chambers with flexible membranes showed that oxygen consumption was significantly higher in chambers with flexible tops ($p < 0.005$) than in chambers with solid tops. The difference in the respective fluxes [18.5 ± 2.7 (95 % CI) compared to 10.7 ± 4.6 ml O_2 m^{-2} h^{-1}] was positively correlated with the effect of wave action at this medium energy exposed beach. Use of chambers with solid tops could result in underestimates in oxygen consumption of >50% at the study site. It is concluded that wave action, with its resultant interstitial water flow, can significantly affect the oxygen consumption of shallow water sediments.

INTRODUCTION

Measurement of exchanges of dissolved compounds between sediments and overlying waters in high or medium energy environments is not a simple procedure. The passage of surface waves causes a fluctuation of bottom hydrostatic pressures in shallow seas (Putnam & Johson 1949, Carstens 1968, Steele et al. 1970), which induces water movement in permeable deposits (Putnam 1949, Webb & Theodor 1968, 1972, Steele et al. 1970, Liu 1973, Swart & Crowley 1983). The biological and chemical importance of this 'subtidal pump' has been described by several authors (Riedl et al. 1972, Rutgers van der Loeff 1981, McLachlan 1983). Further, turbulence induced by stirring in overlying water increases oxygen consumption of sediments (Carey 1967, Martin & Bella 1971, James 1974, Davies 1975, Snodgrass & Fay 1987).

Interference with the hydrodynamic environment is one of the main disadvantages of using in situ chambers to measure metabolism of, or flux of dissolved gases and nutrients across, the benthic boundary layer (Hale 1975, Hargrave & Connolly 1978, Rutgers van der Loeff et al. 1981, Lindeboom et al. 1984). Clearly benthic oxygen consumption measurements should be made under conditions that mimic the natural water flow (Hale 1975, Gust 1977, Boynton et al. 1981). Despite the importance of water movement, the effects of wave action on benthic oxygen exchange have not been quantified in chamber studies of benthic metabolism.

The aim of this paper is 2-fold. Firstly, to introduce a simple chamber that does not impair wave-induced water flow through the sea bed in shallow high energy systems. Secondly, to present preliminary data testing the hypothesis that this interstitial water flow alters the oxygen flux in this nearshore coastal marine system. A detailed investigation comparing oxygen consumption and production measured in situ using chambers with that of cores and theoretical fluxes is nearing completion, but is not reported on here.

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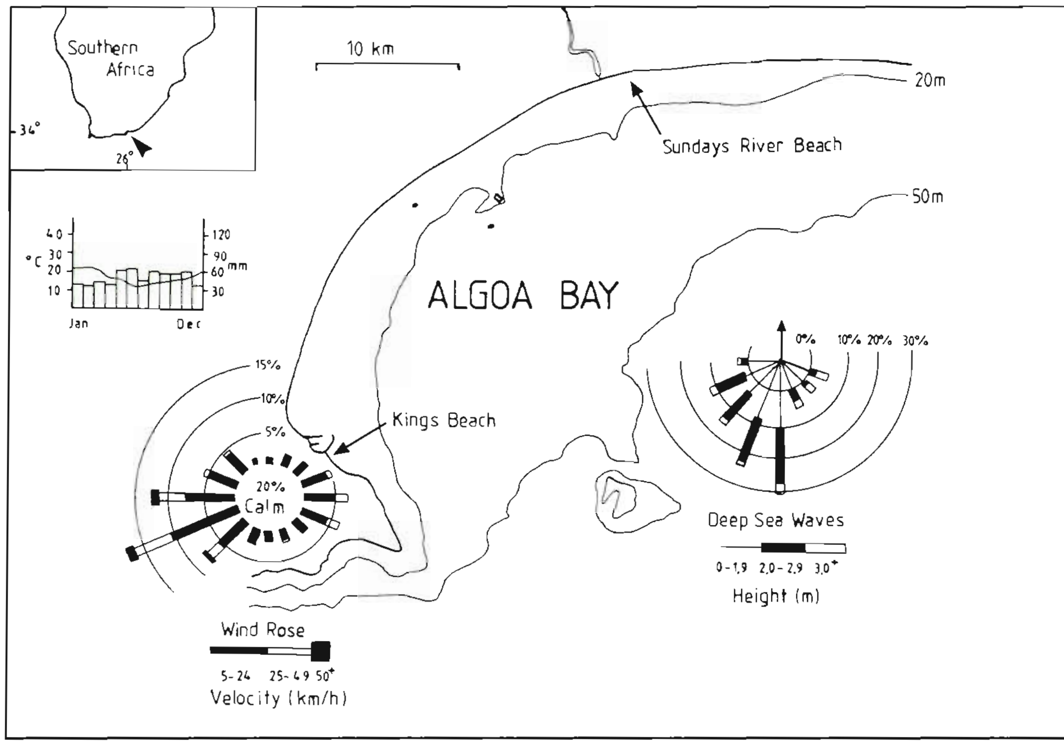

Fig. 1. Location of study site, showing wave and wind roses, temperature and rainfall near Kings Beach, South Africa (adapted from Beckley 1988)

MATERIALS AND METHODS

Study area. All sampling was conducted at Kings Beach (33° 58′ 25″ S; 25° 38′ 50″ E) in the corner of Algoa Bay, South Africa (Fig. 1). Kings Beach is the least exposed sandy beach near Port Elizabeth, but it nevertheless experiences continual wave action and may be considered medium energy by global standards. It is an exposed beach with a rating of 12.5 according to a 20-point exposure rating system suggested for sandy beaches (McLachlan 1980). Depending on weather conditions the surf zone extends out 50 to 100 m, with an average breaker height of ca 1 m. Mean spring tide range equals 1.65 m (McLachlan et al. 1984). Seasonal variations in sea water temperature can be considered mild, ranging maximally from 12 to 24 °C (Beckley 1988).

Kings Beach has fine (average Mz = 220 µm) well-sorted sand with a high $CaCO_3$ content (average 60 %) (Table 1). Organic matter and subsieves (the fraction passing through a 63 µm sieve) average 2.2 % and 2.7 % respectively. The pH and oxygen saturation decrease with depth into the sediment, but no anoxic conditions are encountered to a depth of 60 cm (the greatest depth sampled) (Malan & McLachlan 1985). These authors further showed that meiofaunal dry biomass averages 1119 mg m^{-2} with nematodes dominating and harpacticoid copepod numbers being low. Bacterial biomass averages 6197 mg m^{-2} and increases in an offshore direction. More information on this beach may be found in McLachlan et al. (1984) and Malan & McLachlan (1985).

Oxygen permeability of plastic and glass syringes. Oxygen permeability was determined for 20 ml plastic and glass syringes. Pure nitrogen was bubbled through filtered sea water (0.2 µm Nucleopore) to lower the oxygen content (Malan 1986) to ca 25 mm Hg. Triplicate sets of syringes were incubated in air-equilibrated sea water (20 °C, 35 ‰) and oxygen content monitored over a 36 h period.

In a separate experiment triplicate glass syringes were filled with 0.2 µm filtered sea water, unfiltered sea water and unfiltered sea water of low oxygen content (ca 25 mm Hg). The syringes were incubated under similar conditions to the above. Oxygen readings were periodically recorded on a Radiometer acid-base analyzer over 6 h.

Oxygen permeability of volume compensation bags. Most authors use chambers of solid construction for measurement of benthic metabolism. It is therefore necessary to allow for some form of volume compensation to prevent interstitial water from flowing into the

Table 1. Average sediment parameters for Kings Beach, all values on a dry mass basis (from Malan & McLachlan 1985)

Station depth (m)	Median (µm)	Graphic mean (Mz) (µm)	Inclusive graphic standard deviation	Inclusive graphic skewness	Percentage subsieves	Percentage $CaCO_3$	Percentage organics	Porosity (%)	Permeability (min.)	Remarks
1	239 ± 13	238 ± 15	0.48 ± 0.09	0.00 ± 0.07	3.0 ± 0.8	57 ± 13	1.9 ± 0.6	29.3 ± 5.6	7.1 ± 0.6	Fine sand, well-sorted, near-symmetrical
4	195 ± 7	202 ± 8	0.47 ± 0.05	−0.15 ± 0.09	2.5 ± 1.0	59 ± 3	2.3 ± 0.1	32.1 ± 2.0	8.3 ± 1.2	Fine sand, well-sorted, coarse-skewed
8	214 ± 22	217 ± 16	0.49 ± 0.04	−0.10 ± 0.15	2.4 ± 0.7	63 ± 4	2.6 ± 0.4	33.9 ± 2.9	8.1 ± 0.9	Fine sand, well-sorted, near-symmetrical
Average	217 ± 24	220 ± 20	0.48 ± 0.06	−0.10 ± 0.13	2.7 ± 0.8	60 ± 8	2.3 ± 0.5	31.7 ± 4.2	7.8 ± 1.0	Fine sand, well-sorted, near-symmetrical

chamber during sample removal. Although most authors do not compensate for the volume of sample removed (Table 2), some authors have allowed water to enter from outside (Hallberg et al. 1972, Schippel et al. 1973, Propp et al. 1980, Hopkinson & Wetzel 1982, Pregnall & Miller 1988, Alongi et al. 1989, Jahnke & Christiansen 1989), while others have employed collapsible bags (Hartwig 1976, Dyrssen et al. 1984, Anderson et al. 1986, Dyrssen 1986) or a small 'expansion chamber' (Kelly 1984, Oviatt et al. 1984).

Condoms, polyethylene bags (Hartwig 1976, Klump and Martens 1981, Anderson et al. 1986) and a nylon/polyethylene co-extrusion bag (see below) were evaluated as possible means of volume compensation. A number of bags were completely filled with 150 ml low oxygen content sea water, incubated in air-equilibrated sea water and oxygen content monitored.

Testing of flexible membranes. To allow for wave-induced pumping of water through the sediment a flexible membrane top chamber was designed. As this membrane had to be practically impermeable to oxygen, a co-extrusion consisting of a 45 µm polyethylene layer, a 15 µm bonding agent and a 25 µm nylon layer used for vacuum-packing in the meat industry was evaluated. The membrane was fixed on either side of a 30 cm long Perspex cylinder. The cylinder was completely filled with low oxygen content sea water and incubated in air-equilibrated sea water at 20 °C and the oxygen content monitored. A 75 µm polyethylene membrane was used in the tests for comparative reasons, as this material has been used in chamber studies by other authors (Hartwig 1976, Klump & Martens 1981, Anderson et al. 1986).

Chamber construction and general procedures. Four slightly different types of chambers were constructed. Firstly, chambers were constructed of transparent Perspex cylinders (28.8 cm inside diameter and 6.1 mm wall-thickness) with a transparent 10 mm thick rigid Perspex top. Secondly, a transparent co-extruded membrane was fixed to similar cylinders to provide a flexible top. Thirdly, chambers were constructed of opaque 30 cm inside diameter PVC pipe with a 10 mm rigid Perspex top and lastly a similar PVC chamber was constructed with a co-extruded membrane top. In the latter 2 chambers black plastic linings eliminated light penetration. A diagram of a generalized chamber is presented in Fig. 2.

A 2.2 cm aperture on the side of each chamber enabled the water to escape from the chamber during careful placement by divers using SCUBA, minimizing bow-wave effects. After an equilibrium period of 20 min the aperture was sealed off with a rubber stopper. Samples were removed through a luer-lock plastic tap on the side of the chamber. A partial collapse of the chambers with membranes did compensate for the

Table 2. A comparison of chambers used for in situ flux studies

No.	Volume[a] (l)	Area (cm²)	Flange depth	Transparency	Mixing	Shape	Material	Measurements	Volume compensation	Equilibrium time (min)
1	60.0	1963	5	Opaque	Stir (60 rpm)	Cylinder	Plexiglass	–[b]	Polyethylene bag	–
2	4.7/18.0	600–700	13–30	Opaque/trans	–	–	–	Beginning/end	–	–
3	2094.0	31400	20	Transparent	Stir	Hemisphere	Plexiglass	Continuous	–	–
4	4.2	209	3	Opaque	–	Cylinder	Acrylic	Beginning/end	–	60
5	38.0	3000	–	Opaque	Pump (10 cm s^{-1})	Cylinder	Plexiglass	Periodic	–	15
6	32.0	1600	10	–	Stir (5–10 cm s^{-1})	Square	Plexiglass	Periodic	None	15
7	10.0	774	–	–	–	Cylinder	Stainless Steel	–	–	–
8	11.0	–	–	Transparent	Stir (2–20 cm s^{-1})	Annular	Plastic	Periodic/continuous	None	–
9	2.5–5.0	412	–	Opaque	Stir (30–45 rpm)	Box	Stainless Steel	Periodic	Admitted outside water	30–90
10	12.7	707	4	–	Stir	Cylinder	Plexiglass	Continuous	–	–
11	62.0	3100	–	Transparent	Pump (1–3 cm s^{-1})	Cylinder	Plexiglass	Periodic/contiunous	Open tube to outside	–
12	18.0	700	–	Opaque	Pump (300 ml min^{-1})	–	Fibre-glass	Periodic	–	–
13	27.0	2400	4	Opaque	Stir at sampling	Half cylinder	PVC	Beginning/end	None	–
14	24.4	1875	–	Transparent	Pump	Tunnel (1.3 m)	Plexiglass	Continuous (pump)	Flushing	–
15	7.9	707	6	Opaque	Stir (25–30 rpm)	Cylinder	Aluminium	Periodic	None	60–120
16	17.6	1452	6	Opaque	Stir (30 rpm)	Cylinder	Aluminium	Periodic	None	60–120
17	9.0	900	5	–	None	Square	Plastic	–	Collapsible bag/plungers	–
18	6.1	700	–	Transparent	Stir	–	Acrylic	Continuous	None	–
19	3.5	443	4	Opaque	Stir	Cylinder	Aluminium (coated)	End	–	8 h
20	32.0	2000	6	Opaque	Stir	Hemisphere	Acrylic	Periodic/continuous	Admitted outside water	–
21	47.5	2500	6	Opaque	Stir	Hemisphere	Acrylic	Periodic	Admitted outside water	15–30
22	30.0 m	–	–	–	None	Tunnel	Plastic sheet	–	None	–
23	–	–	–	–	Pump (1–4 m s^{-1})	Pointed rectangle	Epoxy-coated metal	Periodic	None	15
24	50.0	5030	–	Opaque	Stir	Cylinder	PVC	–	–	–
25	8.0	280	–	Opaque	Stir	Cylinder	–	Periodic/continuous	Admitted outside water	–
26	29.4	3600	6	Opaque	Pump (0.25 l s^{-1})	Pyramid	Welded steel	Periodic	–	15
27	25.0	1960	–	–	Pump	Cylinder	Acrylic	–	Admitted outside water	–
28	35.0	3850	–	–	Pump	Cylinder	Acrylic	–	Admitted outside water	–
29	0.9–1.6	412	–	Opaque	–	Box	Stainless Steel	Periodic	Admitted outside water	10–20
30	52.5	1590	–	–	Stir	Cylinder	Plexiglass	Continuous	Opened at 2–4 h interval	–
31	9.6	284	–	–	Stir	Cylinder	Plexiglass	Continuous	Opened at 2–4 h interval	–
32	4.0	400	10	–	None	Tent	Plastic	Periodic	None	–
33	43.0	2376	–	Opaque/trans	Stir/no stir	Hemisphere	–	Beginning/end	Opened during sampling	–
34	0.8	60	–	Opaque/trans	Stir	–	Acrylic	Periodic	–	–
35	2–4	570	5/none	Side/t; lid/o	Stir	Cylinder	Plexiglass/PVC	Continuous	None	–
36	0.6	215	5	Opaque/trans	Stir	Bottles	Glass	Beginning/end	–	–
37	7.3	731	10	Opaque/trans	Stir at sampling	Cylinder	Perspex/PVC	Periodic	Admitted outside water	20–30
38	0.5	–	–	Transparent	Stir	Rectangle	Perspex	Continuous	Flushing	–
39	6.5	661	–	–	Pump	Dome	Plexiglass	Periodic	–	–
40	0.5	45	20	Opaque	–	Cylinder	PVC	Periodic	Admitted outside water	–
41	15.0	500	Few cm	Transparent	–	Bottle	Glass	Periodic (pump)	Replaced after sampling	–
42	2.0	500	–	Opaque/trans	–	Bottle	Glass	Periodic; begin/end	–	–
43	1.0	64	6	Opaque/trans	–	Cylinder	Plexiglass	Beginning/end?	–	–
44	7.5	730	–	–	Stir	–	–	Beginning/end	–	–
45	± 25.0	1600	± 24	Transparent	Stir	Cube	Plexiglass	Weekly	Replaced through valve	1 wk
46	11.0	731	–	Opaque	Stir	Cylinder	Plexiglass	Continuous	–	–
47	1.9	240	4	Opaque/trans	Stir	Rectangle	Plexiglass	Periodic	None	10
48	1.9–7.5	299	Seal edges	–	Stir at sampling	Cylinder	Plexiglass	–	None	–
49	98.2	1964	20	Opaque	–	Cylinder	Stainless steel	Periodic	Balloons	–
50	2.5	651	10	Trans/Opaque	Stir at sampling	Cylinder	Perspex	Periodic	Collapse of flexible top	15

[a] Volume to the nearest 0.1 l
[b] Not mentioned or none

volume of the sample removed (cf. Klump & Martens 1981) and prevented high nutrient interstitial water flowing into the chamber. In all cases the volume of sample removed (ca 10 ml) was <0.5 % of the total volume.

The chamber penetrated the sediment to 10 cm with ca 3.8 cm protruding above the surface. It had a volume of 2.5 l and enclosed an area of 651 cm². These values differed slightly for the dark chambers, but were taken into consideration during flux calculations.

Table 2 (continued)

No.	Exposure time (h)	H_2O column correction	Flux	Sampling area	Region	Source
1	60 d	–	O_2 + nutrients	Fjord	Gullmarsfjorden, Western Sweden	Anderson et al. (1986)[c]
2	2–6	Yes	Nutrients	Nearshore	Königshafen, Wadden Sea, North Sea	Asmus (1982, 1986)
3	63 d	–	O_2 + nutrients	Bight	Kiel Bight, Western Baltic	Balzer et al. (1983), Balzer (1984)
4	24	–	O_2	Nearshore	Santa Barbara, California, USA	Bauer et al. (1988)
5	1–3	Yes	O_2 + nutrients	Estuary	Patuxent estuary, Chesapeake Bay, USA	Boynton et al. (1980)[d]
6	3	Yes	Nutrients	Estuary	Potomac river estuary, Chesapeake Bay, USA	Callender (1982)[e]
7	–	–	O_2	–	North Sea + laboratory	Cramer (1989)
8	24	–	O_2 + nutrients	Open sea loch	Loch Thurnaig, Scotland	Davies (1975)
9	16–24	–	Nutrients	Offshore	Skan Bay, Alaska and Mexico cont. shelf	Devol (1987)
10	–	–	O_2	Baltic, lakes, rivers	Baltic and lakes	Edberg & Hofsten (1973)
11	2–4	–	O_2 + nutrients	Estuaries	North Carolina, USA	Fisher et al. (1982)
12	≥ 3	–	O_2 + NH_3	Offshore	Northwestern Gulf of Mexico	Flint & Kamykowski (1984)
13	2–4	Yes	O_2 + nutrients	Estuary	Narragansett Bay, Rhode Island, USA	Hale (1975)[f]
14	1–10 d	Yes	O_2 + P	Tidal pond	Long Island, New York, USA	Hall et al. (1979)
15	24	Yes	O_2 + CO_2 + P	–	–	Hargrave & Connolly (1978)[g]
16	24	Yes	O_2 + CO_2	Estuary	Eastern passage, Halifax Harb., NS, Canada	Hargrave & Phillips (1981)
17	≤ 6	Yes	Nutrients	Nearshore	La Jolla Bight, USA	Hartwig (1976)
18	24	Yes	O_2	Nearshore	Gulf of Trieste, Northern Adriatic Sea	Herndl et al. (1989)
19	–	–	O_2 + nutrients	Offshore	North Atlantic deep-sea	Hinga et al. (1979)
20	4	Yes	O_2 + nutrients	Nearshore	Georgia Bight, USA	Hopkinson & Wetzel (1982)
21	4	Yes	Nutrients and O_2	Nearshore	Georgia Bight, USA	Hopkinson (1987)[h]
22	–	–	O_2	Streams	England, various sites	James (1974)
23	–	–	O_2	Streams and lakes	England, various sites	James (1974)
24	–	–	O_2	Nearshore	Seto inland sea, Japan	Kawana et al. (1987)
25	10 d	Yes	O_2 + nutrients	Lake	Lake Grevelingen, Netherlands	Kelderman et al. (1988)
26	1–3	Yes	O_2	Estuary	Chesapeake Bay, USA	Kemp & Boynton (1981)
27	–	Yes	NH_3 + P	Nearshore	Cape Lookout Bight, N Carolina, USA	Klump & Martens (1981)
28	–	Yes	NH_3 + P	Nearshore	Cape Lookout Bight, N Carolina, USA	Klump & Martens (1981)
29	15	–	O_2 + methane	Lake	Lake Washington, Seattle, USA	Kuivila et al. (1988)
30	48	Yes	O_2	Nearshore	Flores Sea, Indonesia	Lindeboom & Sandee (1989)
31	48	Yes	O_2	Nearshore	Flores Sea, Indonesia	Lindeboom & Sandee (1989)
32	1–2	–	Methane	Nearshore	Cape Lookout Bight, N Carolina, USA	Martens & Klump (1980)
33	3–4	Yes	O_2 + nutrients	Lagoon	Colorado lagoon, Long Beach, Calif. USA	Murphy & Kremer (1985)
34	4	Yes	O_2 + nutrients	–	Chesapeake Bay, USA	Murray & Wetzel (1987)
35	2– >6	–	O_2	Near/offshore	Puget Sound, Washington, USA	Pamatmat & Fenton (1968)[i]
36	0.5–1.5	Yes	O_2	Intertidal sandflat	False Bay, San Juan Is., Washington, USA	Pamatmat (1968)
37	2–22	–	–	–	–	Patching & Raine (1983)
38	24–36	–	O_2	–	Caribbean	Pearson et al (1984)
39	2–4	Yes	O_2	Infralittoral	Aqaba Gulf, Red Sea	Peres (1982)
40	4–6.5	Yes	Nutrients	Nearshore	Nahant Bay, Massachusetts, USA	Pregnall & Miller (1988)
41	9–10	Yes	O_2 + nutrients	Nearshore	Vostok Bay, Sea of Japan	Propp et al. (1980)
42	5–26	Yes	O_2 + nutrients	Bay	Vostok Bay, Sea of Japan	Propp (1977)
43	1–3	Yes	O_2	Estuary	York River, Chesapeake Bay, USA	Rizzo & Wetzel (1985)
44	–	–	O_2 + nutrients	–	Cap Blanc, Spanish Sahara	Rowe et al. (1977)
45	Months	–	O_2, pH, Eh, Es	–	–	Schippel et al. (1973)
46	4	–	O_2	Nearshore	Castle Harbor, Bermuda	Smith et al. (1972)
47	6	Yes	DIC	Lake	Canadian lake	Sweerts et al. (1986)
48	24	–	O_2	Lake	Char Lake, N Canada	Welch & Kalff (1974)
49	–	Yes	Nutrients	Nearshore	Hiuchi Nada, Suho Nada and Beppu Bay, Japan	Yamada & Kayama (1987)
50	3	Yes	O_2	Nearshore	Algoa Bay, South Africa	This study

[c] Also used by Rutgers van der Loeff et al. (1984), Sundby et al. (1986), Hall (1984), Hall et al. (1989) and Westerlund et al. (1986)
[d] Also used by Callender & Hammond (1982) and Boynton et al. (1981)
[e] Also used by Callender & Hammond (1982)
[f] Also used by McCaffrey et al. (1980), Nixon et al. (1976, 1980) and Elderfield et al. (1981)
[g] Also used by Keizer et al. (1989) (but volume ca 17 l) and Hargrave & Phillips (1986)
[h] Also used by Fallon et al. (1983) and Hopkinson (1985)
[i] Also used by Pamatmat & Banse (1969)

This small volume to area ratio increased exchanges during shorter incubation periods and inhibited the build-up of concentration gradients. This, and the wave action at these shallow stations, eliminated the need for stirring. Stirring was also omitted because the aim of this study was to examine the effect of wave action and different stirring speeds can drastically influence flux rates (Dye 1979, Boynton et al. 1981, Callender & Hammond 1982, Olah et al. 1987) with even more pronounced effects when sediment resus-

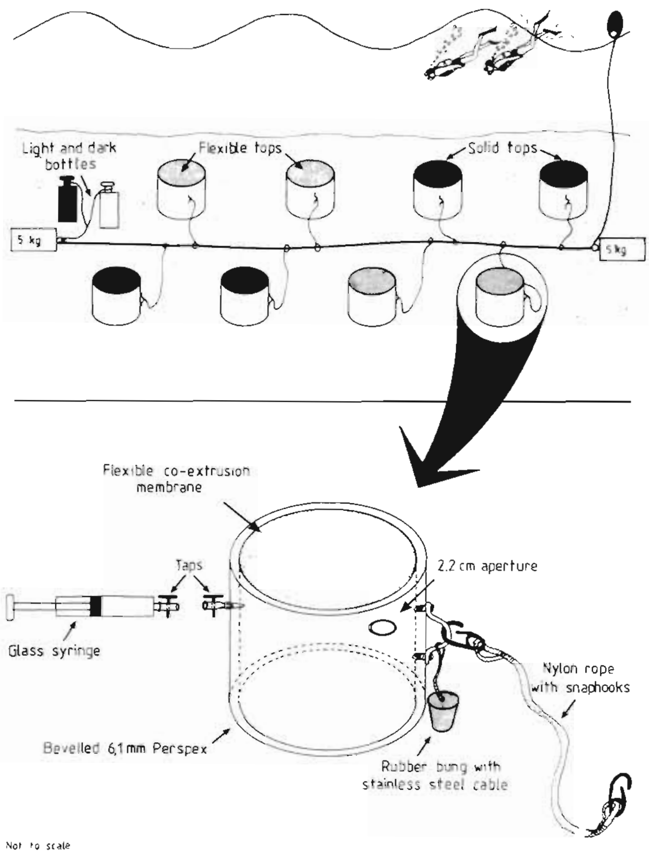

Fig. 2. Schematic representation of setup during chamber employments, with detailed inset of a chamber

pension occurs (Edwards & Rolley 1965, Pamatmat 1977, Boynton et al. 1981).

Oxygen flux determinations, at 18 ± 2 °C, were performed at 0.5 m and 5 m depth below low-water spring tide (ca 20 m and 150 m offshore), representing respectively the inner and outer turbulent zones of this beach (McLachlan et al. 1984) In situ oxygen flux determinations were usually conducted simultaneously with 6 to 8 chambers. The side-wash and visibility, however, influenced the number of chambers that could be successfully employed.

The general procedure followed is clear from Fig. 2. After an equilibration time of 20 min oxygen samples were taken at 30 to 45 min intervals during the total incubation time of 2 to 4 h. Samples were taken with acid-cleaned glass syringes equipped with plastic stopcocks, after gently mixing the contents of the chamber with a 50 ml syringe. Dye studies showed this method of mixing to be adequate. The syringes were stored at between −2 and +2 °C without freezing and immediately analyzed on arrival at the laboratory. Oxygen flux was calculated using chamber volume, area, incubation time and results of light and dark bottles for correction of uptake in overlying water.

Statistics. In general the data was checked for normality and homoscedasticity. This was normally followed by a 1-way analysis of variance and a multiple range test. In certain cases the independent variable had to be transformed $[X_1 = (X + 0.5)^{0.5}]$ to yield a straight line before the slopes were compared. Intercepts were not compared as the experimental design sometimes resulted in differing initial oxygen concentrations.

RESULTS

Oxygen permeability of different materials

The permeability of plastic and glass syringes to oxygen diffusion differed significantly ($p < 0.001$). Both makes of plastic syringes were highly permeable to oxygen, even at small gradients (Fig. 3). The different makes of plastic syringes also varied in oxygen permeability. The all-glass syringes were virtually impermeable to oxygen. The slight increase in oxygen observed in the latter is probably the consequence of oxygen penetrating through the plastic stopcocks.

Storage time had little effect on oxygen concentrations of water samples in glass syringes (Fig. 4). In this experiment, conducted at 20 °C (compare actual transport conditions of < 2 °C), there was a slight oxygen reduction in the unfiltered sea water samples. This effect might be increased, or decreased, during days of varying activity in the water column. Under the conditions tested, glass syringes may be used to collect and store oxygen samples for periods up to 12 h, without inducing errors.

The oxygen permeability of the materials investigated for volume compensation differed significantly ($p < 0.001$) (Fig. 5). Whilst the experimental oxygen gradients were far steeper than would be expected under field conditions, clearly condoms (Latex rubber) and polyethylene are not suitable materials. The co-extrusion was significantly less permeable to oxygen, but still showed some leakage. The success of this co-extrusion used for the flexible membrane chamber lies in the fact that the nylon layer retards oxygen diffusion, while the polyethylene layer supplies strength. According to Brydson (1975), Nylon 6 is 145 times less permeable to oxygen than low density polyethylene.

Oxygen penetration through the 2 materials initially considered for the flexible membrane, polyethylene and the co-extrusion, differed significantly ($p < 0.001$) (Fig. 6). The co-extrusion membrane should also perform better under field conditions where the oxygen gradients would be considerably reduced. Opaque chambers left in the sediment for extended periods resulted in complete oxygen removal. This indicated that signifi-

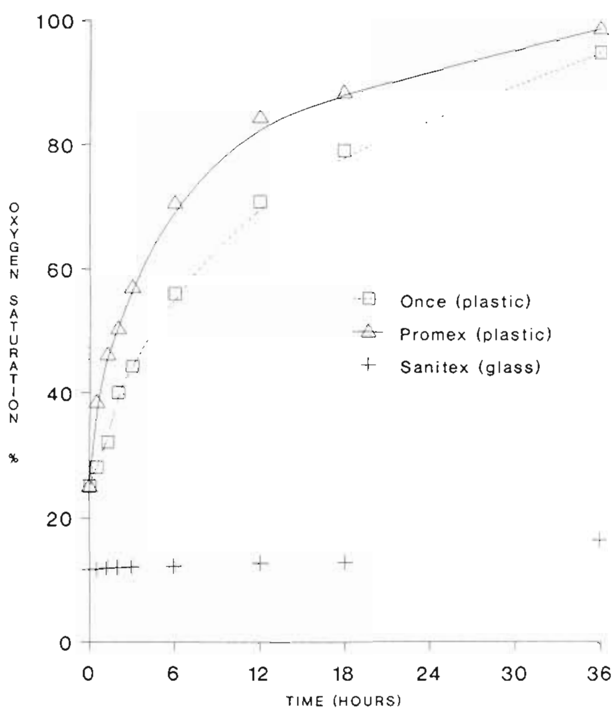

Fig. 3. Oxygen permeability of plastic and glass syringes

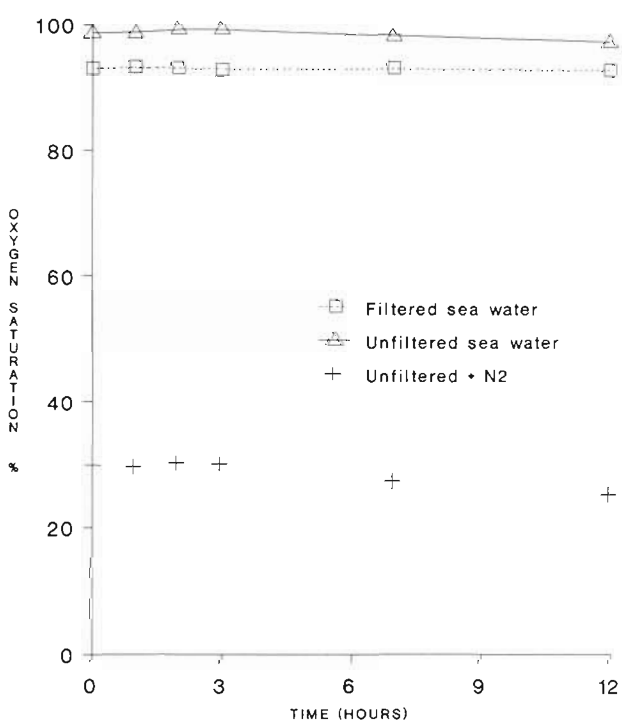

Fig. 4. Effect of time delay before oxygen analysis of water samples transported at 20 °C in glass syringes

cant amounts of oxygen did not penetrate through the membrane, or that depletion was faster than leaking. In contrast, oxygen concentrations in chambers with polyethylene tops were never reduced to zero.

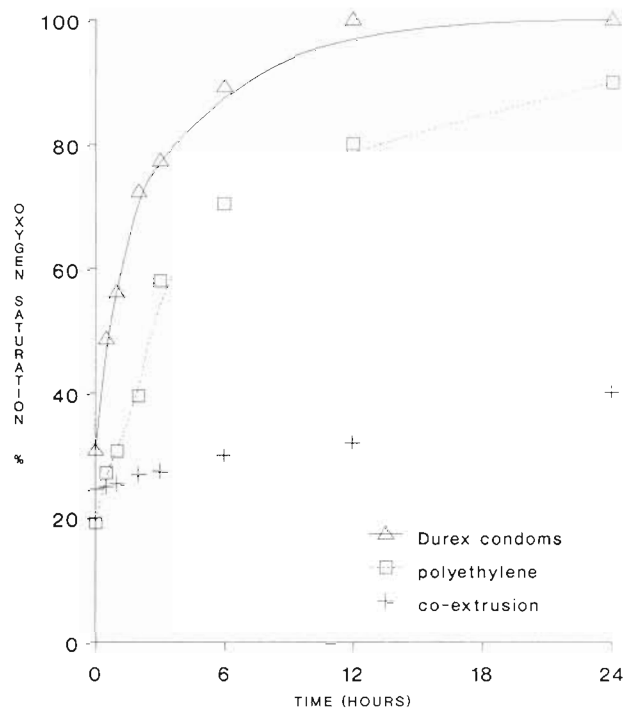

Fig. 5. Oxygen permeability of different materials investigated for volume compensation purposes

Oxygen consumption

ANOVA and multiple range analysis (Zar 1974) of the oxygen flux data revealed that there was no statistically significant difference ($p > 0.05$) between the 2 stations. Light and dark chambers with flexible tops showed no statistically significant difference (ANOVA and multiple range analysis, $p = 0.20$). Similarly the light and dark chambers with solid tops were homogeneous ($p = 0.97$). Data from all flexible top chambers and all solid top chambers were therefore pooled. ANOVA and multiple range analysis showed that the oxygen depletion in the flexible chambers was significantly different from the solid chambers ($p < 0.005$). The oxygen fluxes in the flexible and solid top chambers were respectively 18.5 ± 2.7 (95 % CI) and 10.7 ± 4.6 ml O_2 m^{-2} h^{-1} (average of 123 chamber values).

Using the results of the flexible membrane chambers at the Kings Beach 4 m station, a comparison was made between oxygen consumption during very calm (<0.25 m) and average (1 m) wave conditions. Despite a small sample size for the calm condition ($n_1 = 20$; $n_2 = 97$), there was a significant (ANOVA, $p < 0.05$) difference between these 2 physical conditions. Oxygen consumption during the very calm sampling periods averaged 9.4 ± 6.1 ml O_2 m^{-2} h^{-1} compared to 16.0 ± 2.8 ml O_2 m^{-2} h^{-1} during slightly rougher conditions.

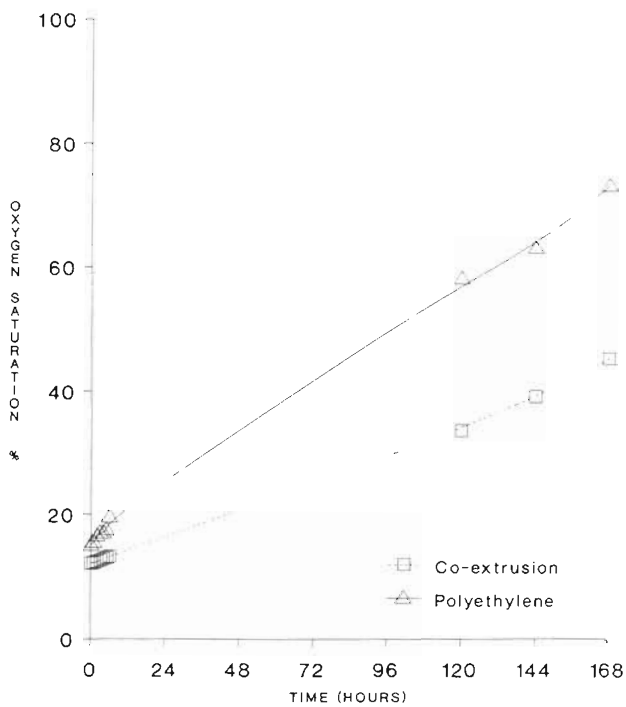

Fig. 6. Oxygen permeability of different materials investigated for the flexible membrane of the chamber

DISCUSSION

Kings Beach sediments are porous (Table 1) with oxygen penetrating to depths exceeding 60 cm (Malan & McLachlan 1985). There must therefore be considerable water exchange between the interstitial system and the overlying water. Measurement of the oxygen consumption of this benthic system therefore needs to include the pumping effect of the waves.

The many different methods used to investigate benthic metabolism have been reviewed by several authors (Bowman & Delfino 1980, Patching & Raine 1983). Despite this, there is still wide-spread disagreement about the best method to determine oxygen consumption. We felt that under our environmental conditions a fairly large in situ chamber with a flexible top would yield the best results, because such a chamber would: (1) most closely mimic the natural changes in hydrostatic pressure caused by surface waves passing overhead, (2) reduce the spatial variability of bottom fauna, (3) preclude unnaturally high consumption figures caused by handling, (4) preserve interstitial profiles, (5) emulate natural light and temperature regimes and (6) avoid decompression problems.

Materials and equipment used for the construction of chambers or used during sampling and analysis must be impermeable to oxygen. The permeability of different materials to oxygen varies tremendously (Brydson 1975). Plastic (Welch & Kalff 1974, Hargrave & Connolly 1978) and PVC syringes (Flint & Kamykowski 1984) have previously been used during experiments for determination of the oxygen content in water samples. Welch & Kalff (1974) found considerable variation in oxygen consumption values and attributed this to the blood-gas analyzer used. This variability could have been due to oxygen diffusion through their plastic syringes. Hargrave & Connolly (1978) mentioned that their plastic syringes were permeable to oxygen, but did not apply any correction for this. Martens & Klump (1980) estimated that the loss of methane through their plastic syringes was <11 %. Pamatmat & Banse (1969) and Pamatmat (1971) considered their oxygen consumption rates underestimates, since the 1.6 mm thick Tenite core liners used were permeable to dissolved oxygen. Laane et al. (1985) conducted laboratory studies to determine oxygen consumption resulting from photo-oxidizing processes. Oxygen concentrations were monitored in 'blood transfusion bags'. These authors, however, did not mention if these bags were impermeable to oxygen. Glass syringes have been used by many people for collecting oxygen samples (Hargrave 1972, Anderson et al. 1986, Sundby et al. 1986, Bender et al. 1989), and proved to be very effective in this study (Fig. 4), even at steep oxygen concentration gradients (Fig. 3).

The evidence presented here on the leakage of oxygen through plastic syringes and many of the materials previously used in chamber construction shows that there have been serious shortcomings in some authors' equipment. Although many authors have compensated for the permeability of their equipment, for example plastic syringes (McLachlan 1977, Martens & Klump 1980), others have ignored it or appear to have been unaware of the problem. Although the initial oxygen gradients in the current experiments were large, considerable leakage occurred even at gradients that would normally be expected under field conditions (Figs. 3 & 5). It is thus clear that some of the oxygen consumption, production, carbon budgets etc. previously reported on in the literature could be suspect. This aspect becomes even more serious if one considers the large variabilities and small sample sizes, often less than 5 to 10 measurements, that many authors report on (Malan & McLachlan unpubl.).

If the data represented in Table 2 is a fair reflection of the wide range of chambers used during in situ chamber deployments, several interesting facts emerge. Less than 30 % of the chambers have volumes smaller than 5 l, whilst 50 % are smaller than 10 l. The other 50 % range between 10 and >60 l. The average volume (excluding the largest chamber of over 2000 l) of the chambers presented here is 19 ± 21 l. Only a small percentage (25 %) of the chambers cover a sediment surface of ≤ 500 cm^2, with the majority falling in the range 500 to 2000 cm^2. It is further noticeable that the chambers often do not penetrate deep into the sediment. While this might be suitable under low energy and anaerobic sediment conditions, it might present problems under high energy conditions with considerable interstitial water flow. Although it was sometimes possible to keep chambers in place for more than a day, only the first few hours of the data could be used. After this period the sediment surrounding the chambers was scoured away causing a leakage of oxygen and hence unreliable results.

Plexiglass is the most popular construction material for chambers and the preferred shape is cylindrical. Although some authors used both transparent and opaque chambers, most make use of opaque materials. Roughly half of the studies in Table 2 made allowance for compensation of water column activity, with even fewer making allowance for the effect of sample removal. Whereas some authors recorded variables continuously, the majority took periodic readings or only initial and final values. Roughly 60 % of the investigators used some method to mix the volume of water enclosed inside their chambers. These methods range from pumps and paddles to magnetic stirrers, all with different flow and stirring speeds, making it very difficult to compare data. Some researchers only stirred the water to prevent the formation of concentration gradients, while others attempted to mimic natural conditions. For example, Murphy & Kremer (1985) matched mixing rates both within and outside their chamber, by comparing the erosion weight loss from $CaSO_4$ chips. Although this will not compensate for the effect of the sub-tidal pump, it is an improvement on the normal procedures. Buchholtz-ten Brink et al. (1989) went to great lengths to calibrate the performance of their stirred benthic chamber.

Few authors allowed any equilibrium time before measurements commenced. The importance of this has clearly been shown before, especially if the sediment surface is covered in a fine flocculent material. It can only be assumed that most authors do in fact allow for this, but neglect to mention it in their papers. Examination of the different exposure times suggests 3 groupings. Firstly, short-term exposures in the range 1 to 4 h, secondly exposures of about 24 h and thirdly exposure of 10 and more days are found. The physical conditions and depth of the sampling site play an important role in determining exposure time. Shallow areas are frequently affected by tidal currents, wave climate and scouring with intermediate depths restricting bottom time of SCUBA divers. Deeper sampling stations require specialized and costly equipment such as free-vehicle respirometers and submersibles (Smith & Teal 1973, Smith 1974, Smith & Baldwin 1984).

From the above and Table 2 it is clear that a large variety of different chambers, construction materials and methods, stirring speeds, depth of penetration and equilibrium times are being used. Many authors further fail to adequately report on their materials and methods. This makes comparison with other data extremely difficult. It is unlikely that anybody will one day develop the ideal chamber that is inexpensive, simple to construct, will operate under all conditions, mimic environmental conditions exactly and will be accepted by all researchers. It is, however, urged that authors do at least report as much detail as possible regarding their equipment, sampling procedures and environmental conditions as this will help in the interpretation of their data and make comparisons easier and more reliable.

The preliminary data presented here on oxygen consumption indicated that values are in the same range as reported by other authors for nearshore sandy sediments (Smith et al. 1972, Rowe et al. 1977, Propp et al. 1980). The data further showed that flux in the flexible chambers was 73 % higher than flux in the solid top chambers. We propose that the differences in the respective fluxes can be entirely attributed to the effect of wave action. To test this hypothesis the station with the most data was used to compare 2 different wave regimes. Although the difference in wave height was only 0.75 m, this represented a 4-fold increase in wave height at this shallow station. This resulted in a 70 % increase in oxygen consumption during the more exposed conditions. We feel that the large difference found between flexible and solid top chambers, together with the similarly large difference found under different wave regimes, indicates that wave action influences oxygen consumption at our study site.

A large majority of workers have not tried to measure respiration in shallow high energy environments. Sampling sites are often in deeper and/or calmer areas and these authors have not previously had to deal with the effect of wave action. It should also be pointed out that sediment characteristics and water depth of many of the study sites recorded in Table 2 are probably of such a nature that interstitial water flow is possibly not a very important factor. Nevertheless, the effect of interstitial water flow resulting from hydrostatic pressure fluctuations caused by passing surface waves can clearly not be ignored in shallow areas. Although Asmus (1982) equipped his bell jars with a polyethylene-polyamide plastic film to transfer wave action to the contents of the jars, to the best of our knowledge no authors have previously experimentally determined the effect of the 'sub-tidal pump' on oxygen consumption. We infer that, depending on such factors as wave action, water depth, sediment porosity and permeability, authors working in shallow areas could have under-estimated oxygen flux rates by as much as 50 %. It is our opinion that this effect caused by the pumping effect of the waves could potentially play an important rôle in all benthic systems where the sampling depth is less than half the wave length. In the nearshore coastal region it is expected to correspond roughly with the outer limit of the dynamic swept prism at a depth of about 15 m (Chapman 1983, Swart 1983). Beyond this depth the importance of the sub-tidal pump will rapidly diminish, although Riedl et al. (1972) mentioned that it could be effective to the 200 m isobath.

The oxygen fluxes presented here for the Kings Beach study site should be considered conservative estimates, since sampling only took place under relatively calm conditions. Further, although the effects of wave action were included by using flexible membrane tops on the chambers, the effect of the bottom surge (which is normally present at these shallow stations) was excluded by the solid vertical walls of the chamber.

In conclusion it can be said that the chamber introduced is inexpensive, easy to construct and appears to adequately allow for the interstitial pumping effect of waves in this shallow marine area studied. It has further been shown that waves have a pronounced effect on oxygen consumption in this shallow high energy coast. Evidence presented demonstrated that many of the materials and equipment previously used are highly permeable to oxygen and unsuitable for oxygen-related studies.

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LITERATURE CITED

Alongi, D. M., Boto, K. G., Tirendi, F. (1989). Effect of exported mangrove litter on bacterial productivity and dissolved organic carbon fluxes in adjacent tropical nearshore sediments. Mar Ecol. Prog. Ser 56: 133–144

Anderson, L. G., Hall, P. O. J., Iverfeldt, A., Rutgers van der Loeff, M. M., Sundby, B., Westerlund, S. F. G. (1986). Benthic respiration measured by total carbonate production. Limnol. Oceanogr. 31: 319–329

Asmus, R. (1982). Field measurements on seasonal variation of the activity of primary producers on a sandy tidal flat in the Northern Wadden Sea. Neth. J. Sea Res. 16: 389–402

Asmus, R. (1986). Nutrient flux in short-term enclosures of intertidal sand communities. Ophelia 26: 1–18

Balzer, W. (1984). Organic matter degradation and biogenic element cycling in a nearshore sediment (Kiel Bight). Limnol. Oceanogr 29: 1231–1246

Balzer, W., Grasshoff, K., Dieckmann, P., Haardt, H., Petersohn, U. (1983). Redox-turnover at the sediment/water interface studied in a large bell jar system. Oceanol. Acta 6: 337–344

Bauer, J. E., Montagna, P. A., Spies, R. B., Prieto, M. C., Hardin, D. (1988). Microbial biogeochemistry and heterotrophy in sediments of a marine hydrocarbon seep. Limnol. Oceanogr. 33: 1493–1513

Bay, D. (1982). Biologie marine – Etude in situ du metabolisme de trois communautes benthiques infralittorales du Golfe d'Aqaba-Mer Rouge. C.R. Acad. Sci., Paris 294: 463–466

Beckley, L. E. (1988). Spatial and temporal variability in sea temperature in Algoa Bay, South Africa. S. Afr Tydskr. vir Wetenskap 84: 67–69

Bender, M., Jahnke, R., Weiss, R., Martin, W., Heggie, D. T., Orchardo, J., Sowers, T (1989). Organic carbon oxidation and benthic nitrogen and silica dynamics in San Clemente Basin, a continental borderland site. Geochim. Cosmochim. Acta 53: 685–697

Bowman, G. T., Delfino, J. J. (1980). Sediment oxygen demand techniques: a review and comparison of laboratory and in situ systems. Wat. Res. 14: 491–499

Boynton, W R., Kemp, W. M., Osborne, C. G. (1980). Nutrient fluxes across the sediment-water interface in the turbid zone of a coastal plain estuary. In: Kennedy, V. S. (ed.) Estuarine perspectives. Academic Press, New York, p. 93–109

Boynton, W R., Kemp, W. M., Osborne, C. G., Kaumeyer, K. R., Jenkins, M. C. (1981). Influence of water circulation rate on in situ measurements of benthic community respiration. Mar Biol. 65: 185–190

Brydson, J. A. (1975). Plastic materials. Whitefriars Press Ltd, London

Buchholtz-ten Brink, M. R., Gust, G., Chavis, D. (1989). Calibration and performance of a stirred benthic chamber. Deep Sea Res. 36: 1083–1101

Callender, E. (1982). Benthic phosphorus regeneration in the Potomac river estuary. Hydrobiol. 92: 431–446

Callender, E., Hammond, D. E. (1982). Nutrient exchange across the sediment water interface in the Potomac River Estuary. Estuar coast. Shelf Sci. 15: 395–413

Carey, A. G. Jr (1967). Energetics of the benthos of Long Island Sound. 1 Oxygen utilization of sediment. Bull. Bingham Oceanogr. Coll. 19: 136–144

Carstens, T (1968). Wave forces on boundaries and submerged bodies. Sarsia 34: 37–60

Chapman, D. M. (1983). Sediment reworking on sandy beaches. In. McLachlan, A, Erasmus, T (eds.) Sandy beaches as ecosystems. Junk, The Hague, p. 45–62

Cramer, A. (1989). A common artefact in estimates of benthic community respiration caused by the use of stainless steel. Neth. J. Sea Res. 23: 1–6

Davies, J. M. (1975). Energy flow through the benthos in a Scottish Sea loch. Mar. Biol. 31: 353–362

Devol, A. H. (1987). Verification of flux measurements made with in situ benthic chambers. Deep Sea Res. 34: 1007–1026

Dye, A. H. (1979). Measurement of biological oxygen demand in sandy beaches. S. Afr Tydskr. Dierk. 14: 55–60

Dyrssen, D. (1986). Chemical processes in benthic flux chambers and anoxic basin waters. Neth. J. Sea Res. 20: 225–228

Dyrssen, D., Hall, P., Westerlund, S. (1984). Benthic chamber chemistry. Symposium on inorganic analysis in environmental research and protection, Juelich (FRG), 13–16 June 1983. Fresenius Z. Anal. Chem. 317: 380–382

Edberg, N., Hofsten, B. V (1973). Oxygen uptake of bottom sediments studied in situ and in the laboratory. Wat. Res. 7: 1285–1294

Edwards, R. W., Rolley, H. L. J. (1965). Oxygen consumption of river mud. J. Ecol. 53 1–19

Elderfield, H., Luedtke, N., McCaffrey, R. J., Bender, M. (1981). Benthic flux studies in Narragansett Bay. Am. J. Sci. 281 768–787

Fallon, R. D., Newell, S. Y., Hopkinson, C. S. (1983). Bacterial production in marine sediments: will cell-specific measures agree with whole-system metabolism? Mar. Ecol. Prog. Ser. 11: 119–127

Fisher, T R., Carlson, P. R., Barber, R. T. (1982). Sediment nutrient regeneration in three North Carolina estuaries. Estuar. coast. Shelf Sci. 14: 101–116

Flint, R. W., Kamykowski, D. (1984). Benthic nutrient regeneration in South Texas coastal waters. Estuar. coast. Shelf Sci. 18: 221–230

Gust, G. (1977). Turbulence and waves inside flexible-wall systems designed for biological studies. Mar Biol. 42: 47–53

Hale, S. S. (1975). The role of benthic communities in the nitrogen and phosphorous cycles of an estuary. In: Howell, F. G., Gentry, F. G., Smith, M. H. (eds.) Proceedings of a symposium on mineral cycling in Southeaster ecosystems. Publ. Tech. Information Centre: U.S. Energy and Development Admin., Augusta, Georgia, p. 291–308

Hall, C. A. S., Tempel, N., Peterson, B. J. (1979). A benthic chamber for intensely metabolic lotic systems. Estuaries 2: 178–183

Hall, P. (1984). Chemical fluxes at the sediment-seawater interface; in situ investigations with benthic chambers. Ph. D. thesis, Chalmers University of Technology and University of Goteborg

Hall, P. O. J., Anderson, L. G., Rutgers van der Loeff, M. M., Sundby, B., Westerlund, S. F. G. (1989). Oxygen uptake kinetics in the benthic boundary layer. Limnol. Oceanogr 34: 734–746

Hallberg, R. O., Bågander, L. E., Enguall, A.-G., Schippel, F. A. (1972). Method for studying geochemistry of sediment-water interface. Ambio 1: 71–72

Hargrave, B. T. (1972). Oxidation-reduction potentials, oxygen concentration and oxygen uptake of profundal sediments in a eutrophic lake. Oikos 23: 167–177

Hargrave, B. T., Connolly, G. F. (1978). A device to collect supernatant water for measurement of the flux of dissolved compounds across sediment surfaces. Limnol. Oceanogr. 23: 1005–1010

Hargrave, B. T., Phillips, G. A. (1981). Annual in situ carbon dioxide and oxygen flux across a subtidal marine sediment. Estuar. coast. Shelf Sci. 12: 725–737

Hargrave, B. T., Phillips, G. A. (1986). Dynamics of the benthic food web in St. Georges Bay, southern Gulf of St. Lawrence. Mar. Ecol. Prog. Ser. 31: 277–294

Hartwig, E. O. (1976). The impact of nitrogen and phosphorus release from a siliceous sediment on the overlying water. In: Wiley, M. (ed.) Estuarine processes, Vol. 1. Uses, stresses, and adaptations to the estuary. Academic Press, New York, p. 103–117

Herndl, G. J., Peduzzi, P., Fanuko, N. (1989). Benthic community metabolism and microbial dynamics in the Gulf of Trieste (Northern Adriatic Sea). Mar. Ecol. Prog. Ser. 53: 169–178

Hinga, K. R., Sieburth, J. M., Heath, G. R. (1979). The supply and use of organic material at the deep-sea floor J. mar. Res. 37: 557–579

Hopkinson, C. S. Jr (1985). Shallow-water benthic and pelagic metabolism: evidence of heterotrophy in the nearshore Georgia Bight. Mar. Biol. 87: 19–32

Hopkinson, C. S. Jr (1987). Nutrient regeneration in shallow-water sediments of the estuarine plume region of the nearshore Georgia Bight, USA. Mar. Biol. 94: 127–142

Hopkinson, C. S. Jr, Wetzel, R. L. (1982). In situ measurements of nutrient and oxygen fluxes in a coastal marine benthic community. Mar Ecol. Prog. Ser 10: 29–35

Jahnke, R. A., Christiansen, M. B. (1989). A free-vehicle benthic chamber instrument for sea floor studies. Deep Sea Res. 36: 625–637

James, A. (1974). The measurement of benthal respiration. Wat. Res. 8: 955–959

Kawana, K., Hoshika, A., Tanimoto, T (1987). Water quality monitoring system for oxygen consumption studies in the benthic boundary layer of the Seto inland sea. Proceedings of: 'Oceans 87. The ocean an international workplace' symposium. McNab, Halifax, p. 194–199

Keizer, P. D., Hargrave, B. T., Gordon, D. C. Jr (1989). Sediment-water exchange of dissolved nutrients at an intertidal site in the upper reaches of the Bay of Fundy, Canada. Estuaries 12: 1–12

Kelderman, P., Lindeboom, H. J., Klein, J. (1988). Light dependent sediment-water exchange of dissolved reactive phosphorus and silicon in a producing microflora mat. Hydrobiologia 159: 137–147

Kelly, J. R. (1984). Microcosms for studies of sediment-water interactions. In: Persoone, G., Jaspers, E., Claus, C. (eds.) Ecotoxicological testing for the marine environment, Vol. 2. State Univ. Ghent and Inst. Mar Scient. Res., Bredene, p. 315–330

Kemp, W M., Boynton, W. R. (1981). External and internal factors regulating metabolic rates of an estuarine benthic community. Oecologia (Berl.) 51: 19–27

Klump, J. V., Martens, C. S. (1981). Biogeochemical cycling in an organic rich coastal marine basin – II. Nutrient sediment-water exchange processes. Geochim. Cosmochim. Acta 45: 101–121

Kuivila, K. M., Murray, J. W., Devol, A. H., Lidstrom, M. E., Reimers, C. E. (1988). Methane cycling in the sediments of Lake Washington. Limnol. Oceanogr. 33: 571–581

Laane, R. W. P. M., Gieskes, W W C., Kraay, G. W., Eversdij, A. (1985). Oxygen consumption from natural waters by photo-oxidizing processes. Neth. J. Sea Res. 19: 125–128

Lindeboom, H. J., Sandee, A. J. J. (1989). Production and consumption of tropical seagrass fields in Eastern Indonesia measured with bell jars and microelectrodes. Neth. J. Sea Res. 23: 181–190

Lindeboom, H. J., De Klerk, H. A. J., Sandee, A. J. J. (1984). Mineralization of organic carbon on and in the sediment of Lake Grevelingen. Neth. J. Sea Res. 18: 492–510

Liu, P. L. F. (1973). Damping of water waves over porous bed. J. Hydraulics Div., Proc. Am. Soc. Civ. Eng. 99: 2263–2271

Malan, D. E. (1986). Effects of Qatar Light crude oil on adult saltmarsh crab *Sesarma catenata* and implications in the field: respiration, oxygen diffusion and hypoxia. S. Afr. J. mar Sci. 4: 265–275

Malan, D. E., McLachlan, A. (1985). Vertical gradients of meiofauna and bacteria in subtidal sandy sediments from two high-energy surf zones in Algoa Bay – South Africa. S. Afr. J. mar. Sci. 3: 43–53

Martens, C. S., Klump, J. V. (1980). Biogeochemical cycling in an organic-rich coastal marine basin – I. Methane sediment-water exchange processes. Geochim. Cosmochim. Acta 44: 471–490

Martin, D. C., Bella, D. A. (1971). Effect of mixing on oxygen uptake rate of estuarine bottom deposits. J. Wat. Pollut. Control Fed. 43: 1865–1876

McCaffrey, R. J., Myers, A. C., Davey, E., Morrison, G., Bender, M., Leudtke, N., Cullen, D., Froelich, P., Klinkhammer, G. (1980). The relation between pore water chemistry and benthic fluxes of nutrients and manganese in Narragansett Bay, Rhode Island. Limnol. Oceanogr 25: 31–44

McLachlan, A. (1977). Studies on the psammolittoral meiofauna of Algoa Bay, South Africa. 1. Physical and chemical evaluation of the beaches. Zool. Afr 12: 15–32

McLachlan, A. (1980). The definition of sandy beaches in relation to exposure: a simple rating system. S. Afr. J. Sci. 76: 137–138

McLachlan, A. (1983). Sandy beach ecology – a review. In: McLachlan, A, Erasmus, T (eds.) Sandy beaches as ecosystems. Junk, The Hague, p. 321–380

McLachlan, A., Cockcroft, A. C., Malan, D. E. (1984). Benthic faunal response to a high energy gradient. Mar. Ecol. Prog. Ser 16: 51–63

Murphy, R. C., Kremer, J. M. (1985). Bivalve contribution to benthic metabolism in a California lagoon. Estuaries 8: 330–341

Murray, L., Wetzel, R. L. (1987). Oxygen production and consumption associated with the major autotrophic components in two temperate seagrass communities. Mar. Ecol. Prog. Ser. 38: 231–239

Nixon, S. W., Kelly, J. R., Furnas, B. N., Oviatt, C. A., Hale, S. S. (1980). Phosphorus regeneration and the metabolism of coastal marine bottom communities. In: Tenore, K. R., Coull, B. C. (eds.) Marine benthic dynamics. University of South Carolina Press, Columbia, p. 219–242

Nixon, S. W., Oviatt, C. A., Hale, S. S. (1976). Nitrogen regeneration and the metabolism of coastal marine bottom communities. In: Anderson, J. M., MacFadyed, A. (eds.) Proc. 17th Symposium, British Ecological Soc. Blackwell Scientific Publication, London, p. 269–283

Olah, J., Sinha, V R. P., Ayyappan, S., Purushothanan, C. S., Radheyshyam, S. (1987). Sediment oxygen consumption in tropical undrainable fish ponds. Int. Revue ges. Hydrobiol. 72: 297–305

Oviatt, C. A., Pilson, M. E. Q., Nixon, S. W., Frithsen, J. B., Rudnick, D. T., Kelly, J. R., Grassle, J. F., Grassle, J P. (1984). Recovery of a polluted estuarine system: a mesocosm experiment. Mar Ecol. Prog. Ser. 16: 203–217

Pamatmat, M. M. (1968). Ecology and metabolism of a benthic community on an intertidal sandflat. Int. Revue ges. Hydrobiol. 53: 211–298

Pamatmat, M. M. (1971). Oxygen consumption by the seabed. IV. Shipboard and laboratory experiments. Limnol. Oceanogr. 16: 536–550

Pamatmat, M. M. (1977). Benthic community metabolism: a review and assessment of present status and outlook. In: Coull, B. C. (ed.) Ecology of marine benthos. Univ. of South Carolina Press, Columbia, p. 89–111

Pamatmat, M. M., Banse, K. (1969). Oxygen consumption by the seabed. II. In situ measurements to a depth of 180 m. Limnol. Oceanogr. 14: 250–259

Pamatmat, M. M., Fenton, D. (1968). An instrument for measuring subtidal benthic metabolism in situ. Limnol. Oceanogr. 13: 537–540

Patching, J. W., Raine, R. C. T (1983). Benthic metabolism and the supply of organic material to the sea-bed. In. MacDonald, A. G., Priede, I. G. (eds.) Experimental biology at sea. Academic Press, New York, p. 311–345

Pearson, M. P., Burns, M. D., Spencer Davies. P. (1984). An underwater respirometer and programmable data logger for in situ energy budget studies. J. exp. mar. Biol. Ecol. 74: 231–239

Pregnall, A. M., Miller, S. L. (1988). Flux of ammonium from surf-zone and nearshore sediments in Nahant Bay, Massachusetts, USA in relation to free-living *Pilayella littoralis*. Mar. Ecol. Prog. Ser 50: 161–167

Propp, M. V (1977). Exchange of energy, nitrogen and phosphorus between water, bottom and ice in a near-shore ecosystem of the Sea of Japan. Helgoländer wiss. Meeresunters. 30: 598–610

Propp, M. V., Tarasoff, V G., Cherbadgi, I. I., Lootzik, N. V (1980). Benthic-pelagic oxygen and nutrient exchange in a coastal region of the sea of Japan. In: Tenore, K. R., Coull, B. C. (eds.) Marine benthic dynamics. Univ. of South Carolina Press, Columbia, p. 265–284

Putnam, J. A. (1949). Loss of wave energy due to percolation in a permeable sea bottom. Trans. Am. Geophys. Un. 30: 349–356

Putnam, J. A., Johson, J. (1949). The dissipation of wave energy by bottom friction. Trans. Am. Geophys. Un. 30: 67–74

Riedl, R. N., Huang, N., Machan. R. (1972). The subtidal pump: a mechanism of interstitial water exchange by wave action. Mar. Biol. 13: 210–221

Rizzo, W. M., Wetzel, R. L. (1985). Intertidal and shoal benthic community metabolism in a temperate estuary: studies of spatial and temporal scales of variability. Estuaries 8: 342–351

Rowe, G. T., Clifford, C. H., Smith, K. L. (1977). Nutrient regeneration in sediments off Cap Blanc, Spanish Sahara. Deep Sea Res. 24: 57–63

Rutgers van der Loeff, M. M. (1981). Wave effects on sediment-water exchange in a submerged sand bed. Neth. J. Sea Res. 15: 100–112

Rutgers van der Loeff, M. M., Anderson, L. G., Hall, P. O. J., Iverfeldt, A., Josefson, A. B., Sundby, B., Westerlund, S. F. G. (1984). The asphyxiation technique: an approach to distinguishing between molecular diffusion and biologically mediated transport at the sediment-water interface. Limnol. Oceanogr 29: 675–686

Rutgers van der Loeff, M. M., Van Es, F. B., Helder, W., De Vries, R. T P. (1981). Sediment water exchanges of nutrient and oxygen on tidal flats in the Ems-Dollard Estuary. Neth. J. Sea Res. 15: 113–129

Schippel, F. A., Bagander, L. E., Hallberg, R. O. (1973). An apparatus for subaquatic in situ measurements of sediment dynamics. Stockholm Contrib. Geol. 24: 7–16

Smith, K. L. Jr (1974). Oxygen demands of San Diego through sediments: an in situ study. Limnol. Oceanogr 19: 939–944

Smith, K. L. Jr, Baldwin, R. J. (1984). Seasonal fluctuations in deep-sea sediment community oxygen consumption: central and eastern North Pacific. Nature, Lond. 307: 624–626

Smith, K. L. Jr, Burns, K. A., Teal, J. M. (1972). In situ respiration of benthic communities in Castle Harbour, Bermuda. Mar Biol. 12: 196–199

Smith, K. L. Jr, Teal, J. (1973). Deep-sea benthic community respiration: an in situ study at 1850 m. Science 179: 282–283

Snodgrass, W. J., Fay, L. A. (1987). Values of sediment oxygen demand measured in the central basin of Lake Erie, 1979. J. Great Lakes Res. 13: 724–730

Steele, J. H, Munro, A. L. S., Giese, G. S. (1970). Environmental factors controlling the epipsammic flora on beach and sublittoral sands. J. mar biol. Ass. U.K. 50: 907–918

Sundby, B., Anderson, L. G., Hall, O. J., Iverfeldt, A., Rutgers van der Loeff, M. M., Westerlund, F. G. (1986). The effect of oxygen on release and uptake of cobalt, manganese, iron and phosphate at the sediment-water interface. Geochim. Cosmochim. Acta 50: 1281–1288

Swart, D. H. (1983). Physical aspects of sandy beaches – a review. In: McLachlan, A., Erasmus, T (eds.) Sandy beaches as ecosystems. Junk, The Hague, p. 5–44

Swart, D. H., Crowley, J. B. (1983). Wave-generated water flow through a porous sea bed. In: McLachlan, A., Erasmus, T. (eds.) Sandy beaches as ecosystems. Junk, The Hague, p. 177–189

Sweerts, J. P., Rudd, J. W. M., Kelly, C. A. (1986). Metabolic activities in flocculent surface sediments and underlying sandy littoral sediments. Limnol. Oceanogr 31 330–338

Webb, J. E., Theodor, J. (1968). Irrigation of submerged marine sands through wave action. Nature, Lond. 220: 682–683

Webb, J. E., Theodor, J. (1972). Wave-induced circulation in submerged sands. J. mar. biol. Ass. U.K. 52: 903–914

Welch, H. E., Kalff, J. (1974). Benthic photosynthesis and respiration in Char Lake. J. Fish. Res. Bd Can. 31. 609–620

Westerlund, S. F. G., Anderson, L. F., Hall, P. O. J., Iverfeldt, A., Rutgers van der Loeff, M. M., Sundby, B. (1986). Benthic fluxes of cadmium, copper nickel, zinc and lead in the coastal environment. Geochim. Cosmochim. Acta 50: 1289–1296

Yamada, H., Kayama, M. (1987). Liberation of nitrogenous compounds from bottom sediments and effect of bioturbation by small bivalve, *Theora lata* (Hinds). Estuar coast. Shelf Sci. 24: 539–555

Zar, J. H. (1974). Biostatistical analysis. Prentice-Hall Biological Science Series, Englewood Cliffs

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