International Council
for the Exploration of the Sea

C.M. 1974/K.33
Shellfish and Benthos Committee

COMPARISON OF BENTHIC INVERTEBRATE BIOMASS AND OXYGEN CONSUMPTION BY MARINE SEDIMENTS

by

Barry T. Hargrave

Fisheries Research Board of Canada
Marine Ecology Laboratory
Bedford Institute of Oceanography
Dartmouth, Nova Scotia

Introduction

Measures of oxygen uptake by undisturbed sediment have been carried out in a variety of marine locations to provide an index of energy flow through benthic communities (Hargrave 1973, Pamatmat 1973, Smith *et al.* 1973a). All of these previous studies are predicated on the belief that such measures of community metabolism represent an integrated measure of the combined effects of hydrographic factors (temperature, salinity, pressure) and the supply of oxidizable organic matter on the size and composition of the benthic community. To date, only indirect evidence supports a causal link between sediment oxygen uptake and organic matter supply. Sediment in areas of equivalent depth with higher rates of annual primary production have increased rates of oxygen consumption (Hargrave 1973); there are seasonal differences after temperature corrections which imply input of organic material from primary production (Pamatmat 1971) and sediments receiving sewage discharge have higher rates of oxygen uptake than those in adjacent areas not receiving sewage effluent (Smith *et al.* 1973a).

Current studies are being carried out in different bays along the Nova Scotian coast in eastern Canada to examine quantitative relations between sedimentation and benthic community structure and metabolism. No previous studies have simultaneously assessed these variables which could provide predictive relationships between such factors as the rate of supply of carbon/nitrogen, oxygen availability, rates of anaerobic and aerobic sediment community metabolism, and changes in macrofauna biomass. The present review summarizes preliminary attempts to quantify some relations between rates of oxygen uptake by undisturbed sediment cores from a variety of marine locations and invertebrate macrofauna biomass in the same sediments. A positive correlation between invertebrate biomass and sediment oxygen uptake would suggest that organic matter supply controlled both macrofauna abundance and rates of community metabolism and/or that macrofauna serve a functional role in energy flow through bottom communities which is proportional to community metabolism. If such a relation exists, macrofauna biomass and its change with time could be used as an indicator of the flux of organic matter to bottom communities.

Methods

Estimates of macrofauna biomass have all been derived from sediment taken in core or grab (van Veen, 0.1 m^2) samples sieved through 0.8 mm mesh. Three embayments (references 8, 9, 10; Table 1) located along the Atlantic coast of Nova Scotia, Canada, have been sampled throughout the past five years. Macrofaunal communities in St. Margaret's Bay have been most extensively studied (see Hughes *et al.* 1972, Peer 1970) while central basin areas of Bedford Basin and Petpeswick Inlet have been sampled less frequently throughout a single year. One station in the Gulf of St. Lawrence, 15 km offshore from Ellerslie, Prince Edward Island, was sampled on two occasions during the summer of 1973. Except for some data taken from Pamatmat and Banse (1969) (Reference 2, Table 1), animals larger than 1 g/individual have not been included in biomass estimates since these are not sampled quantitatively by small core or grab samples. All weights are express on an ash-free dry weight basis which if not measured directly by ashing (550 C, 1-2 hr) is assumed equivalent to 10% of the fresh (wet) weight.

Methods used to measure rates of oxygen uptake by undisturbed sediment are summarized by Hargrave (1973), Pamatmat (1973), and Smith *et al.* (1973a). It is now apparent (Smith and Teal 1973b), particularly for measurements with deep sea sediments, that *in situ* (bell jar) methods give the most accurate measures of natural rates of sediment community oxygen uptake. For shallow-water coastal sediments, however, freshly taken core samples incubated under laboratory conditions give comparable results to *in situ* measurements (Pamatmat 1973), despite problems of experiment duration and the effect of stirring of overlying water during incubation. All measures of oxygen uptake reported here, if not derived from *in situ* measurements, result from laboratory incubations with freshly collected cores under *in situ* temperature and oxygen conditions. Stirring by means of magnetic bars prevents stratification during incubation and total rates of oxygen uptake (corrected for any consumption occurring in supernatant water removed from over intact sediment cores) have been calculated by following the decrease in dissolved oxygen concentration in water over undisturbed cores held in the dark for periods up to six hours.

Total oxygen uptake by undisturbed sediment cores is compartmentalized into chemical oxidation and biological respiration by treatment with buffered formalin (final concentration of 1-2% in water over sediment). Oxygen uptake due to biological activity is halted by this treatment and only oxygen consumption due to oxidation of reduced compounds such as H_2S and HS^- remains. While this treatment permits a measure of respiration associated with organisms, the significance of measures of chemical oxidation is obscure. A direct correlation exists with the concentration of reduced substances in the upper few centimetres of sediment, yet chemical oxygen consumption underestimates anaerobic metabolism indexed by measures of dehydrogenase activity (Pamatmat and Bhagwat 1973). No attempt was made during the present study to use measures of chemical oxygen uptake in an absolute manner. Since relationships between sediment oxygen uptake and macrofauna biomass were to be considered, the measurements only represent residual oxygen uptake after removal of biological respiration.

Results

There is no significant correlation between macrofauna biomass and total oxygen uptake by undisturbed sediment cores using data from single locations (references 2, 6, 9) or with data from all areas combined (Table 1). The lack of any relationship is clearly shown by comparing seasonal changes in biomass and sediment oxygen uptake. Macrofauna biomass in a Sapelo Island sublittoral area remains approximately constant from July to November while total benthic community metabolism decreases from 93 to 65 ml O_2 m^{-2} hr^{-1} (reference 6, Table 1). Also, at Tropp Island, St. Margaret's Bay, monthly samples of macrofauna biomass show little seasonal variation (mean 4.2 g ash-free m^{-2}) yet total sediment oxygen uptake ranges from 7 to 39 ml O_2 m^{-2} hr^{-1} (reference 8, Table 1). Sediments from near a sewage outfall in Bedford Basin consume oxygen at a moderately high rate, yet invertebrate biomass is equivalent to that found at 1850 m on the North Atlantic continental slope where rates of total community metabolism are two orders-of-magnitude lower (reference 4 compared with 9c, Table 1).

There is also no relation either seasonally or in different areas between biological respiration in sediment cores and macrofauna biomass. Approximately similar rates of respiration occur where there are order-of-magnitude differences in invertebrate biomass and conversely, similar amounts of biomass are observed in sediments with significantly different rates of biological respiration (references 3, 5; Table 1).

An inverse hyperbolic relation between macrofauna biomass and residual oxygen uptake after poisoning with formalin (chemical oxidation) is apparent when data from various locations are compared. Transformation of data by plotting on logarithmic axes (Fig. 1) makes the relationship clearer although data from areas in which no chemical oxidation occurs cannot be plotted. Usual incubation techniques do not permit rates of oxygen uptake less than 0.5 ml O_2 m^{-2} hr^{-1} to be quantified accurately (Pamatmat 1973) and thus some chemical oxidation below this level may occur in sediments having no measurable residual oxygen consumption after formalin treatment. For comparative purposes data for macrofauna biomass from these areas (references 3, 4; Table 1) are plotted at this lower limit of sensitivity for measurements of oxygen uptake.

Discussion

Previous attempts to correlate levels of macrofauna biomass with measures of total sediment oxygen uptake have shown no direct relation, just as neither parameter shows any consistent change with sediment organic content (Pamatmat and Banse 1969, Hargrave 1969a, and Smith 1973). Soklova (1972), on the other hand, using the weight of deep-sea benthic fauna as a basis for mapping trophic regions in the Pacific and Indian Oceans, has observed a semilogarithmic relation between heterotrophic activity of surface sediment microflora as indexed by radiochemical and oxygen uptake (total biological oxygen consumption) methods. The use of stirred sediments for these measurements prevents comparison with data summarized in Table 1.

Several problems exist with attempts to compare measures of bottom fauna abundance in various locations on an absolute basis. Collection efficiency which differs for various types of bottom sampler depending on sediment type (Flannagan 1970) is seldom quantified. Comparisons in St. Margaret's Bay, however, indicate a close similarity (±15%) in biomass estimates in van Veen and gravity and diver-retrieved core samples (Hargrave and Peer, unpublished data). Serious errors may also arise from significant seasonal changes in biomass not observed with limited sampling. Shallow-water littoral benthic populations may have up to a twofold variation in biomass throughout the year (Pamatmat 1968, Massé 1972, Smith 1973) while deeper water communities show far less seasonal variation (Lie 1969, Hargrave and Peer, unpublished data).

Direct comparison of macrofauna biomass and oxygen uptake in the same sediment core sample (references 2, 3, 5, 6, 8-11, Table 1) avoids some of these problems but the present review also combines results of different studies where biomass and oxygen uptake were measured at approximately similar locations but at different times (references 1, 4, 7, Table 1). Separation of the data on this basis still does not produce any significant relation between the variables.

Part of the difficulty with such comparisons is that a dynamic measure (oxygen uptake) is being compared with standing crop estimates which may not reflect the flux of oxidizable organic material into the sediment. Also, instantaneous changes in temperature will considerably alter rates of sediment oxygen consumption (Hargrave 1969a) while invertebrate biomass or sediment organic content would remain unaffected.

While total oxygen uptake is not related to invertebrate biomass it seems surprising that no relationship exists with biological respiration. Estimates of macrofauna respiration in a variety of benthic communities have shown that extrapolated laboratory measurements of invertebrate oxygen uptake could account for from 8 to 40% of total community oxygen consumption (Smith 1973) with the remaining respiration attributable to meiofauna, microfauna, and microflora. Macrofauna thus seem to represent the least important metabolic component of benthic communities and the relative size of their contribution to energy flow, indexed by respiration, appears to vary with location. Bacterial (antibiotic sensitive) oxygen consumption, on the other hand, which has been estimated to account for from 30 to 60% of total community respiration in different areas, closely parallels seasonal changes in total sediment oxygen uptake (Hargrave 1969b, Smith 1973).

The inverse hyperbolic relation between macrofauna biomass and chemical oxidation (Fig. 1), while not without considerable variation, shows a definite trend both seasonally within one area (reference 6) and between areas in one location (reference 9) to reduced fauna biomass at high and low rates of chemical oxidation with greatest biomass occurring in sediments consuming between 5 and 10 ml O_2 m^{-2} hr^{-1} after formalin treatment. If chemical oxidation reflects the amount of reduced organic and inorganic material in sediments, as Pamatmat's (1971) observations suggest, the inverse relation may reflect the response of invertebrate fauna to the combined effects of organic supply, sediment type and degree of oxidation.

Mud-silt which predominates in cores having high rates of chemical oxidation (references 2, 5b, 8b, 9b, c; Table 1) prevents deep penetration of dissolved oxygen into interstitial water. Reduced material accumulates in such sediment and organic content is relatively high due to incomplete oxidation of organic matter added through sedimentation. Macrofauna biomass is reduced under these conditions presumably in response to reduced conditions and the lack of an adequate oxygen supply.

Invertebrate biomass is also low in sediments with little or no measurable chemical oxidation. Sand predominates in these areas (references 1, 3, 4, 11) and except for the observation by Pamatmat (1968) that reducing conditions occur below 2 cm in False Bay sand cores, sediments from these areas appear to be well supplied with oxygen with little accumulation of reduced compounds in surface layers. Oxidation of organic matter must therefore be largely complete and in these locations macrofauna biomass may be controlled by factors such as the rate of supply of organic matter and physical factors such as water turbulence which prevents the formation of a stable sediment-water interface. The degree of exposure of littoral sediments to wave action determines particle size, sorting and compaction, all of which can influence the extent of water movement through sediments (Steele *et al.* 1970) and the size and composition of the faunal community (Massé 1972). Thus, sediments subject to high turbulence have reduced biomass due primarily to the physical effects of water motion. Deep water benthic communities, on the other hand, are limited in biomass due to low rates of organic supply (Sanders and Hessler 1969).

In both the present (Table 1) and previous studies (Massé 1972, Sanders, 1956) high levels of macrofauna biomass in excess of 10 g dry weight m^{-2} are associated with relatively stable fine sand sediments which receive ample oxygen supply. There may be some imbalance between organic input and utilization in these sediments since reduced material accumulates as reflected by measurable chemical oxidation (Fig. 1). The hyperbolic nature of the relationship implies that optimum conditions for development of high biomass exist where organic input slightly exceeds utilization.

The interaction between oxygen availability, total benthic community metabolism and macrofauna biomass has been nicely demonstrated by Bagge (1969) in a polluted estuary. Reduced fauna biomass occurred in areas of low oxygen concentration and in sediments with high rates of oxygen consumption. Although undifferentiated as to chemical oxidation, high rates of oxygen uptake by polluted sediments containing sulphite wastes obviously reflect the oxygen debt of accumulated reduced compounds which severely limit colonization by invertebrate fauna. The observations demonstrate the fruitful combination of viewing benthic communities from a structural and functional point of view. Massé (1972) cautions against the use of macrofauna biomass estimates for characterizing bottom communities, stressing that variability influenced by exposure and trophic conditions prevents meaningful comparisons. Biomass estimates, however, accompanied by data on sediment organic content, oxidation-reduction potentials and rates of community metabolism, do provide meaningful indices of the effects of numerous factors which affect benthic community structure through integrated action.

From the present comparisons, macrofauna biomass appears to indicate long-term steady state conditions between organic supply and oxidation within sediments of a given area. Rates of community oxygen consumption, on the other hand, reflect the instantaneous short-term effect of conditions of temperature, turbulence and recent organic supply. Current studies being carried out in St. Margaret's Bay are designed to provide a quantitative relationship between sedimentation and the utilization of sedimented organic matter within a benthic community. Simultaneous observations of changes in abundance and biomass of macrofauna will provide data for a more complete description of benthic food chain dynamics than has to date been possible.

Acknowledgements

I thank Mr. Robert Branton for assistance with collection and analysis of core samples from Petpeswick Inlet and St. Margaret's Bay.

Table 1. Comparison of total macrofauna biomass and sediment oxygen uptake with and without formalin poisoning of biological respiration in various marine benthic communities. + indicates dry weight estimated as 10% of weight wet.

Ref. No.	Location		Sediment oxygen uptake ml O_2 m^{-2} hr^{-1}			Macrofauna biomass g/m^2
			total	- chemical	= respiration	
1.	False Bay		15.0	0.09	14.9	6.0
2.	Puget Sound	a	19.0	11.4	7.6	4.6
		b	35.0	21.0	14.0	6.6
		c	35.0	21.0	14.0	9.3
		d	33.0	19.8	13.2	10.6
		e	17.0	10.7	6.3	19.6
		f	25.0	15.3	9.7	31.4
3.	Castle Harbour, Bermuda	a	24.6	0	24.6	1.4
		b	27.0	0	27.0	0.4
4.	N. Atlantic slope		0.5	0	0.5	0.6^{+}
5.	Woods Hole	a	54.6	7.8	46.8	11.6^{+}
		b	67.8	15.0	52.8	1.6^{+}
6.	Sapelo Island sublittoral	J	97.2	8.5	84.2	9.0
		S	89.5	7.1	82.4	8.0
		O	81.4	8.1	73.3	7.0
		N	64.1	6.4	67.7	9.0
		D	69.9	4.1	65.8	10.0
		J	53.9	2.8	51.1	14.0
		F	59.1	3.1	56.0	17.0
		M	65.3	4.5	60.8	19.5
		A	73.0	5.6	67.4	16.5
		M	85.1	7.6	77.5	15.0
7.	N. Pacific coast	a	5.0	1.5	2.0	4.0
		b	6.0	2.0	4.0	3.9
		c	5.0	3.0	2.0	4.5
8.	St. Margaret's Bay	a	20.0	11.4	8.6	4.2
		b	34.0	17.1	16.9	1.8
9.	Bedford Basin	a	21.0	10.3	10.7	5.7
		b	38.9	33.0	5.9	0.8
		c	46.8	42.5	4.3	0.6
10.	Petpeswick inlet		5.4	1.0	4.4	1.7
11.	Ellerslie (offshore)		1.5	0.6	0.9	1.1

Table 1 continued

References

1. Pamatmat (1968). Intertidal sandflat, San Juan Island, Washington. Station 3. Single estimate of chemical oxidation during December. 7-8 C. Macrofauna biomass estimate from January sample.

2. Pamatmat and Banse (1969). Mean of 3-7 *in situ* measurements during August-September at various locations. Mean value for chemical oxidation (60% of total oxygen uptake) taken as average of 23 stations in Puget Sound (Pamatmat 1971). Estimates of macrofauna biomass include large animals not sampled representatively.

3. Smith *et al.* (1972). Mean of two subtidal stations, 1.5 m depth, during May.

4. Smith and Teal (1973). North Atlantic continental slope, 1850 m depth. Mean of 10 *in situ* measurements of total oxygen uptake and two measurements of chemical oxidation, 4.5 C. Macrofauna biomass from Wigley and McIntyre (1964).

5. Smith *et al.* (1971). Two stations, 14 m depth. (a) Buzzards Bay, mean of four determinations; (b) sewage outfall, 182 m offshore, mean of 12 determinations.

6. Smith (1973). Monthly means (10 replicates) with cores taken from 7 m sublittoral zone off Sapelo Island, Georgia.

7. Pamatmat (1973). Northeast Pacific coast, single determinations at various locations. (a) Washington coast, Sta. 23, macrofauna biomass from Lie (1969), Sta. 20; (b), (c) Oregon coast, Yaquina Head, 50 and 100 m depth, macrofauna biomass from Carey (1972).

8. Present study (a) 13 m Troop Island, annual mean from bimonthly core samples incubated at *in situ* temperatures; (b) 68 m central St. Margaret's Bay, average spring, summer, fall and winter measurements.

9. Present study (a) Wright's Cove, average of four replicates, 13 m; (b) central basin, 70 m depth, six replicates during June; (c) near sewage outfall, 8 m depth, average of four replicates. All measurements at *in situ* temperatures (1.5-8 C).

10. Present study. Sampling site at 8 m depth inshore basin. Five measurements with cores collected during June-August, incubation at 5 C.

11. Present study. Mean of four cores taken on two occasions during summer at 12 m depth off Malpeque Bay, Prince Edward Island. Incubation at 5 C, 17 hr after collection.

Literature Cited

Bagge, P. 1969. Effects of pollution on estuarine ecosystems. I. Effects of effluents from wood-processing industries on the hydrography, bottom and fauna of Saltkällefjord (W. Sweden). Merentutkimuslait. Julk./ Havsforskningsinst. Skr. No. 228: 3-118.

Carey, A.G., Jr. 1972. Ecological observations on the benthic invertebrates from the central Oregon continental shelf, p. 422-443. *In* A.T. Pruter and D.L. Alverson (eds.), The Columbia River estuary and adjacent ocean waters: bioenvironmental studies. Univ. of Washington Press.

Flannagan, J.F. 1970. Efficiencies of various grabs and corers in sampling freshwater biota. *J. Fish. Res. Board Can. 27:* 1691-1700.

Hargrave, B.T. 1969a. Similarity of sediment oxygen uptake by benthic communities. *Limnol. Oceanogr. 14:* 801-805.

Hargrave, B.T. 1969b. Epibenthic algal production and community respiration in the sediments of Marion Lake. *J. Fish. Res. Board Can. 26:* 2003-2026.

Hargrave, B.T. 1973. Coupling carbon flow through some pelagic and benthic communities. *J. Fish. Res. Board Can. 30:* 1317-1326.

Hughes, R.N., D.L. PEER, and K.H. MANN. 1972. Use of multivariate analysis to identify functional components of the benthos in St. Margaret's Bay, Nova Scotia. *Limnol. Oceanogr. 17:* 111-121.

Lie, U. 1969. Standing crop of benthic infauna in Puget Sound and off the coast of Washington. *J. Fish. Res. Board Can. 26:* 55-62.

Massé, H. 1972. Quantitative investigations of sand-bottom macrofauna along the Mediterranean north-west coast. *Mar. Biol. 15:* 209-220.

Pamatmat, M.M. 1968. Ecology and metabolism of a benthic community on an intertidal sandflat. *Int. Rev. Geo. Hydrobiol. 53:* 211-298.

Pamatmat, M.M. 1971. Oxygen consumption by the seabed. VI. Seasonal cycle of chemical oxidation and respiration in Puget Sound. *Int. Rev. Geo. Hydrobiol. 56:* 769-793.

Pamatmat, M.M. 1973. Benthic community metabolism on the continental terrace and in the deep sea in the North Pacific. *Int. Rev. Geo. Hydrobiol. 58:* 345-368.

Pamatmat, M.M., and K. Banse. 1969. Oxygen consumption by the seabed. II. In situ measurements to a depth of 188 m. *Limnol. Oceanogr. 14:* 250-259.

Pamatmat, M.M., and A.M. Bhagwat. 1973. Anaerobic metabolism in Lake Washington sediments. *Limnol. Oceanogr. 18:* 611-627.

Peer, D.L. 1970. Relation between biomass, productivity, and loss to predators in a population of a marine benthic polychaete, *Pectinaria hyperborea. J. Fish. Res. Board Can. 27:* 2143-2153.

Sanders, H.L. 1956. Oceanography of Long Island Sound, 1952-1954. X. The biology of marine bottom communities. Bull. Bingham Oceanogr. Collect. Yale Univ. 15: 345-414.

Sanders, H.L., and R.R. Hessler. 1969. Ecology of the deep-sea benthos. *Science 163:* 1419-1424.

Sokolova, M.N. 1972. Trophic structure of deep-sea macrobenthos. *Mar. Biol. 16:* 1-12.

Smith, K.L., Jr. 1973. Respiration of a sublittoral community. *Ecol. 54:* 1065-1075.

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

Smith, K.L., Jr., G.T. Rowe, and J.A. Nichols. 1973a. Benthic community respiration near the Woods Hole sewage outfall. *Est. and Coastal Mar. Sci. 1:* 65-70.

Smith, K.L., Jr., and J.M. Teal. 1973b. Deep-sea benthic community respiration: an *in-situ* study at 1850 m. *Science 179:* 282-283.

Steele, J.H., A.L.S. Munro, and G.S. Giese. 1970. Environmental factors controlling the epipsammic flora on beach and sublittoral sands. *J. Mar. Biol. Ass. U.K. 50:* 907-918.

Wigley, R.L., and A.D. McIntyre. 1964. Some quantitative comparisons of offshore meiobenthos and macrobenthos south of Martha's Vineyard. *Limnol. Oceanogr. 19:* 485-493.

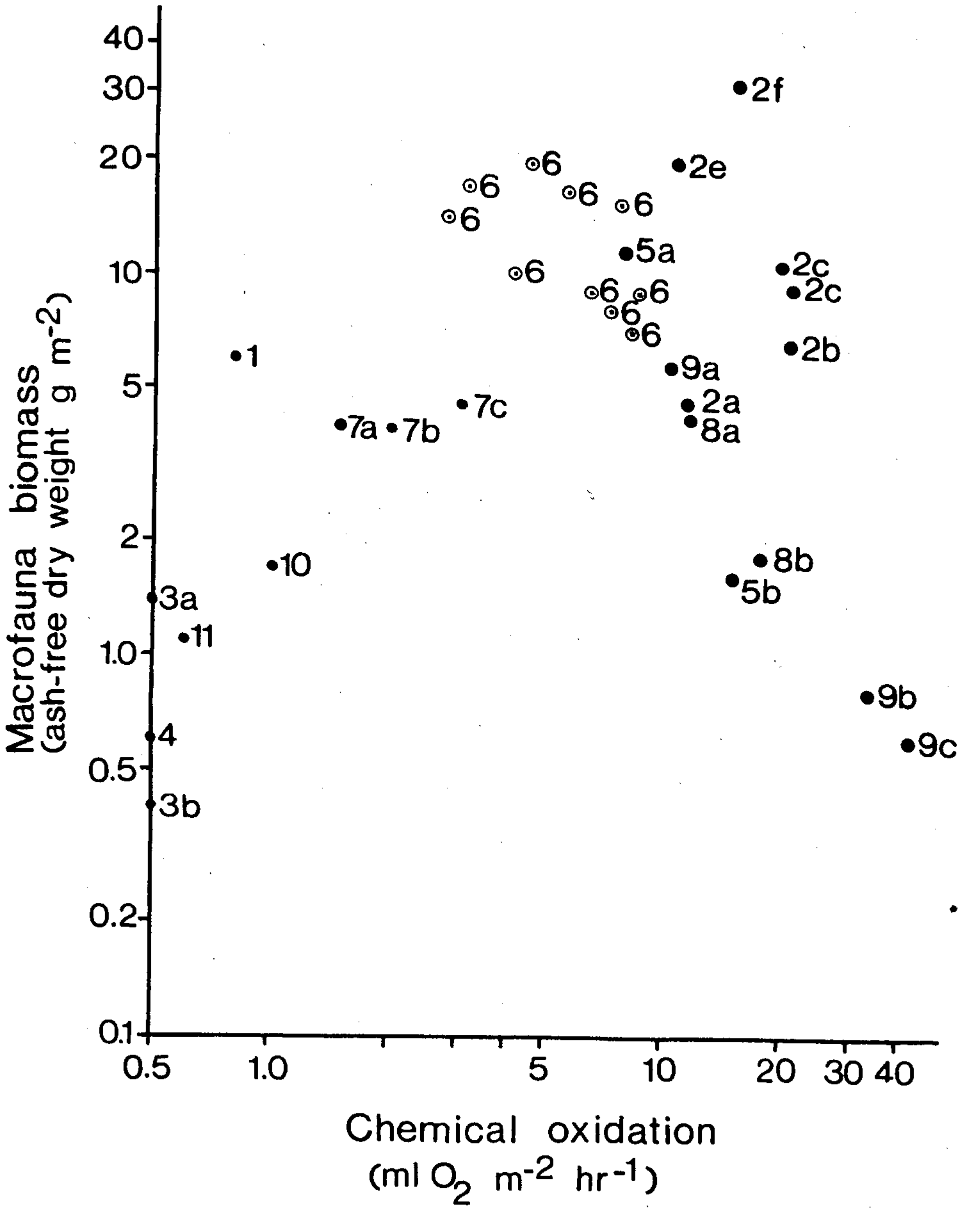

Figure 1. Comparison of estimates of macrofauna biomass dry weight and residual oxygen uptake by undisturbed sediment cores after formalin treatment in sediments from various marine locations. Numbered references from Table 1.