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Biomass, Productivity and Nutrient Requirements of Microphytobenthos

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EXECUTIVE SUMMARY

Microphytobenthos (MPB) or benthic microalgae are common components of shallow aquatic systems world-wide. Diatoms, dinoflagellates, cyanobacteria and occasionally chlorophyte algae are the most common components of the MPB. Colonisation by MPB can provide physical stability to sedimentswhilst the metabolic processes of this group of micro-algae can regulate oxygen conditions and nutrient exchange across the sediment/water column interface.

The biomass and productivity of MPB in a range of shallow marine and estuarine habitats from around the world have been examined. MPB biomass, as determined by chlorophyll *a* distribution in sediments, averages 86 mg chlorophyll *a* m^{-2} in shallow water systems and productivity by these organisms has a mean value of 55 mg C m^{-2} h^{-1}. Annual production by MPB from a number of studies shows a mean value of 135 g C.m^{-2} y^{-1} which is greater than production by oceanic or coastal phytoplankton. MPB are significant components of marine and estuarine ecosystems, contributing more than 30% of the total primary productivity in some situations.

There is considerable variation around the mean biomass and productivity figures quoted above. Whilst in global terms there are no significant correlations between biomass/productivity and latitude/habitat type, there are locally significant correlations between MPB distribution and environmental factors such as depth, sediment type and nutrient availability. The large variation in MPB biomass and productivity within and between different marine ecosystems preclude application of published data to Port Phillip Bay. The ecological significance of MPB to the Bay will require direct investigation rather than extrapolation from data obtained from other areas.

1. INTRODUCTION

Importance of microphytobenthos

In recent years it has been recognised that the microalgae attached to or found within sediment particles (the microphytobenthos or MPB) can make a significant contribution to the overall primary productivity of aquatic environments (Pomeroy et al. 1981; Taasen & Hoisaeter 1981; Masini 1990).

Water column production of well mixed ecosystems is often greatly augmented by displaced MPB during re-suspension events (Lukatelich & McComb 1986; Shaffer & Sullivan 1988). Benthic microalgae are grazed directly by higher level consumers (Daehnick et al. 1992) and stable isotope studies increasingly point to the importance of MPB, as opposed to macroalgae and seagrasses, in the transfer of carbon to higher trophic levels (Moncreiff et al. 1992). The MPB has also been shown to provide physical stability to intertidal (Paterson et al. 1990) and subtidal (Madsen et al. 1993) sediments.

The importance of MPB has been reported from environments as disparate as the sub-arctic (Bjork-Ramburg 1983) to tropical coral reefs (Sournia 1976). Marine and freshwater systems exhibit dominant MPB floras (Bjork-Ramburg 1983; Nienhuis and DeBree 1984; Stevenson 1984; Wetzel 1964). Within the marine environment, MPB are important components of both intertidal and subtidal habitats (Masini 1990).

Although benthic microalgae contribute a small percentage of the annual total productivity compared to macroalgal components of many shallow water ecosystems, they nonetheless show much more rapid rates of turnover and recycling resulting in a corresponding relatively high nutrient requirement (Walker et al. 1988). The MPB has long been implicated in the mineralisation and recycling of nutrients from particulate organic matter to the water mass (Nixon 1981). Furthermore, the role that the microphytobenthos plays in regulating oxygen conditions and nutrient exchange at the sediment/water column interface has been demonstrated in several environments (Rizzo 1990; Sundbäck et al. 1991).

The organisms

Diatoms are usually the most abundant components of MPB populations. A broad range of diatom species are usually found in sediments and the most common genera include *Navicula, Nitzchia, Achnathes* and *Amphiprora.* In some circumstances dinoflagellates can comprise a significant proportion of the MPB population. Genera noted include *Prorocentrum* (Masini 1990) and *Amphidinium* and *Gymnodinium* (Axelrad et al. 1979). Cyanobacteria, usually of the genera *Oscillatoria, Calothrix* and *Rivularia,* can occasionally form microbial mats on marine sediments. *Merismopedia* can also be common (Whitton & Potts 1982). Occasionally, chlorophyte algae such as marine species of the genus *Chlamydomonas* are recorded (Axelrad et al. 1979). A range of species in Port Phillip Bay has been noted by various authors and is summarised by Light and Woelkerling (1992). The organisms can exist either in the interstitial water of the sediment (in which case they may be relatively easily resuspended into the water column) or attached to the sediment particles.

Aims and scope of this review

The aim of this review is to provide an overview of the likely extent and primary productivity of microphytobenthos in Port Phillip Bay and to assess the contribution of these organisms to nutrient cycling in the Bay.

It should be stated at the outset of this report that there are very few data in the literature pertaining directly to any aspect of microphytobenthos in Port Phillip Bay. Most of the information in the review is therefore derived from studies on other systems and its applicability to Port Phillip Bay must be inferred.

2. ESTIMATES OF MICROPHYTOBENTHOS BIOMASS IN SHALLOW MARINE ECOSYSTEMS

Biomass of MPB has almost invariably been determined as chlorophyll per unit weight of sediment or, more commonly, as chlorophyll per unit area (mg chlorophyll m^{-2}). There are a few exceptions. For instance Walker et al. (1988) cite biomass as the weight of algae per unit area (g algae m^{-2}) whilst several data sets also provide direct cell counts (e.g. Masini 1990; Sundbäck et al. 1991). In the data presented in this review, biomass has been expressed as chlorophyll *a* per unit area
(mg chlorophyll *a* .m^{-2}), except in several instances where insufficient detail was provided in publications to enable conversions from a weight to an areal basis.

Four studies on MPB (Axelrad et al. 1979; Hargrave et al.1983; Lukatelich & McComb 1986; Pollard & Kogure 1993) have presented chlorophyll *a* values uncorrected for pheopigments (i.e. no attempt was made to determine the contribution of the degradation product pheophytin to estimations of chlorophyll *a* concentrations). For the purpose of this review, chlorophyll data from these studies has not been used in subsequent calculations. Unless specifically stated, all values of chlorophyll quoted hereafter refer to chlorophyll *a* corrected for the presence of pheophytin.

Microphytobenthos biomass from a range of different habitats is presented in Tables A1-A4, representing values from sub-tidal marine, sub-tidal estuarine, intertidal marine and intertidal estuarine/saltmarsh environments respectively. Most data are from latitudes 32^{o}S to 57^{o}N, but a few data sets have been generated from tropical or sub-polar habitats.

The range of values is noteworthy. Chlorophyll concentrations in sediments range from less than 1 mg chl m^{-2} to more than 1000 mg chl m^{-2} . This variation is found both within and between individual studies and reflects differences in depth, nutrient loading, light penetration and sediment grain size as well as seasonal effects (see Section 5 for details). Analysis of the data from depths shallower than 20 m (thereby excluding values from deep water with extremely low light penetration), gives mean biomass for the four different habitats of 57 to 107 mg chl m^{-2} (Table 1).

Table 1: Summary of microphytobenthic biomass, expressed as mg chl m^{-2}, in different environments (n = number of estimates).

	Sub-tidal Marine n = 62	Sub-tidal Estuarine n = 29	Intertidal Marine n = 12	Intertidal Estuarine/saltmarsh n = 25
Minimum	0.04	4	0.04	0.23
Maximum	1030	558	500	324
Mean (s.d.)	107 (185)	98 (119)	82 (137)	57 (76)

There appears no marked differences in the distribution of biomass between the four different environments (Figure 1). Whilst values from tropical and sub-polar environments appear to be at the low end of the range (Figure 2), we do not consider this variation in mean biomass with latitude to be 'real' and believe that the observed distribution is partially a reflection of the fewer number of studies conducted at these latitudes. Unusually high values (outliers) could be explained by the use of varying sediment thicknesses; in most instances the uppermost 5 or 10mm of sediment was extracted for chlorophyll. However, several studies (e.g. Vilbaste 1992) failed to specify depth of sediment examined. Outliers could also be attributed to the occasional poor detail provided in methodologies; several publications refer to chlorophyll *a* values which leave the reader unsure as to whether corrections for pheopigments have been made.

To date, the only study conducted on MPB in Port Phillip Bay is that of Axelrad et al. (1979). These authors reported MPB biomass off shore from Werribee to vary between 60 and 130 mg chl m^{-2} whereas values ranging from 12-28 mg chl m^{-2} were reported at Portarlington. These values are comparable to those of other studies from similar habitats. Our own more recent studies in Port Phillip Bay (Light, Beardall and Black, unpublished) have indicated MPB biomass levels higher than those of Axelrad et al. (1979) with values for functional chlorophyll *a* of up to 253 mg chl m^{-2}. However, most samples yielded biomass values in the range 0-50 mg chl *a* m^{-2} (mean 19 mg chl *a* m^{-2}). High MPB biomass was found at sites near Werribee and Corio Bay whereas biomass values in the lower range were obtained at sites over most of the rest of the Bay. Estimates of chlorophyll concentrations made without correction for the pheophytin content of the sediment result in considerably higher values, with highest concentrations of more than 500 mg chl m^{-2} and a mean value for the Bay of 152 mg chl m^{-2}. These latter values provide the better direct comparison with the data set of Axelrad et al. (1979) in which functional chl *a* and pheophytin were not differentiated (see Section 6).

3. ESTIMATES OF PRIMARY PRODUCTIVITY OF MICROPHYTOBENTHOS

3.1. Photosynthetic Characteristics of MPB

Photosynthesis is the major determinant of primary productivity and because the organisms of the MPB are frequently found at considerable depth where light is a major limiting factor, an assessment of photosynthetic characteristics could help predict the likely performance of the MPB *in situ*. Average values for the parameters describing the photosynthesis vs irradiance relationship are given in Table 2.

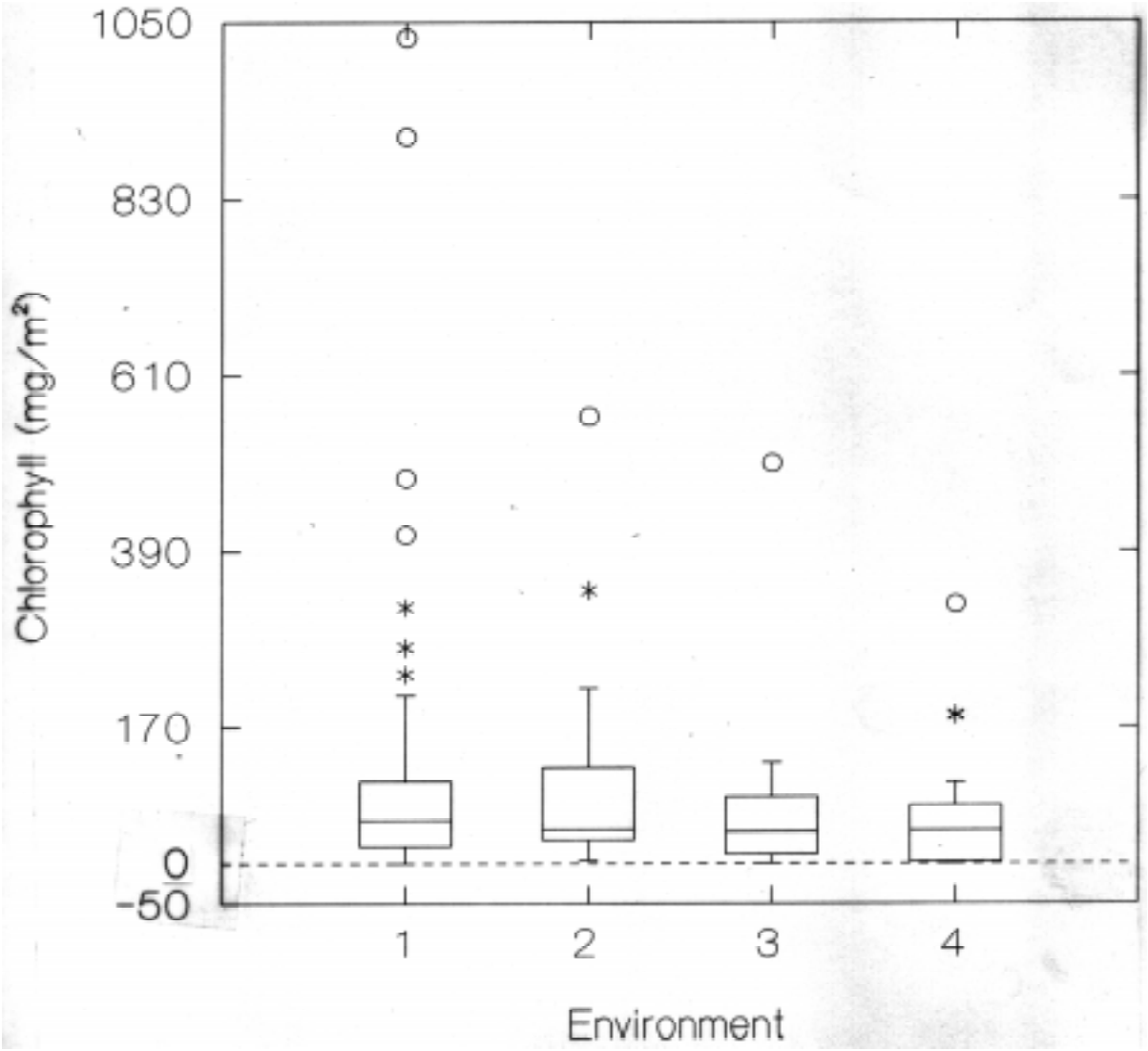

Figure 1. Values of microphytobenthos biomass (expressed as chlorophyll m^{-2}) in different environments. Key to Environments: 1 = Subtidal marine; 2 = Subtidal estuarine; 3 = Intertidal marine; 4 = Intertidal estuarine. Values are expressed as box plots where the central horizontal line box is the median value and the top and bottom of the box represents the 75 and 25 percentiles respectively. The lines above and below the box represent values within the range 1.5x that within the box. Values represented as "*" are outliers and those shown by "o" are extreme outliers.

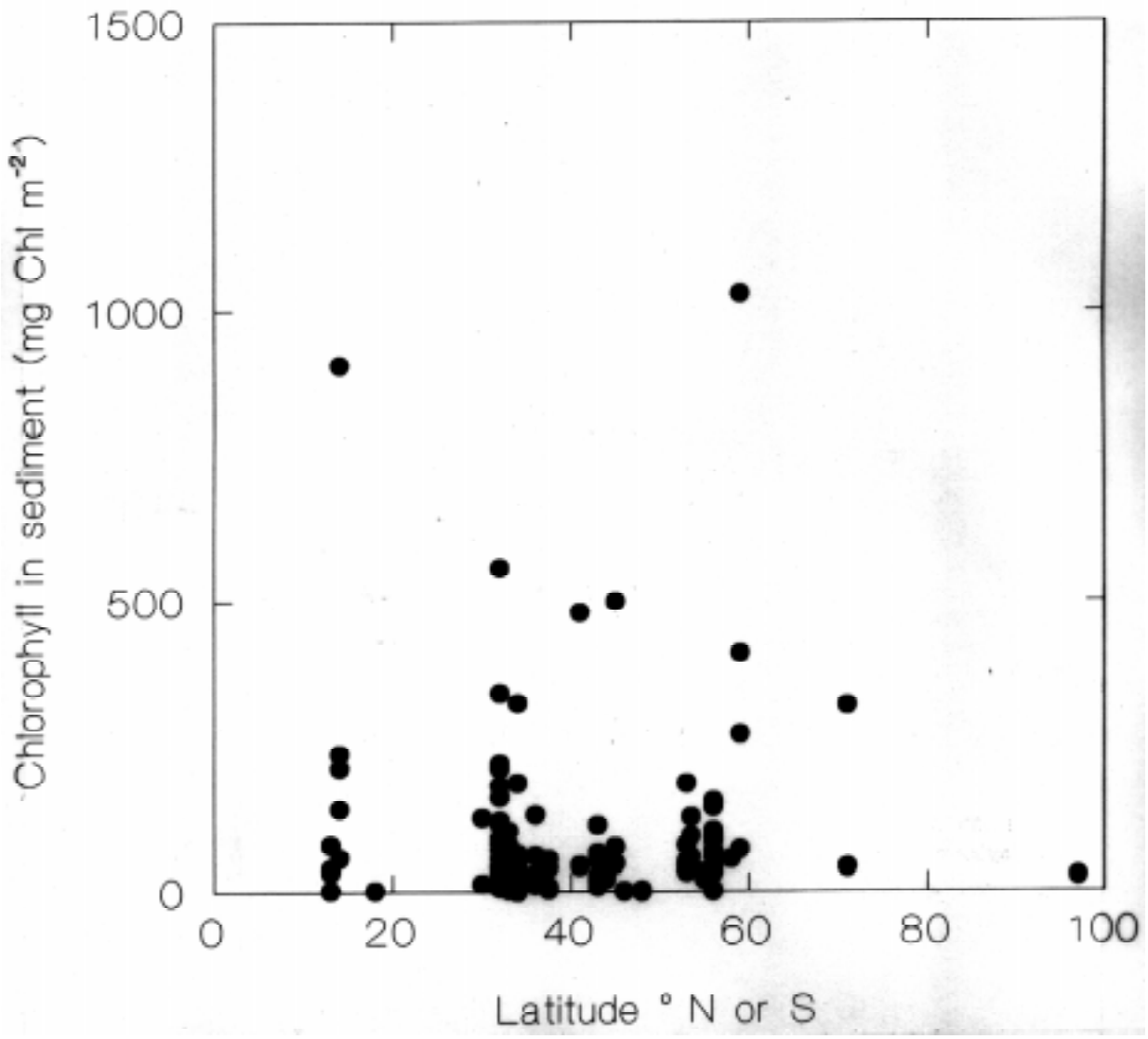

Figure 2. Distribution of MPB biomass (chlorophyll *a*. m^{-2}) as a function of latitude.

The assimilation numbers for benthic microalgae quoted in Table 2 are, on average, considerably lower than those of phytoplankton which range from 1.6 to more than 20 mg C mg chl^{-1} h^{-1} (Falkowski 1981; Glover 1980). This difference may be attributed to the low light environment to which the organisms are often subjected.

Table 2. Photosynthetic parameters for benthic microalgae. (Data abstracted from Blanchard & Montagna 1992, Colijn & de Jonge 1984, Davis & McIntire 1983, Masini 1990, Mills & Wilkinson 1986, Pinckney & Zingmark 1993c, Rasmussen et al. 1983 and Steele & Baird 1968)

	Assimilation Number (mgC mg chl^{-1} h^{-1}) (n = 45)	Alpha (mgC mg chl^{-1} h^{-1}) /(µEin m^{-2} s^{-1}) (n = 9)	I_c (Ein m^{-2} s^{-1}) (n = 10)	I_k (Ein m^{-2} s^{-1}) (n = 13)	I_m (Ein m^{-2} s^{-1}) (n = 9)
Mean	1.408	0.0442	38.9	256	848
SE	0.152	0.0189	4.043	77	
Min	0.110	0.0019	13	48	419
Max	3.64	0.158	53	810	1668

The compensation point (I_c) is the light intensity where respiration balances photosynthesis. The mean value for I_c (38.9 Ein m^{-2} s^{-1}) is considerably higher than values obtained for microalgae grown in culture (Richardson et al. 1983). The high I_c value for MPB most likely reflects the high respiratory loading in the benthic community inhabiting the sediment rather than the inherent inability of benthic microalgae to function efficiently at low light levels.

The values for I_k (the photon flux at which photosynthesis starts to become light saturated - represented by the intersect between the initial slope, alpha, and maximum photosynthetic rate P_{max}) and I_m (the photon flux giving maximal photosynthesis rate) are highly variable and reflect a range of populations which are adapted to low light (low values for these parameters) or high light (I_m full sunlight). Using the mean values for all parameters results in a Photosynthesis vs Irradiance curve as shown in Figure 3. (The different lines are photosynthetic rates calculated on mean standard errors of the parameters given in Table 2). Interestingly, the light environments measured at the shallow sites at Werribee and Indented Head would fall in the light saturated region of the curve, whilst the deeper sampling sites (Great Sands and Werribee) would be at approximately 0.5 and 0.25 saturation respectively. Thus productivity at the shallow sites may not be as dependent on seasonal fluctuations in light availability as those in deeper waters.

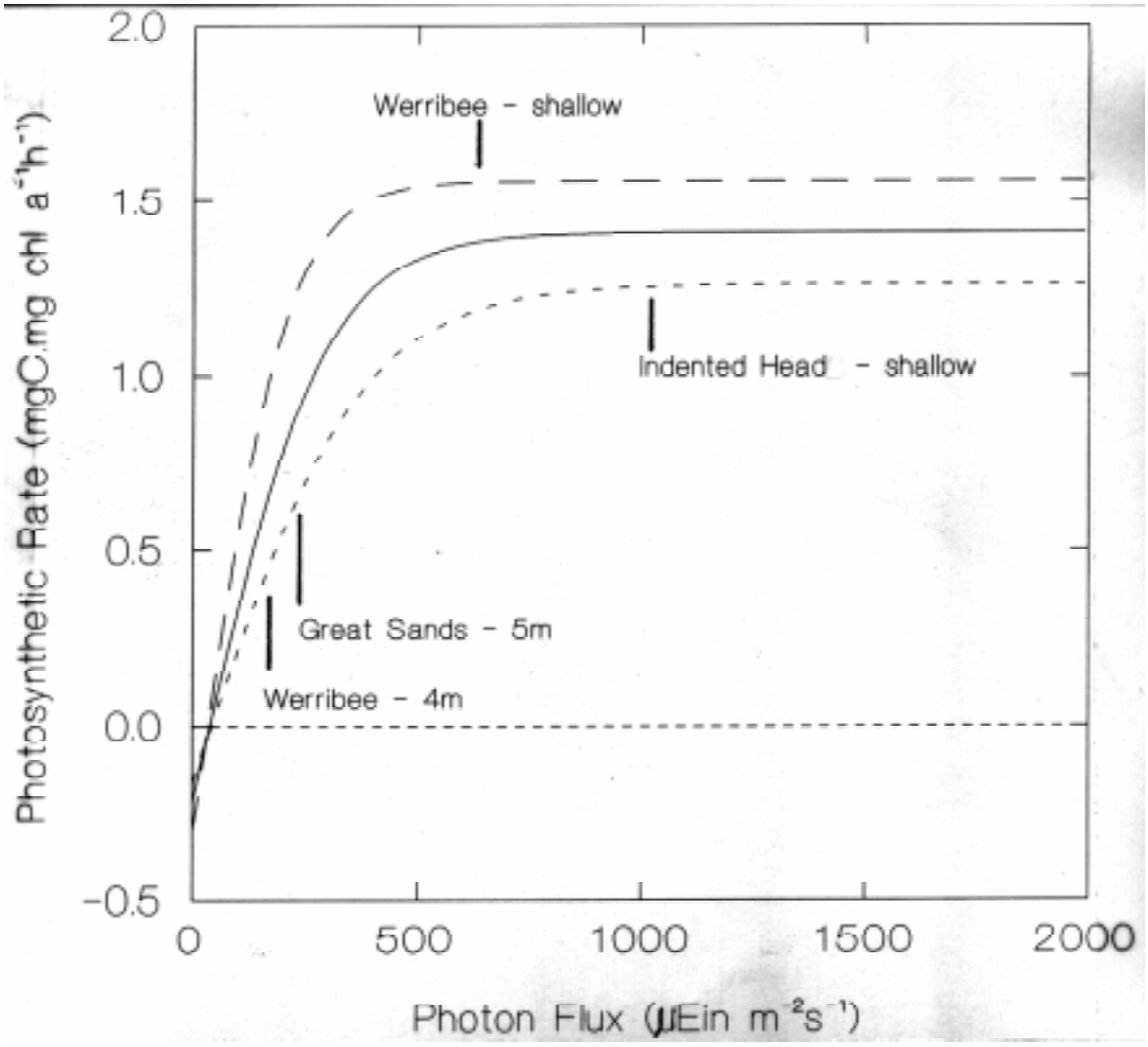

Figure 3. Photosynthesis as a function of photon flux as determined from the mean values (—) of the photosynthetic parameters given in Table 2. Curves marked (-----) and (– – –) represent values calculated ± the standard errors quoted in Table 2. *In situ* photon fluxes measured at a number of sites in Port Phillip Bay during August 1994 are shown for comparison. Clearly, the shallow sites at Weribbee and Indented Head are saturated and less likely to be affected by seasonal variation in light availability than the deeper sites.

3.2. Estimates of MPB Primary Productivity

3.2.1 Rates of primary productivity

World-wide values for primary productivity in various sub-tidal marine, sub-tidal estuarine, intertidal marine and intertidal estuarine environments are summarised in Tables A5 to A8 respectively. Values range from 1 mgC m^{-2} h^{-1} (Colijn & deJonge 1984) to 276 mgC m^{-2} h^{-1} (Daehnick et al. 1992). Mean values from each of these environments are presented in Table 3.

Table 3: Gross primary productivity of MPB from various marine environments. Data are abstracted from Tables A5 to A8. Units are mgC m^{-2} h^{-1} (n = number of estimates).

	Sub-tidal Marine n=14	**Sub-tidal Estuarine n=12**	**Intertidal Marine n=3**	**Intertidal Estuarine/saltmarsh n=14**
Minimum	2.1	10	23	1
Maximum	276	178	75	120
Mean (s.d.)	59(72)	65 (57)	49 (26)	48 (33)

As with biomass, there appear to be no consistent trends in productivity between the different environments (Figure 4) or at different latitudes (Figure 5).

Published studies of MPB in Port Phillip Bay are limited to the single investigation by Axelrad et al. (1979) who reported gross productivity rates ranging from 290 to 1060 mgC m^{-2} d^{-1}. These rates represent the higher end of the range for global MPB populations presented in Tables A5 to A8. Our preliminary studies in Port Phillip Bay of the photosynthetic capacity of resuspended sediments, give light saturated rates of photosynthesis to 600 mgC m^{-2} h^{-1}, which is well in excess of those of Axelrad et al. (1979) and most of those in Tables A5 to A8. However, it must be noted that our data are likely to be higher than those of previous studies because they represent resuspended sediments rather than intact cores. In the latter, due to shading, a smaller proportion of the population would be exposed to light. Other studies involving intact sediment cores, currently in progress, have resulted in rates of up to 80 mgC m^{-2} h^{-1} for Indented Head and 160 mgC m^{-2} h^{-1} for Werribee.

The effects of environmental factors on rates of primary productivity of MPB are discussed in Section 5.

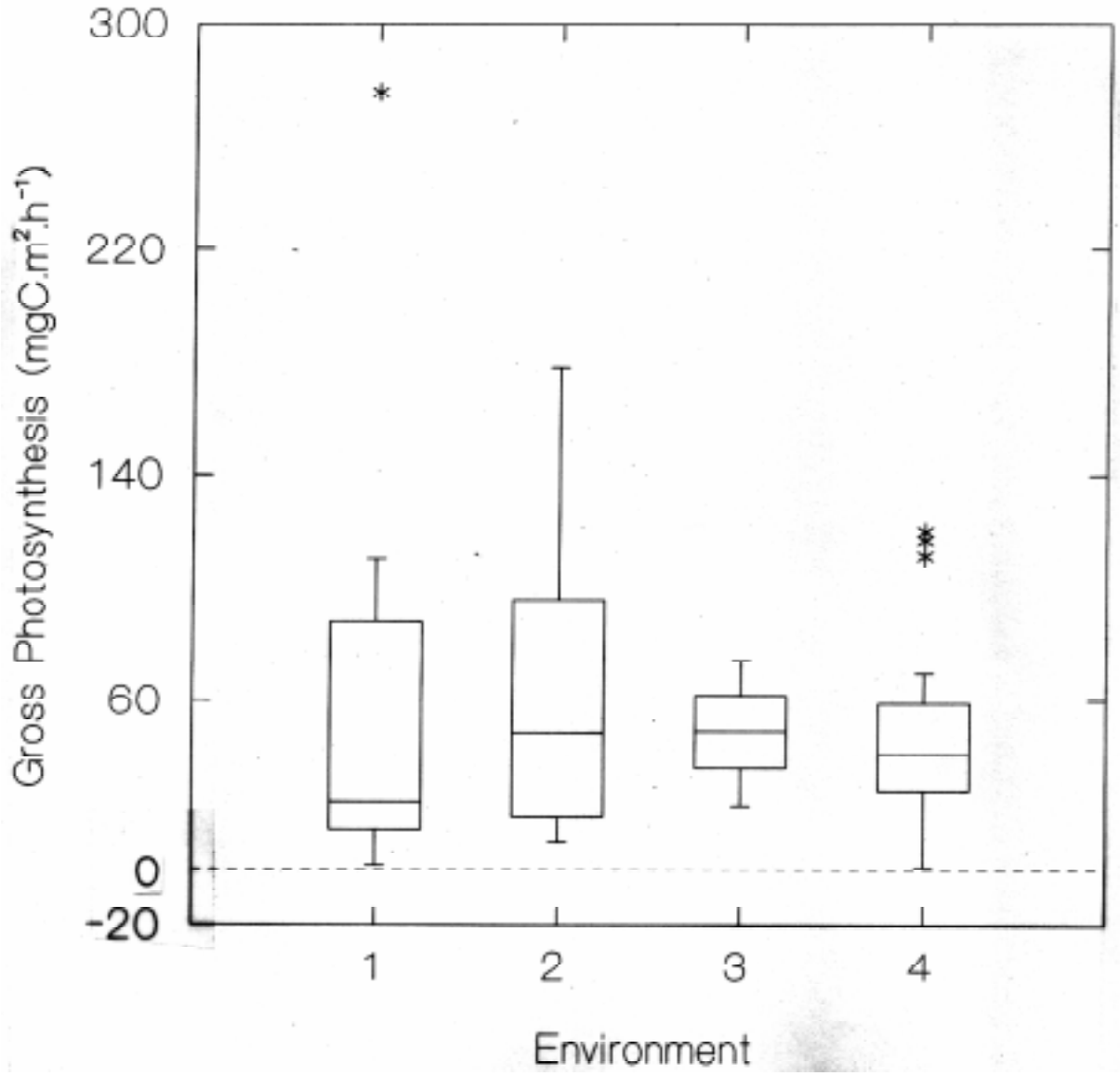

Figure 4. Values of microphytobenthos productivity (expressed as $mgC.m^{-2}.h^{-1}$) in different environments. Key to Environments: 1 = Subtidal marine; 2 = Subtidal estuarine; 3 = Intertidal marine; 4 = Intertidal estuarine. Values are expressed as box plots where the central horizontal line box is the median value and the top and bottom of the box represents the 75 and 25 percentiles respectively. The lines above and below the box represent values within the range 1.5x that within the box. Values represented as "*" are outliers and those shown by "o" are extreme outliers.

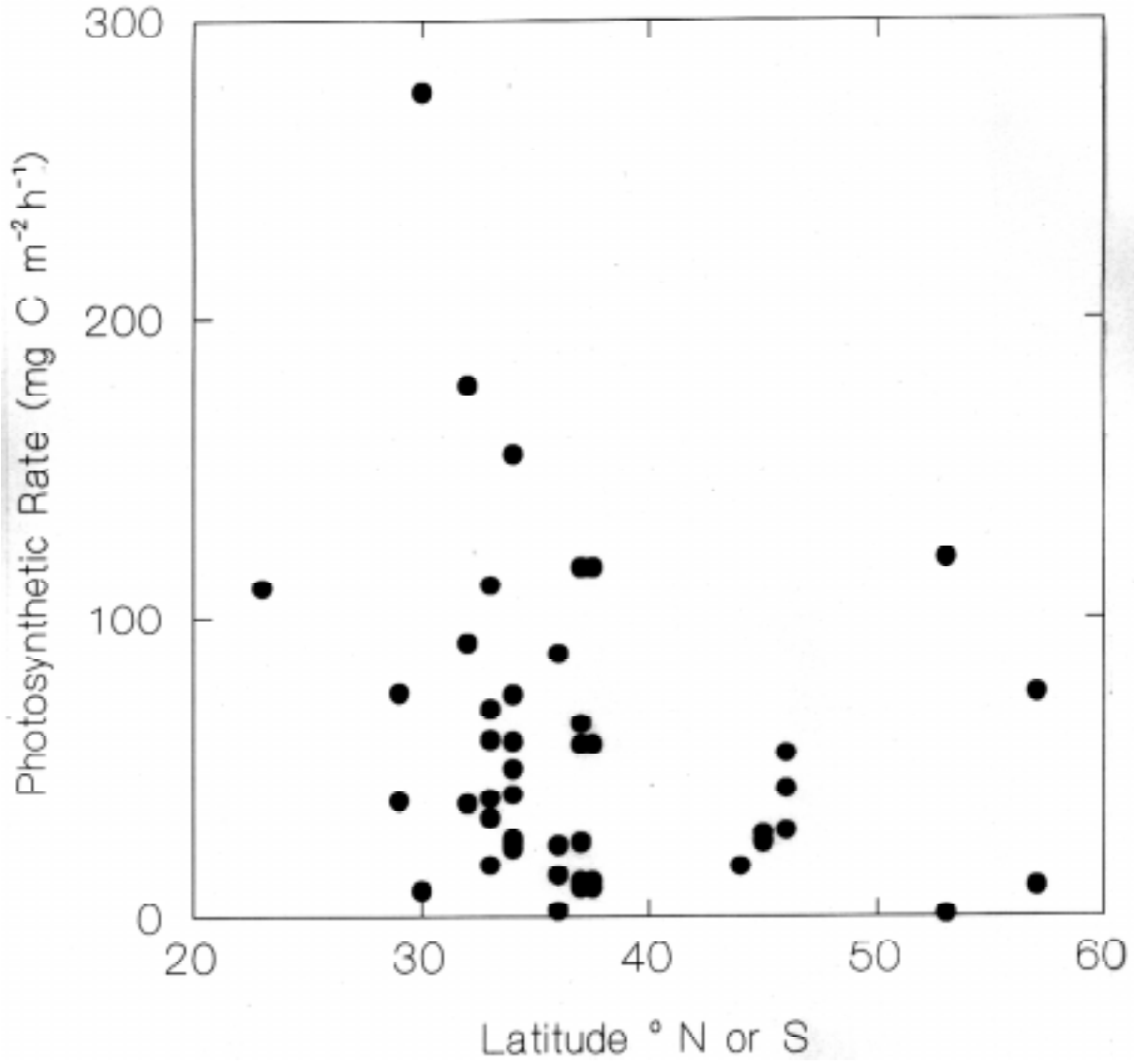

Figure 5. Distribution of MPB biomass (expressed as $mgC.m^{-2.}.h^{-1}$)) as a function of latitude.

3.2.2. Annual production by MPB

The MPB can make a significant contribution to the overall carbon budget of shallow marine environments. For instance, the study by Walker et al. (1988) estimated that MPB could contribute up to 6% of the total annual primary production in shallow waters surrounding Rottnest Island in Western Australia. A mean value of 135 gC $m^{-2}y^{-1}$ for various MPB populations worldwide (Table 4) represents an approximate three fold increase on the estimates for oceanic phytoplankton (Morris 1974). In coastal systems the corresponding overall value for phytoplankton has been estimated at 100 gC m^{-2} y^{-1} (Morris 1974) with higher values generally being recorded in estuarine ecosystems. Data presented by Pinckney & Zingmark (1993a) indicate that the contributions of MPB, phytoplankton, macroalgae and *Spartina* to overall system production in North Inlet, South Carolina (33^{o} N) were 22-38%, 15-27%,10-17% and 30-59% respectively.

4. EFFECTS OF MICROPHYTOBENTHOS ON NUTRIENT EXCHANGE BETWEEN SEDIMENTS AND THE OVERLYING WATER COLUMN

Few studies in the literature allow a critical, quantitative assessment of the effects of microphytobenthos on nutrient fluxes across the sediment/water interface. A number of authors (e.g. Rizzo 1990) report that nutrient exchange in dome experiments is different between darkened and illuminated domes although little attempt is made to quantify rates of uptake attributable to microphytobenthos. Typically however, release of dissolved inorganic nitrogen, phosphorus and silicate to the water column has been shown to be decreased by autotrophic activity in the sediments (Graneli & Sundbäck 1985; Kelderman et al. 1988; Rizzo 1990; Sundbäck et al. 1991).

The most detailed and thorough studies of the interaction between microphytobenthos and nutrient exchange are those of Sundbäck and her colleagues (Graneli & Sundbäck 1985, Sundbäck et al. 1991). These clearly show the contribution of light-dependent microphytobenthic metabolic activity to nutrient fluxes between sediments and the overlying water column. Data from these and other studies are summarised in Table 5.

Values range from 27 to more than 200 mol $N.m^{-2}.h^{-1}$ and from 1.0 to 27 mol $P.m^{-2}.h^{-1}$, the range presumably being linked in part to differences in microalgal biomass (although chlorophyll values are not given in every case) and also to temperature and depth variations between studies.

Table 4. Estimates of annual production by MPB from different localities. Values are for net production except for the data of Pinckney & Zingmark (1993a) which are expressed as gross production.

Location	Annual Production ($g\ C\ m^{-2}\ y^{-1}$)	Reference
Danish Fjords (55ºN)	231	Grøntved (1960)*
Danish Wadden Sea (55ºN)	571-892	Grøntved (1962)*
Loch Ewe Scotland (58ºN)	4-9	Steele and Baird (1968)
Ythan estuary Scotland (57ºN)	31	Leach (1970)
Chuchi Sea USA (71ºN)	5	Matheke and Horner (1974)
Falmouth Bay USA (41ºN)	106	van Raalte et al. (1976)
Balgzand, Wadden Sea (53ºN)	85	Cadee and Hegeman (1977)
Madagascar (13ºS)	66-150	Plante-Cuny (1978)
Wadden Sea Netherlands (53ºN)	58-177	Cadee (1980)
Port Phillip Bay Victoria (38ºS)	46-236	Axelrad et al. (1981)
Port Hacking, New South Wales (34ºS)	46-65	Giles (1983)
False Bay USA (48ºN)	143-226	Pamatmat (1968)
Ems-Dollard estuary (53ºN)	69-314	van Es (1982)
Netarts Bay Oregon (45ºN)	21-53	Davis and McIntire (1983)
Bay of Fundy Canada (45ºN)	47-83	Hargrave et al. (1983)
Columbia River estuary (45ºN)	72	McIntire and Amspoker (1986)
Swan River estuary WA (32ºS)	109	Masini (1990)
Peel Harvey estuary WA (32ºS)	46-206	Masini (1990)
North Inlet, South Carolina (33ºN)	56-234	Pinckney & Zingmark (1993b)
Sylt, Germany (55º N)	115	Asmus (1982)
Ems-Dollard, The Netherlands (53ºN)	50-250	Colijn and de Jonge (1984)
Dutch Wadden Sea (53ºN)	101	Cadee and Hegeman (1974)
Ria de Arosa, Spain (42º N)	79	Varela and Penas (1985)
Graveline Bay, Mississippi (30º N)	28-151	Sullivan and Moncreiff (1988)
Bolsa Bay, California (34ºN)	115-246	Riznyk et al. (1978)
Southern New England (41ºN)	81	Marshall et al. (1971)*
Lynher River, England (50ºN)	143	Joint (1987)
Lewes, Delaware (39º N)	79-99	Gallagher and Daiber (1974)
Langebaan, South Africa (33ºS)	63-253	Fielding et al. (1988)
Southern Baltic Sea (58º N)	75	Wasmund (1986)
Mugu Lagoon, California (34º N)	170	Shaffer and Onuf (1985)
Boston, Massachusetts (42º N)	250	Gould and Gallagher (1990)
Sapelo Island, Georgia (31ºN)	200	Pomeroy (1959)
		(* Cited in Colijn and de Jonge, 1984)

Table 5. Available data on rates of primary productivity and N and P fluxes attributable to photoautotrophic activity in sediments. (Figures in parentheses are the fluxes relative to P,which is set at 1.0).

C Assimilation (mol. $m^{-2}.h^{-1}$)	**N uptake by MPB** (mol. $m^{-2}.h^{-1}$)	**P uptake by MPB** (mol. $m^{-2}.h^{-1}$)	**Reference**
244 (152)	57 (36)	1.6 (1)	Sundbäck et al. 1991 (mud)
215 (215)	27 (27)	1.0 (1)	Sundbäck et al. 1991 (sand)
3438 (128)	Not measured	26.9 (1)	Kelderman et al. 1988
1570 (109)	225 (16)	14 (1)	Walker et al. 1988
544 (155)	130 (37)	3.5 (1)	Rizzo 1990

The data in Table 5 can be used to derive approximate values for nutrient use by MPB. From these studies, the mean value for C:N:P flux ratio in benthic microalgae is calculated to be 152:29:1. This has slightly higher C:P and N:P ratios than the Redfield ratio of 106:16:1 commonly quoted for composition of phytoplankton, but seems closer to real values for nutrient fluxes *in situ*. Using this ratio and the values for primary productivity (C flux) from Table 2, values for N and P fluxes attributable to MPB may be derived. Thus, for a mean C assimilation rate of 55 mg C m^{-2} h^{-1} (4604 mol C m^{-2} h^{-1}; see Table 3), fluxes for N and P of 159 mol N m^{-2} h^{-1} and 30.3 mol P m^{-2} h^{-1} are obtained. Alternatively, the mean assimilation number for MPB (Table 2) of 1.41 mg C mg chl^{-1} h^{-1} translates into 22.5 mol N mg chl^{-1} h^{-1} and 0.8 mol P mg chl^{-1} h^{-1}. A mean functional chlorophyll *a* content in Port Phillip Bay of 19 mg m^{-2} (Light, Beardall and Black, unpublished) in turn can be converted into mean potential N and P fluxes of 428 mol N m^{-2} h^{-1} and 15 mol P m^{-2} h^{-1}. The foregoing analysis must, of necessity, be approximate and ignores non-biological effects of MPB on nutrient flux effected by changes in the redox potential of the sediments (Nixon 1981).

Graneli & Sundbäck (1985) estimated that microphytobenthos assimilated approximately 40-60% of the inorganic nitrogen supplied to their experimental cores (1-1.5 mmol $N.m^{-2}$ d^{-1}). Sediments typically also supply 16-35% and 25-53% of the requirements of phytoplankton for N and P respectively (Callender & Hammond 1982; Fisher et al. 1982; Hopkinson & Wetzel 1982; Rizzo 1990).

5. ENVIRONMENTAL FACTORS CONTROLLING MPB DISTRIBUTION AND PRODUCTIVITY

The following is intended as a summary of the major correlations between environmental factors and MPB biomass and productivity. Full details are given in Section 7 (Tables A1-A8).

5.1. Depth (Light availability)

Whilst some studies have been unable to demonstrate a clear correlation between depth and MPB biomass or productivity, a large number of authors have reported a strong negative relationship between biomass and various factors limiting light availability. For instance, depth in the water column has been shown to be negatively correlated with MPB biomass (Cahoon et al. 1990; Cahoon et al. 1992; Delgado 1989; Lukatelich & McComb 1986; Sundbäck 1984). Furthermore, all studies which have examined the relationship between MPB distribution within the sediment have shown a marked decrease in biomass with increasing depth in the sediment. Water turbidity was noted as a controlling factor in the studies of Masini (1990) and Pinckney & Zingmark (1993a, 1993c), and density of the overlying macrophyte canopy influenced MPB biomass in the study by Daehnick et al. (1992).

Pinckney & Zingmark (1993c) and Schaffer & Onuf (1983) have presented evidence that seasonal variation in MPB production is affected by total sunlight availability and water turbidity. Kristensen (1993) reported that seasonal changes in MPB production could be explained primarily by seasonal changes in daylength and temperature. In the study by Pinckney & Zingmark (1993c), turbidity in the area was affected mainly by phytoplankton population density. Hence there can be interactions between the productivity of phytoplankton and that of benthic microalgae.

5.2. Sediment type

A positive correlation between grain size and MPB biomass was reported by Sundbäck (1984), Lukatelich and McComb (1986), Masini (1987) and Riznyk et al. (1978) whilst, by contrast, Shaffer and Onuf (1983) noted that sediments with smaller grain size harboured greater biomass.

Grain size affects sediment mobility and hence the ability of MPB to be resuspended into the water column. A negative correlation has been reported between mobility and MPB biomass (Plante et al. 1986). Not surpisingly, physical exposure has proved to be of importance (Fielding et al. 1988; LeGuellec & Bodin 1992) and it has been noteworthy that one of the Port Phillip Bay transect sites (Carrum), in which the shallow sediments are frequently disturbed, has repeatedly shown much lower MPB productivity than other areas (Light & Beardall unpublished).

Sundbäck et al. (1991) reported that muddy sediments had 2.5 times the chlorophyll content and cell density of sandy sediments although net productivity was not significantly different between the two sediment types.

5.3. Nutrient availability

A number of studies have shown a strong positive relationship between enhanced nutrient input and MPB biomass (Axelrad et al. 1979; Flothmann & Werner 1992; Graneli & Sundbäck 1985; Lukatelich & McComb 1986; Riznyk et al. 1978; Vilbaste 1992). Fewer investigations have reported enhanced MPB productivity by higher nutrient levels and Sundbäck (1983) reported a negative correlation between biomass and inorganic N concentration. Although Axelrad et al. (1979) correlated differences in productivity between Werribee and Portarlington with levels of inorganic N and P, there are insufficient data to determine the general likelihood of nutrient limitation of MPB in Port Phillip Bay.

5.4. Seasonality in MPB biomass and/or production

There appears be a lack of universal seasonality for MPB biomass and productivity in the published literature.

For instance Pinckney and Zingmark (1993b) showed that monthly production rates by MPB in intertidal sandflats and shallow sub-tidal habitats in Northern Inlet, South Carolina, were fairly constant over the year. However, in mudflats and within *Spartina* beds, peaks in MPB biomass and production were evident in late winter/early spring. In other studies, peaks in biomass and/or productivity have been observed in spring (Gallagher & Daiber 1974; Rizynk et al. 1978; Sullivan & Moncrieff 1988), summer (Axelrad et al. 1979; Daehnick et al. 1992; Kristensen 1993), winter (Kristensen 1993; Masini 1990; Plante-Cuny 1973) or autumn (Plante et al. 1986; Sundbäck 1983). In some studies, peaks have been observed in more than one season (Davis & McIntire 1983; Riznyk et al. 1978). In many instances however, seasonal variation can be minor (McIntire & Amspoker 1986; Rizzo & Wetzel 1985; Sundbäck & Jonsson 1988).

Seasonal variation would be expected from a number of (possibly interacting) factors including temperature (Daehnick et al. 1992; Kristensen 1993; Masini 1990), total sunlight availability and water turbidity (Pinckney & Zingmark 1993a) or daylength (Kristensen 1993).

6. COMMENTS ON TECHNIQUES APPLICABLE TO STUDIES OF MICROPHYTOBENTHOS COMMUNITIES

The aim of this section is to identify problems associated with methodologies applied to various aspects of the study of MPB. Some of these problems involve technique, others experimental design and recognition of the natural heterogeneity of MPB populations.

6.1. Spatial heterogeneity in MPB populations

With several notable exceptions (e.g. Masini 1990), many of the studies on MPB have taken single cores or effected dome deployments without consideration of the spatial variability of MPB populations. However, the small scale (several metres) variation in biomass and productivity can be marked (Schaffer & Cahoon 1987; Schaffer & Onuf 1895). Future studies into aspects of the biology of MPB must take such variability into consideration when planning both experimental and descriptive work.

6.2. Biomass

Most studies into the biomass of MPB populations have used chlorophyll *a* as the index of microalgal biomass. However, there are a range of techniques for chlorophyll analysis from sediments and an equal number of equations used to determine chlorophyll *a* concentration in extracts. Of major importance in regard to MPB is the issue of whether measurements take into account the amount of degraded chlorophyll (usually pheophytin) in the sediments. Since, because of the large proportion of detrital plant matter in sediments, chlorophyll *a* to pheophytin ratios can be as low as 0.06 (Masini 1990) and are frequently 1, techniques which do not differentiate between chlorophyll *a* and pheopigment could significantly overestimate MPB biomass. This is one possible reason why assimilation numbers for MPB are frequently less than those for phytoplankton (Section 3.1).

Spectrophotometric techniques exist that determine pheophytin levels following acidification of pigment extracts (e.g. Whatley & Darley 1979). These have recently been shown to overestimate chlorophyll *a* concentrations by 16% (Pinckney et al. 1994) when compared to HPLC techniques. However, such overestimation was consistent across all samples examined.

6.3. Primary productivity

A number of techniques have been applied to the measurement of MPB primary productivity. There are certain advantages and disadvantages associated with each. This section attempts to provide a brief overview of the available methodologies.

Incorporation of ^{14}C-HCO_3^-

Some studies have measured primary productivity of MPB by incubation of cores with radioactively labelled bicarbonate and calculating productivity from ^{14}C incorporated into organic matter. Whilst this technique is relatively simple and is inexpensive to conduct, the problem of uneven diffusion of ^{14}C-bicarbonate throughout the core must be recognised. This can lead to inaccuracy in estimating the specific activity of the label and hence in determining true rates of inorganic C assimilation. This can be compounded by an inability to correct for CO_2 released from the sediments by benthic respiration. In an attempt to overcome this problem, several studies have distributed the radioactive label into a sediment slurry. This of course destroys the integrity of the cores and exposes the MPB to a totally unrealistic light environment.

The technique does have the advantage that experiments can be conducted *in situ*, although problems of environmental contamination arise. *In situ* experiments are particularly prone to the problems outlined above (Masini pers. comm.; Beardall unpublished observations).

O_2-microelectrodes

These are very useful for examining small-scale distribution of photosynthetic capacity and characteristics within sediments. They have the advantage of being able to measure photosynthesis within the surface layers of sediments that receive most of the the light incident on sediments. Concomitant measurements of light penetration enable the actual relationship between *in situ* photosynthesis and irradiance to be determined. However, the techniques involved can be difficult to standardise and the time taken to process each core could raise difficulties in processing the large number of replicate cores necessary to achieve statistically valid data sets.

Oxygen sensors / probes

O_2 based measurements using intact cores have been used in a number of studies (e.g. Masini 1990). Generally these involve measurements of oxygen concentration in water overlying the sediment. Whilst these techniques cannot provide the spatial resolution of microelectrodes, they do have the advantages of being able to rapidly examine the relationship between incident irradiance and photosynthesis in intact cores. Appropriate design of incubation chambers allows multiple cores to be incubated together, thereby making allowance for spatial heterogeneity of MPB populations.

Oxygen electrodes deployed within domes incubated on the sediment have frequently been used. This approach has the benefit of examining whole community responses to light and other environmental variables. It is still susceptible to problems with the heterogeneity of MPB populations unless multiple dome deployments are made at each site. The technique can also be more expensive, requiring increased vessel time and data logging equipment.

7. BIBLOGRAPHY

Asmus, R., (1982). Field measurements on seasonal variation of the activity of primary producers on a sandy tidal flat in the northern Wadden Sea. *Netherlands Journal of Sea Research*, **16**: 389-402.

Axelrad, D.M., Hickman, N.J., Gibbs, C.F., (1979). Microalgal productivity as affected by treated sewage discharge to Port Phillip Bay. Port Phillip Bay Environmental Study Werribee Project (PO1), Environmental Studies Series No. 241. Ministry for Conservation, Victoria.

Axelrad, D.M., Poore, G.C.B., Arnott, G.H., Bauld, J., Brown, V., Edwards, R.R.C. and Hickman, N.J., (1981). The effects of treated sewage discharge on the biota of Port Phillip Bay, Victoria, Australia. In. *Estuaries and Nutrients*. (eds B.J. Neilson and L.E. Cronin), pp 279-306. Humana Press, Clifton, New Jersey.

Bjork-Ramburg, S., (1983). Production of epipelic algae before and during lake fertilisation in a subarctic lake. *Holarctic Ecology*, **6**: 349-55.

Blanchard, G.F. and Montagna, P.A., (1992). Photosynthetic response of natural assemblages of marine benthic microalgae to short- and long-term variations of incident irradiance in Baffin Bay, Texas. *Journal of Phycology*, **28**: 7-14.

Burford, M.A., Long, B.G. and Rothlisberg, P.C., (1994). Sedimentary pibments and organic carbon in relation to microalgal and benthic faunal abundance in the Gulf of Carpentaria. *Marine Ecology Progress Series*, **103**: 111-7.

Cadee, G.C., (1980). Reappraisal of the production and import of organic carbon in the western Wadden Sea. *Netherlands Journal of Sea Research*, **14**: 305-22.

Cadee, G. and Hegeman, J., (1974). Primary production of the benthic microflora living on tidal flats in the Dutch Wadden Sea. *Netherlands Journal of Sea Research*, **8**: 260-91.

Cadee, G. and Hegeman, J., (1977). Distribution of primary production of the benthic microflora and accumulation of organic matter on the tidal flat area, Balgzad, Dutch Wadden Sea. *Netherlands Journal of Sea Research*, **11**: 24-41.

Cahoon, L.B., Beretich, G.R., Thomas, C.J. and McDonald, A.M., (1993). Benthic microalgal production at Stellwagen Bank, Massachusetts Bay, USA. *Marine Ecology Progress Series*, **102**: 179-85.

Cahoon, L.B. and Cooke, J.E., (1992). Benthic microalgal production in Onslow Bay, North Carolina, USA. *Marine Ecology Progress Series*, **84**: 185-96.

Cahoon, L.B. and Laws, R.A., (1993). Benthic diatoms from the North Carolina continental Shelf: inner and mid shelf. *Journal of Phycology*, **29**: 257-63.

Cahoon, L.B., Laws, R.A. and Savidge, T.W., (1992). Characteristics of benthic microalgae from the north Carolina outer continental shelf and slope: preliminary results. In: *Diving for Science*, (ed. L.B. Cahoon), pp. 61-7. Proceedings of the American Academy of Underwater Sciences, Costa Mesa, California.

Cahoon, L.B., Redman, R.S., and Tronzo, C.R., (1990). Benthic microalgal biomass in sediments of Onslow Bay, North Carolina. *Estuarine, Coastal Shelf Science*, **31**: 805-16.

Callender, E. and Hammond, D.E., (1982). Nutrient exchange across the sediment-water interface in the Potomac River estuary. *Estuarine, Coastal Shelf Science*, **15**: 395-413.

Colijn, F. and de Jonge, V.N., (1984). Primary production of microphytobenthos in the Ems-Dollard Estuary. *Marine Ecology Progress Series*, **14**: 185-96.

Daehnick, A.E., Sullivan, M.J. and Moncreiff, C.A., (1992). Primary production of the sand microflora in seagrass beds of Mississippi Sound. *Botanica Marina*, **35**: 131-39.

Davis, M.W. and McIntire, C.D., (1983). Effects of physical gradients on the production dynamics of sediment-associated algae. *Marine Ecology Progress Series*, **13**: 103-14.

Delgado, M., (1989). Abundance and distribution of microphytobenthos in the bays of Ebro Delta (Spain). *Estuarine, Coastal Shelf Science*, **29**: 183-94.

Falkowski, P.S., (1981). Light-shade adaptation and assimilation numbers. *Journal of Plankton Research*, **3**: 203-15.

Fielding, P.J., Damstra, K.St.J. and Branch, G.M., (1988). Benthic diatom biomass, production and sediment chlorophyll in Langebaan Lagoon, South Africa. *Estuarine, Coastal Shelf Science*, **27**: 413-26.

Fisher, T.R., Carlson, P.R. and Barber, R.T., (1982). Sediment nutrient regeneration in three North Carolina estuaries. *Estuarine and Coastal Marine Science*, **14**: 101-16.

Flothmann, S., and Werner, I., (1992). Experimental eutrophication of an intertidal sandflat: effects on microphytobenthos, meio- and macrofauna. In: *Marine Eutrophication and Population Dynamics*, (eds G. Colombo *et al.*), pp. 93-100. Proceedings of the 25th EMBS. Olsen and Olsen, Fredensborg, Denmark.

Gallagher, J. and Daiber, F., (1974). Primary production of edaphic algal communities in a Delaware salt marsh. *Limnology and Oceanography*, **19**: 390-5.

Giles, M.S., (1983). Primary production of benthic micro-organisms in the South West Arm, Port Hacking, New South Wales. In *Synthesis and Modelling of Intermittent Estuaries*, (eds W.R. Cuff and M. Tomczac), pp147-66. Lecture Notes on Coastal and Estuarine Studies, Volume 3. Springer-Verlag, Berlin.

Glover, H.E., (1980). Assimilation numbers in cultures of marine phytoplankton. *Journal of Plankton Research*, **2**: 69-79.

Gould, D. and Gallagher, E., (1990). Field measurements of specific growth rate, biomass and primary production of benthic diatoms of Savin Hill Cove, Boston. *Limnology and Oceanography*, **35**: 1757-70.

Graneli, E. and Sundbäck, K., (1985). The response of planktonic and microbenthic algal assemblages to nutrient enrichment in shallow coastal waters, southwest Sweden. *Journal of Experimental Marine Biology and Ecology*, **85**: 253-68.

Grant, J., (1986). Sensitivity of benthic community respiration and primary production to changes in temperature and light. *Marine Biology*, **90**: 299-306.

Hargrave, B., Prouse, N., Phillips, G. and Neame, P., (1983). Primary production and respiration in pelagic and benthic communities at two intertidal sites in the upper Bay of Fundy. *Canadian Journal of Fisheries and Aquatic Science*, **40**: 229-43.

Hopkinson, C.S. and Wetzel, R.L., (1982). *In situ* measurements of nutrient and oxygen fluxes in a coastal marine benthic community. *Marine Ecology Progress Series*, **10**: 29-35.

Jobson, D.J., Zingmark, R.G. and Katzberg, S.J., (1980). Remote sensing of benthic microalgal biomass with a tower-mounted multispectral scanner. *Remote Sensing of Environment*, **9**: 351-62.

Joint, I.R., (1978). Microbial production of an estuarine mudflat, *Estuarine and Coastal Marine Science*, **7**:185-95.

Kelderman, P., Lindeboom, H.J., and Klein, J., (1988). Light dependent sediment-water exchange of dissolved reactive phosphorus and silicon in a producing microflora mat. *Hydrobiologia*, **159**: 137-47.

Kristensen, E., (1993). Seasonal variations in benthic community metabolism and nitrogen dynamics in a shallow, organic-poor Danish Lagoon. *Estuarine, Coastal Shelf Sciences*, **36**: 565-86.

Leach, J.H., (1970). Epibenthic algal production in an intertidal mudflat. *Limnology and Oceanography*, **15**: 514-21.

Le Guellec, C. and Bodin, P., (1992). Meiobenthos of the Bay of Saint-Brieuc (North Brittany, France). I.: quantitative distribution in subtidal and intertidal zones. *Oceanologica Acta*, **15**: 661-71.

Light, B.R. and Woelkerling, W.J., (1992). Literature and information review of the benthic flora of Port Phillip Bay. Technical Report No. 6, CSIRO Port Phillip Bay Environmental Study, Melbourne.

Lukatelich, R.J. and McComb, A.J., (1986). Distribution and abundance of benthic microalgae in a shallow southwestern Australian estuarine system. *Marine Ecology Progress Series*, **27**: 287-97.

Madsen, K., Nilsson, P. and Sundback, K., (1993). The influence of benthic microalgae on the stability of a subtidal sediment. *Journal of Experimental Marine Biology and Ecology*, **170**: 159-177.

Masini, R.J., (1987). Preliminary studies on the productivity of benthic microalgae in the Swan River Estuary. In: *The Swan River Estuary Ecology and Management*, (ed. Jacob John), pp 91-101. Proceedings of a symposium on the Swan-Canning River Estuarine System, Western Australia, Perth, 10-11 October 1986.

Masini, R.J., (1990). The ecological significance of benthic microalgae in Western Australian aquatic ecosystems. Ph.D thesis, University of Western Australia, 194 pp.

Matheke, G.E.M. and Horner, R., (1974). Primary productivity of the benthic algae in the Chukchi Sea near Barrow, Alaska. *Alaskan Journal of Fisheries Research Board, Canada*, **31**: 1779-86.

McIntire, C.D. and Amspoker, M.C., (1986). Effects of sediment properties on benthic primary production in the Columbia River estuary. *Aquatic Botany*, **24**: 249-67.

Mills, D.K. and Wilkinson, M., (1986). Photosynthesis and light in estuarine benthic microalgae. *Botanica Marina*, **29**: 125-9.

Moncreiff, C.A., Sullivan, M.J. and Daehnick, A.E., (1992). Primary production dynamics in seagrass beds of Mississippi Sound: the contributions of seagrass, epiphytic algae, sand microflora, and phytoplankton. *Marine Ecology Progress Series*, **87**: 161-71.

Morris, I., (1974). The limits to the primary productivity of the sea. *Science Progress Oxford*, **61**: 99-122.

Nienhuis, P.H. and DeBree, B.H.H., (1984). Carbon fixation and chlorophyll in bottom sediments of the brackish lake Grevelingen, the Netherlands. *Netherlands Journal of Sea Research*, **18**: 337-359.

Nixon, S.W. (1981). Remineralisation and nutrient cycling in coastal marine ecosystems. In: *Estuaries and Nutrients*, (eds B.J. Neilson and L.E. Cronin), pp. 111-38. Humana Press, New Jersey.

Page, H.M., Dugan, J.E. and Hubbard, D.M., (1992). Comparative effects of infaunal bivalves on an epibenthic microalgal community. *Journal of Experimental Marine Biology and Ecology*, **157**: 247-62.

Pamatmat, M.M., (1968). Ecology and metabolism of a benthic community on an intertidal sandflat. *Internationale Revue der Gesamten Hydrobiologie*, **53**: 211-98.

Paterson, D.M., Crawford, R.M. and Little, C. (1990). Subaerial exposure and changes in the stability of intertidal estuarine sediments. *Estuarine, Coastal Shelf Sciences*, **30**: 541-56.

Pinckney, J. and Zingmark, R.G., (1993a). Modelling the annual production of intertidal benthic microalgae in estuarine ecosystems. *Journal of Phycology*, **29**: 396-407.

Pinckney, J. and Zingmark, R.G., (1993b). Biomass and production of benthic microalgal communities in estuarine habitats. *Estuaries*, **16**(4): 887-97.

Pinckney, J. and Zingmark, R.G., (1993c). Photophysiological responses of intertidal benthic microalgal communities to *in situ* light environments: methodological considerations. *Limnology and Oceanography*, **38**(7): 1373-83.

Plante, R., Plante-Cuny, M. and Reys, J., (1986). Photosynthetic pigments of sandy sediments on the north Mediterranean coast: their spatial distribution and its effect on sampling strategies. *Marine Ecology Progress Series*, **34**: 133-41.

Plante-Cuny, M.R., (1973). Recherches sur la production primaire benthique en milieu marin tropicale. *Cahiers O.R.S.T.O.M. Serie Oceanographie*, **11**: 317-48.

Plante-Cuny, M.R., (1978). Pigments phytosynthetiques et production primaire de fonds meubles neritiques d'une region tropicale (Nosy-Be, Madagascar). *Travaux et Documents de l'O.R.S.T.O.M.*, **96**: 1-359.

Plante-Cuny, M., Salen-Picard, C., Grenz, C., Plante, R., Alliot, E. and Barranguet, C., (1993). Experimental field study of the effects of crude oil, drill cuttings and natural biodeposits on microphyto- and macrozoobenthic communities in a Mediterranean area. *Marine Biology*, **117**: 355-66.

Pollard, P.C. and Kogure, K., (1993). The role of epiphytic and epibenthic algal productivity in a tropical seagrass, *Syringodium isoetifolium* (Aschers.) Dandy, community. *Australian Journal of Marine and Freshwater Research*, **44**: 141-54.

Pomeroy, L.R., (1959). Algal productivity in salt marshes of Georgia. *Limnology and Oceanography*, **4**: 386-97.

Pomeroy, L.R., Darley, W.M., Dunn, E.L., Gallagher, J.L., Haines, E.B., Whitney, D.M. (1981). Primary production. In. *The Ecology of a Salt Marsh*. (eds L.R. Pomeroy and R.G. Wiegert), pp 39-68. Ecological Studies 38. Springer-Verlag, New York.

Rasmussen, M.B., Henriksen, K. and Jensen, A., (1983). Possible causes of temporal fluctuations in primary production of the microphytobenthos in the Danish Wadden Sea. *Marine Biology*, **73**: 109-114.

Richardson, K., Beardall, J. and Raven, J.A., (1983). Adaptation of unicellular algae to irradiance: an analysis of strategies. *New Phytologist*, **93**: 157-91

Riznyk, R.Z., Edens, J.I. and Libby, R.C., (1978). Production of epibenthic diatoms in a southern California impounded estuary. *Journal of Phycology*, **14**: 273-79.

Rizzo, W.M. and Wetzel, R.L., (1985). Intertidal and shoal benthic community metabolism in a temperate estuary: studies of spatial and temporal scales of variability. *Estuaries*, **8**(4): 342-51.

Rizzo, W.M., (1990). Nutrient exchanges between the water column and a subtidal benthic microalgal community. *Estuaries*, **13**(3): 219-26.

Shaffer, G.P., (1988a). K-systems analysis for determining the factors influencing benthic microfloral productivity in a Louisiana estuary, USA. *Marine Ecology Progress Series*, **43**: 43-54.

Shaffer, G.P. and Cahoon, P., (1987). Extracting information from ecological data containing high spatial and temporal variability: benthic microfloral production. *International Journal of General Systems*, **13**: 107-23.

Shaffer, G.P. and Onuf, C.P., (1983). An analysis of factors influencing the primary production of the benthic microflora in a southern California lagoon. *Netherlands Journal of Sea Research*, **17**(1): 126-44.

Shaffer, G.P. and Onuf, C.P., (1985). Reducing the error in estimating annual production of benthic microflora: hourly to monthly rates, patchiness in space and time. *Marine Ecology Progress Series*, **26**: 221-31.

Shaffer, G.P. and Sullivan, M.J., (1988). Water column productivity attributable to displaced benthic diatoms in well-mixed shallow estuaries. *Journal of Phycology*, **24**: 132-40.

Sournia, A., (1976). Primary production of sands in the lagoon of an atoll and the role of foraminiferan symbionts. *Marine Biology*, **37**: 29-32.

Steele, J.H. and Baird, I.E., (1968). Production ecology of a sandy beach. *Limnology and Oceanography*, **13**: 14-25.

Stevenson, R.J., (1984). Epilithic and epipelic diatoms in the Sandusky River with emphasis on species diversity and water pollution. *Hydrobiologia*, **114**: 161-75.

Sullivan, M.J. and Moncreiff, C.A., (1988). Primary production of edaphic algal communities in a Mississippi marsh. *Journal of Phycology*, **24**: 49-58.

Sundbäck, K., (1983). Microphytobenthos on sand in shallow brackish water, Oresund, Sweden. Primary production, chlorophyll-*a* content and species composition (diatoms) in relation to some ecological factors. Ph.D Thesis, University of Lund, Sweden. 209 pp.

Sundbäck, K., (1984). Distribution of microbenthic chlorophyll-*a* and diatom species related to sediment characteristics. *Ophelia*, Suppl. **3**: 229-46.

Sundbäck, K., Enoksson, V., Graneli, W. and Pettersson, K., (1991). Influence of sublittoral microphytobenthos on the oxygen and nutrient flux between sediment and water: a laboratory continuous-flow study. *Marine Ecology Progress Series*, **74**: 263-79.

Sundbäck, K. and Jonsson, B., (1988). Microphytobenthic productivity and biomass in sublittoral sediments of a stratified bay, southeastern Kattegat. *Journal of Experimental Marine Biology and Ecology*, **122**: 63-81.

Taasen, J.P. and Hoisaeter, T., (1981). The shallow-water soft bottom benthos in Lindaspollene, Western Norway, 4. Benthic marine diatoms, seasonal density fluctuations. *Sarsia*, **66**: 293-316.

van Es, F.B., (1982). Community metabolism of intertidal flats in the Ems-Dollard Estuary. *Marine Biology*, **66**: 95-108.

van Raalte, C., Valiela, I. and Teal, J., (1976). Production of epibenthic salt marsh: light and nutrient limitation. *Limnology and Oceanography*, **21**: 862-72.

Varela, M., and Penas, E., (1985). Primary production of benthic microalgae in an intertidal sandflat of the Ria de Arosa, NW Spain. *Marine Ecology Progress Series*, **25**: 111-19.

Vilbaste, S., (1992). Microphytobenthos - a part of the ecosystem of Haapsalu Bay, the Baltic Sea. *Proceedings of the Estonian Academy of Science and Ecology,* **2** (3): 119-26.

Walker, D.I., Masini, R.J., and Paling, E.I., (1988). Comparison of annual production and nutrient status of the primary producers in a shallow limestone reef system (Rottnest Island), Western Australia. Proceedings of the Australian Marine Sciences Association Annual Meeting, 1988.

Wasmund, N., (1986). Ecology and bioproduction in the microphytobenthos of the chain of shallow inlets (boddens) south of the Darss-Zingst Peninsula (Southern Baltic Sea). *Internationale Revue der Gesamten Hydrobiologie*, **71**: 153-78.

Wetzel, R.L., (1964). A comparative study of the primary productivity of higher aquatic plants, periphyton and phytoplankton in a large shallow lake. *Internationale Revue der Gesamten Hydrobiologie*, **49**: 1-61.

Whitney, D.E. and Darley, W.M., (1979). A method for the determination of chlorophyll *a* in samples containing degradation products. *Limnology and Oceanography,* **24**: 183-186.

Whitton, B.A. and Potts, M., (1982). Marine Littoral. In. *The Biology of Cyanobacteria.* (Carr, N.G. and Whitton, B.A. eds), pp 515-42. Botanical Monographs Vol. 19, Blackwell Scientific Publications, Oxford..

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Table A6 **Table A6 (continued)**

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Table A8 **Table A8 (continued)** **Table A8 (continued)**