ISDN 1039-3218

Microphytobenthos in Port Phillip Bay: Distribution and Primary Productivity

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Technical Report No.30

Port Phillip Bay Environmental Study
CSIRO Environmental Projects Office
Canberra, ACT, Australia

GPO Box 1666, Canberra, ACT 2601, Australia

December 1997

EXECUTIVE SUMMARY

The spatial and temporal variation in microphytobenthos biomass and primary productivity has been examined in Port Phillip Bay, Victoria.

Results indicate that microphytobenthos biomass across the Bay is comparable to the highest values recorded from other shallow marine systems elsewhere in the world. Both biomass and primary productivity show a unimodal seasonal trend with a summer maximum. Primary productivity of MPB is high and compare favourably to those of other primary producers in the Bay.

Primary productivity is closely related to benthic community respiratory rates. Over a twelve month period, modelled estimates of microphytobenthos biomass in the Bay was equivalent to 49×10^6 g chlorophyll *a* and gross production was 119.3 g C y^{-1}. Using Redfield stoichiometry, this carbon fixation rate equate to microphytobenthos nitrogen and phosphorus requirements of 21×10^9 and 2.9×10^9 g y^{-1} respectively. These estimates emphasise the importance of microphytobenthos to the energetics and overall nutrient pathways and budgets of the Port Phillip Bay system.

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1. INTRODUCTION

1.1. Importance of microphytobenthos

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

The range of biomass levels attributable to microphytobenthos in shallow waters is noteworthy. Chlorophyll concentrations in sediments range from less than 1 mg chl m^{-2} to over 1000 mg chl m^{-2} . This variation is found both between and within individual studies and reflects differences in depth, nutrient loading, light penetration and sediment grain size as well as seasonal effects (see Beardall and Light 1994). Annual production of microphytobenthos in various regions of the world has been shown to range from 5 to 892 g C m^{-2} with a mean of approximately 141 g C m^{-2}. This level of productivity is comparable with those of other primary producers such as phytoplankton where annual productivities of 50, 100 and 300 g C m^{-2} yr^{-1} have been estimated for oceanic, coastal and upwelling regions respectively (Morris 1974). Pinckney & Zingmark (1993) have shown benthic microalgae to be responsible for 22-38% of the total annual production in an estuarine environment. Similarly, Walker *et al* (1988) examined the contribution of various photoautotrophs to primary productivity of waters <10m deep off Rottnest Island, Western Australia and concluded that microphytobenthos was responsible for more than 6% of the annual production. This value was 5 times the corresponding figure for phytoplankton.

The importance of microphytobenthos appears valid not only for marine systems but also for freshwater lakes and rivers (Bjork-Ramburg, 1983, Nienhuis and DeBree, 1984, Stevenson, 1984, Wetzel, 1964). Microphytobenthos can also be important in habitats as diverse as sub-arctic lakes (Bjork-Ramburg, 1983) and the subtidal region of tropical coral reefs (Sournia, 1976).

Microphytobenthic organisms can also influence the ecology of aquatic ecosystems by their effect on nutrient exchange between sediments and the overlying water column (Graneli and Sundbäck, 1985). Whilst this effect can be attributable in part at least to the nutrient requirements of the microphytobenthic organisms themselves, there have been suggestions in the literature that oxygenic activities mediate bacterial nutrient transformation and exchange processes directly (Sundbäck et al, 1991; Rysgaard *et al*, 1993; Rysgaard-Petersen *et al*, 1994; Rysgaard *et al*, 1995). By increasing the supply of oxygen in the upper layers of sediment, autotrophic activity by MPB can influence the relative rates of nitrification/denitrification in the sediments and hence regulate nitrogen cycling.

1.2. Overall aims of the study

Aspects of the distribution and productivity of microphytobenthic organisms have been thoroughly reviewed by Beardall and Light (1994). These authors pointed out that there have been very few studies on MPB in Port Phillip Bay, and that those investigations that have been carried out are of limited coverage. Consequently the aim of the studies reported here was to thoroughly investigate the distribution and seasonal variation in biomass and primary production of MPB in Port Phillip Bay. Additional studies were designed to get information on the likely effect of MPB activities on nutrient exchange between the sediments and the overlying water column.

1.3. Description of the Study Area.

Located on the central south coast of Victoria, Australia (38° S, 145° E), Port Phillip Bay is a large, shallow marine embayment which has restricted exchange with Bass Strait (Fig. 1). Of the total surface area of Port Phillip Bay (1,950 km^2), approximately half is less than 14 metres deep, providing a high benthic area to total volume ratio. The Bay is generally characterised by particulate sediments with a conspicuous lack of hard, stable substrata, the principal factor in a depauperate macrophyte flora (Light and Woelkerling, 1992). Tides are semi-diurnal with a maximum amplitude of almost 1 metre. Port Phillip Bay is vertically well mixed to the extent that temperature (annual range: 9 to 22° C) and salinity (close to oceanic: 35 ppt) do not commonly stratify. Annual freshwater input is of the order of 5 percent of mean Bay volume and approximates annual evaporation. The largest contributors of fresh water to Port Phillip Bay are the Yarra River and the Western Treatment Plant. Estimated residence time for Port Phillip Bay water is approximately slightly over1 year (Hunter,1992).

2. BAY-WIDE DISTRIBUTION OF SEDIMENT-ASSOCIATED PLANT PIGMENTS

2.1. Objectives

The aim of this initial phase of the study was to obtain a Bay-wide picture of the distribution of plant pigments in the sediments and hence infer the distribution of MPB in relation to water depth and sediment type.

2.2. Methods

2.2.1. Sampling strategy

Sediment associated plant pigment and associated data were determined at a total of 65 subtidal sites in Port Phillip Bay (Fig. 1) throughout a six week period commencing in March 1994. Sediment samples were collected by divers in disposable plastic centrifuge tubes having a small diameter hole drilled through the apex to enable water expulsion during coring. Three sediment cores (10mm inner diameter x 50mm length) were taken by at each site. Cores were capped, returned to the surface and stored in a cool, dark ice box. On return to the laboratory, cores were extruded and the 0-10mm and 10-20mm strata removed with a razor blade. All samples were sealed in aluminium foil, appropriately labelled and frozen at -70°C until extraction. Pigment extraction took place within one month of sample collection.

2.2.2. Determination of plant pigments

Frozen sediment samples were homogenised with 10 ml of 90% acetone, centrifuged and the supernatant collected. A second and third extraction were made, re-suspending the residue in subsequent 10 ml and 5 ml volumes of 90% acetone respectively. The three supernatants were combined to provide a final volume of 25 ml. Strong light and heat were avoided throughout the extraction procedure. Chlorophyll *a* and pheophytin were determined spectrophotometrically following a method modified from that of Lorenzen (1967). The addition of a well defined volume of low concentration acid (Moed & Hallegraeff, 1978), ensured degradation of chlorophyll *a* to pheophytin. Extracted sediments were then dried at 60°C for 72 hours. Chlorophyll *a* and pheophytin data are reported as both areal biomass (mg m^{-2}) and concentration (μg g^{-1} sediment dry weight).

2.2.3. Grain size, total organic matter and ancillary data.

Three additional cores were collected at each of the 65 sites for grain size analysis. The grain size distribution of the uppermost 0-50 mm sediment strata was determined from falling velocities in an automated settling tube system (Greilach et al., 1996). Grain size was assigned to one of three descriptive classes following the Udden-Wentworth sediment scale (Wentworth, 1922).

Total organic matter was determined from loss on ignition. Sediment samples dried to constant weight at 60°C were heated in a muffle furnace at 550°C for 4 hours and loss of mass recorded.

Water depth at each site was recorded with an acoustic echo sounder to the nearest 0.2 m, and the location of each sample site was recorded by Global Positioning System (GPS) incorporating differential correction (± 2.5 m).

2.2.4. Data analysis

The purpose of this task was to provide estimates of sediment associated plant pigments at each site and to examine their Bay-wide distribution in relation to water depth and sediment type. Hence the three measurements at each site were pooled to obtain a mean value and these means were used in statistical tests. Mann-Whitney 'U' tests were used to compare most variables (Chl *a* areal biomass, Chl *a* concentration, pheophytin areal biomass, pheophytin concentration, and functional Chl *a* to total Chl *a* ratio) between the upper (0-10mm) and lower (10-20mm) sediment strata. Two-way ANOVA was used to examine the relationship of water depth (shallow: 2.0 - 8.0m; mid: 8.1 - 14m; deep: 14.1 - 24m) and sediment type (silt - very fine sand, fine sand, coarse - medium sand) to Chl *a* areal biomass, Chl *a* concentration, pheophytin areal biomass, pheophytin concentration, functional Chl *a* to total Chl *a* ratio, and total organic matter areal biomass. In most instances, data required power transformation to eliminate heteroscedascity. For the variable 'autotrophic index', variances were significantly heterogeneous even after transformation. These data were not formally analysed. In the absence of a nonsignificant depth - sediment type interaction term, differences among water depth and sediment type means were compared by posteriori pairwise Bonferroni tests as in Underwood (1981).

2.3. Results

Of 65 sites sampled for sediment associated pigments, 55 contained some measurable functional Chl *a*.

Values for sediment-associated chlorophyll + pheophytin in the first 10mm were greatest in Corio Bay and the northern sites with isolated patches of high concentration (>25 $\mu g\ g^{-1}$ sediment dry weight) off Mornington and Carrum (Fig. 2). High pigment concentrations were also found in deeper water (12 - 20m) in a zone reaching down from Elwood to Mornington (Fig. 2). High pigment concentrations below 10mm were found only in parts of Corio Bay, and in parts of the central area (Fig. 3).

However, when functional chl *a* distributions were considered, high concentrations were found only in the top layers of sediment in Corio Bay, in a zone north of Indented Head and off Carrum (Fig. 4). Below 10 mm, chl *a* concentrations were generally low, with values above 2.5 $\mu g\ g^{-1}$ sediment dry weight being found only in some sites in Corio Bay (Fig.5). Similar patterns were obtained when chl *a* content of the sediments was expressed on an areal basis (Figs 6 and 7).

Total organic matter in sediments on an areal basis was greatest in Corio Bay (particularly the northern region) with high values extending up the coast as far as

Werribee. The area off Carrum also showed high organic matter content as did isolated sites in the north-central Bay and the Great Sands (Fig. 8).

The ratio of functional chlorophyll *a* to total organic matter in the sediments can be taken as an autotrophic index (i.e. a measure of the proportion of organic matter associated with functional MPB populations). Values for this parameter are shown in Fig. 9. High values are found in a region running approximately from Mornington to Wooleys Reef and from Carrum north along the coast to Elwood. Highest values were found in the south western reaches of Corio Bay, in the zone north of Indented Head and in the northernmost sites of Port Phillip Bay (Fig. 9).

The distribution of sediment types is shown in Fig. 10. Most of the Bay sediments were found to consist of fine or very fine sand with significantly sized regions of medium sand. Silty sediments were only found in the central region of the Bay and west of Mornington. Results of particle size analysis are given in Fig. 11 and these essentially mirror the sediment type distributions.

The distribution of parameters in relation to water depth and sediment type is summarised in Table 1. ANOVA and Bonferroni tests (Table 1) indicate that functional Chl *a* has a significantly greater biomass at shallow and mid sites (as compared to deep sites) so that a water depth dissimilarity for Chl *a* concentration was significant. Sediment type and sediment by depth dissimilarities for Chl *a* biomass and concentration were not significant (Table 1).

Table 1: Analysis of variation in benthic microalgal biomass and associated parameters. df = degrees of freedom, MS = mean sums of squares, F = F-ratio, ^{ns}P = not significant, *P < 0.05, **P < 0.001, ***P < 0.0001.

Source	df	MS	F	MS	F	MS	F
		Functional chlorophyll *a*[1]		**Functional chlorophyll *a* to total chlorophyll *a* ratio[2]**		**Autotrophic index[2]**	
Water depth	2	3.994	3.601 *	0.027	2.355 ns	0.000052	1.774 ns
Sediment type	2	0.139	0.125 ns	0.002	0.173 ns	0.000034	1.175 ns
Depth by sediment type	4	0.261	0.235 ns	0.007	0.614 ns	0.000025	0.851 ns
Site/error	45	1.109		0.012		0.000029	
Bonferroni pairwise comparisons Greatest mean value[a]		shallow, mid					
		Pheophytin *a*		**Total chlorophyll *a***		**Total organic matter**	
Water depth	2	2486.05	6.05 *	33126.46	6.04 *	1.747	3.165 *
Sediment type	2	8648.34	2.10 ns	8763.56	1.60 ns	0.320	0.580 ns
Depth by sediment type	4	2589.88	0.63 ns	2047.44	0.37 ns	0.971	1.760 ns
Site/error	55	4108.52		5488.03		0.552	
Bonferroni pairwise comparisons Greatest mean value[a]		shallow, mid		shallow		shallow, mid	

[a] Where two water depths are listed, mean sediment associated parameters were greater than at the third and not siginifcantly different from each other. Bonferroni comparisons had P < 0.05.

[1] Data transformed to Log (x) before analysis, [2]Arcsin $((x)^{0.5})$ transform.

Pooled values for chl *a* presented as both areal biomass and concentration were significantly greater in the upper core stratum (16.3 ± 2.1 mg m^{-2} and 1.17 ± 0.21 μg g^{-1} sediment dry weight respectively) compared to the lower stratum (10.0 ± 2.1 mg m^{-2} and 0.53 ± 0.11 μg g^{-1} sediment dry weight respectively) (Mann-Whitney 'U' test, $P < 0.01$ and $P < 0.001$ respectively).

Pheophytin was recorded at all sites sampled. Pheophytin areal biomass and concentration were significantly greater in the upper core stratum (156 ± 8.53 mg m^{-2} and 13.92 ± 1.33 μg g^{-1} sediment dry weight respectively) compared to the lower stratum 117 ± 8.22 mg m^{-2} and 7.94 ± 0.81 μg g^{-1} sediment dry weight respectively) (Mann-Whitney 'U' test, $P < 0.001$). ANOVA and Bonferroni tests (Table 1) indicate that pheophytin biomass was significantly greater in shallow and mid sites (as compared to deep sites). A water depth dissimilarity for pheophytin concentration was hence significant. Pheophytin concentration was significantly greater when associated with silt-very fine sand (as compared to fine sand and coarse-medium sand) but differences in pheophytin areal biomass between sediment types were not significant (Table 1).

The ratio of functional Chl *a* to total Chl *a* + pheophytin was significantly greater in the upper core stratum (0.081 ± 0.008) compared to the lower stratum (0.059 ± 0.009) (Mann-Whitney 'U' test, $P < 0.001$). ANOVA and Bonferroni tests (Table 1) show a non-significant depth effect, indicating that this ratio is significantly greater at shallow and mid sites (as compared to deep sites). Differences in the functional Chl a to total Chl a ratio between sediment types were not significant (Table 1).

The significance of the distribution of surficial total organic matter (TOM) biomass in relation to water depth and sediment type is also summarised in Table 1. Water depth and sediment type dissimilarity, as tested by ANOVA, were significant for total TOM biomass (Table 1)

2.4. Discussion

It was clear that there was a significant negative relationship between water depth and both chlorophyll *a* and the ratio of chl *a* to functional chlorophyll *a* + pheopigments. At greater depths the available light intensity was presumably insufficient to support the development of large, active MPB populations. A similar conclusion may be reached in relation to the depth within the sediments. Although pheophytin concentrations were highest in the surficial layer (0-10mm), the ratio of functional chlorophyll *a* to total pigment (chl *a* + pheophytin) was always higher in these samples than deeper in the sediments, indicating a healthier photoautotrophic population. It is worth noting that the ratio of functional chl *a*: chl *a* + pheophytin was always far lower in samples taken as part of this sub-task than for later samples in the study. This may reflect the somewhat greater depths for most of the samples taken during this sub-task, a conclusion supported by the observed significant relationship between this ratio and water depth (Table 1).

Whilst some other studies have been unable to show a clear relationship between water depth and MPB biomass or productivity, a large number of authors have reported 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 that have examined the MPB distribution within the sediment have shown a marked decrease in biomass with increasing depth in the sediment, observations that are consistent with our data.

Although our results suggested that larger grain sizes in the sediments were associated with larger MPB biomass, we were unable to show any statistically significant trends in the data. Possibly this relates to the relatively low number of samples in each grain size class and the consequent poor statistical power of the analysis. A positive correlation between grain size and MPB biomass has been reported by Sundbäck (1984), Lukatelich & McComb (1986), Masini (1987) and Riznyk *et al*. (1978) whilst, in contrast, Schaffer & Onuf (1983) noted that sediments with smaller grain size had higher 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 surprisingly, physical exposure has proved to be of importance (LeGuellec & Bodin 1992, Fielding *et al*. 1988) and it has been noteworthy that one of the Port Phillip Bay transect sites (Carrum), in which the shallow sediments are frequently disturbed, repeatedly shows much lower MPB productivity than other areas (see Section 4).

3. SPATIAL VARIATION IN THE DISTRIBUTION OF SEDIMENT-ASSOCIATED CHLOROPHYLL *A*

3.1. Introduction and aims

There is little data available in the literature on the variation in MPB density at different spatial scales. With some notable exceptions (eg. Masini 1990), many of the studies on MPB have taken single cores or dome deployments without consideration of the heterogeneity within populations. However, the small scale (several metres) variation in biomass and productivity can be marked (Schaffer & Onuf 1985, Schaffer & Cahoon 1987). It is critical that investigations use a sampling scheme that gives representative data in relation to variation in MPB parameters with environmental and physical factors.

The second phase of this study was therefore designed to investigate variation, across a range of spatial scales, in sediment-associated microalgal pigments (taken to reflect MPB biomass) and to use this information to generate an optimised sampling design for the later aspects of the work.

3.2. Methods

3.2.1. Sampling strategy

To examine spatial variation in sediment associated chlorophyll *a* distribution, 72 sediment cores were collected in May 1994 from each of two sites (Werribee, Indented Heads; Fig. 1) at a water depth of approximately one metre. At each site, four replicate cores (22.5mm x 70mm length) were sampled from within each of three plots, within each of two stations, within each of three waypoints. Sites, waypoints, stations and plots were in the order of 10's of kilometres, 1 kilometre, 50 meters and 10 meters apart respectively. Plots were 2m x 2m in size.

Sediment cores were collected with polycarbonate tubes with end caps perforated to facilitate the expulsion of water during coring. Cores were capped and stored in a cool, dark ice-box. On return to the laboratory, cores were extruded and the 0-5mm uppermost strata removed with a razor blade. All sediment samples were stored in 25ml glass screw-top bottles, appropriately labelled and frozen at - 70 °C until extraction. Pigment extraction took place within one week of sample collection.

3.2.2. Determination of plant pigments

Frozen sediment samples were homogenised with 18ml of 100% acetone and pigments extracted in the dark over a 24 hour period at 4 °C. The addition of 2ml of distilled water post pigment extraction provided a final volume of 20ml. A sub-sample (5ml) was centrifuged and the supernatant collected. Chlorophyll *a* and pheophytin were determined spectrophotometrically following the method outlined in Section 2.2. Chlorophyll *a* data are reported as biomass per unit area (mg m^{-2}).

3.2.3. Data analysis

Hierarchical ANOVA was used to examine the spatial variation in chlorophyll *a* distribution, with sites, waypoints, stations and plots all considered random, nested factors. The data were log-transformed to eliminate heteroscedascity.

3.3. Results & Discussion

Hierarchical ANOVA revealed that chlorophyll *a* biomass variation differed across the various spatial scales examined (Table 2). Waypoint (spatial scales in the order of 1 kilometre) proved non-significant, whereas sites (10's of kilometres), stations (50 meters) and plots (10 meters) showed significant variation in chlorophyll *a* distribution. Site alone accounted for greater than 90 percent of the variation in chlorophyll *a* distribution, whereas waypoint and plot collectively accounted for only 2 percent variation (Table 2).

Table 2. Results of analysis of spatial variation in chlorophyll *a* distribution.
SS = sums of squares, DF = degrees of freedom, MS = mean square, SIG = significance where ** = significant at 0.01 level, *** = significant at 0.001 level, NS = not significant at 0.05 level, % = variance components[b].

Source	SS	DF	MS	SIG	%
Core/error	107.010	108	0.991		2
Site	2146.626	**1**	2146.626	***	90
Waypoint	118.680	4	29.670	NS	1
Station	155.979	6	25.996	***	6
Plot	52.687	24	2.195	**	1

[b]Variance components are expressed as proportions of variation explained by each factor (see Underwood 1981).

As a consequence of these phenomena, for all subsequent studies on transects at standard sites in the Bay, the sampling scheme comprised 8 cores taken from each of 3 stations at each site. Such a sampling scheme minimises the errors associated with small scale variation in MPB yet provides the statistical power to detect effects associated with site.

4. SEASONAL VARIATION IN MPB BIOMASS AND PRIMARY PRODUCTIVITY

4.1. Introduction and aims

There are no consistent trends reported in the literature on seasonal variation in MPB. In some instances, peaks in MPB populations and productivity are described for summer whereas in other studies winter (Kristensen 1993, Masini 1990, Plante-Cuny *et al* 1993) or autumn (Plante *et al* 1986, Sundback 1983) peaks have been observed. In some studies, peaks were observed in more than one season (Davis and McIntire 1983, Riznyk *et al* 1978). Seasonal variation may be attributable to a number of (possibly interacting) factors including temperature (Daehnick *et al* 1992, Masini 1990), total sunlight availability and water turbidity (Pinckney and Zingmark 1993).

This sub-task was therefore designed to determine the seasonal variation in MPB populations, their photosynthetic characteristics and *in situ* productivity. Such measurements would allow estimation of the overall contribution of MPB to primary productivity and, indirectly, to nutrient cycling in the Bay.

4.2. Methods

4.2.1. Study sites.

Initially four sites were chosen, these being Indented Head, Carrum, Werribee and Great Sands. After four months of the study it was decided that the Great Sands site was too unstable to yield meaningful results. The site depth was continually changing as sand banks were built up and worn down and, in addition, the strong rip in the area made diving hazardous. These factors, together with the fact that chlorophyll levels were always minimal except for isolated patches (eg. Mud Island) led this study site to be discontinued. Details of the remaining sites are given in Table 3 and the positions of the sites are shown in Fig.1.

Table 3: Characteristics of the sites chosen for intensive seasonal studies of MPB

Site	Depth	GPS reference	Sediment type	Organic matter content
Indented Head	1.1m	144.590103, 38.052898	medium sands	low
	5.0 m	144.576096, 38.034599	medium sands	low
	9.5 m	144.558304, 38.038300	coarse shelly sands	low
Carrum	1.0 m	145.118301, 38.076302	medium sands	low
	5.0 m	145.115494, 38.076099	medium sands	low
	10.0 m	145.108795, 38.079498	coarse sands	low
Werribee	0.9m	144.746902, 38.144798	fine silt/sand	high
	5.0 m	144.739700, 38.151699	fine silt/sand	high
	9.5 m	144.717896, 38.168800	fine silt/sand	high

4.2.2. Sampling strategy

Pigments. The three sites (Fig. 1 and Table 3) that were selected for detailed examination of temporal dynamics in sediment associated plant pigments were visited monthly throughout the period September 1994 to September 1995. Three water depths were examined at each site.

As a consequence of the studies in Section 3, eight sediment cores (22mm x 70mm length) were sampled at each of three stations at each of three water depths at each of three sites. Cores were collected by divers, capped, and returned to the laboratory in a cool, dark ice-box. Following photosynthesis *versus* irradiance work (see Section 4.2.4), sediments from four cores were extruded and the 0-5mm uppermost strata removed with a razor blade. All sediment samples were stored in 25ml glass screw-top bottles, appropriately labelled and frozen at - 70 °C until extraction. Pigment extraction took place within one month of sample collection.

b) Primary productivity: For studies of primary productivity of MPB, two water depths were examined at each site. Sampling procedure was otherwise as described in a) above. Measurements of primary productivity were made as soon as cores were returned to the laboratory (and always within 24 hours of sampling).

c) Ancillary field data: At each time of sampling at each site, measurements were taken of bottom water temperature and water column vertical light attenuation.

4.2.3. Determination of plant pigments

Frozen sediment samples were homogenised with 18ml of 100% acetone and pigments extracted in the dark over a 24 hour period at 4 °C. The addition of 2ml of distilled water post pigment extraction provided a final volume of 20ml. A sub-sample (5ml) was centrifuged and the supernatant collected. Chlorophylls (*a*, *b* and *c*) and pheophytin were determined spectrophotometrically following the method outlined in Section 2.2.2. Following pigment extraction, sediments were dried at 60°C for 72 hours. Chlorophyll and pheophytin data are reported as both "concentration" units ($\mu g\ g^{-1}$ sediment dry weight) and "areal biomass" units ($mg\ m^{-2}$).

4.2.4. Measurement of photosynthetic characteristics

Head water was syringed from each core and the uppermost 25mm of sediment extruded into an incubating tube of the same diameter sealed at the base. Eight cores from each station were randomly placed in a purpose built, clear acrylic metabolism chamber. Seawater collected at the same time and location of sampling was filtered through GF/C filters (Whatman International, U.K.) to remove phytoplankton. This filtered seawater was circulated through the chamber via a peristaltic pump, past a Clark-type oxygen electrode (Hansatech, U.K.) and back to the chamber containing the intact sediment cores. The chamber was immersed in a water bath set at *in situ* temperature. The oxygen electrode was connected to a pre-amplification unit (Hansatech, U.K.) and the data logged, stored and managed on PC using in-house developed software.

This system enabled an integrated measure of oxygen production/consumption from each set of eight cores to be measured. A resolution of 0.00016 mg O_2 litre^{-1} can be attained with this equipment configuration.

The light source consisted of a slide projector positioned vertically above the chamber. Neutral density filters enabled varying light intensities up to 850 μEin m^{-2} sec^{-1} to be projected onto the chamber surface.

The system was calibrated at the start of each day. Each set of eight cores was subjected to a series of light intensities from 0 to 850 μEin m^{-2} sec^{-1}. Cores were incubated at each light intensity for approximately 20 minutes with only the last 5 minutes used to calculate the rate of oxygen production/consumption. The water volume circulating through the system was carefully removed and measured at the end of each P-I incubation. Each set of eight cores (stations) were incubated in a random order.

4.2.5. Estimates of daily *in situ* productivity

A continuous record of incident PAR (EPA, Victoria), monthly data on water column attenuation (Section 4.2.2) and calculated photosynthetic characteristics (Pmax and α) were used to model *in situ* primary productivity of MPB over an annual cycle.

In a separate program conducted at one site (Werribee deep), PAR sensors and data loggers, incorporating wiper units to inhibit sensor fouling, were moored for approximately five week periods in winter 1995 and in summer 1996 , to obtain high resolution data on water column attenuation. This was then used to calculate comparable *in situ* primary production for the two periods. Deployment dates and durations are summarised in Table 4.

Table 4. PAR sensor and logger deployment dates and durations at Werribee. Water depth was 9.5 m.

Deployment	Season	Duration
I	winter 1995	28.07.1995 - 05.09.1995
II	summer 1996	12.01.1996 - 19.02.1996

One PAR unit was fixed to the bottom (9.5 metres deep) and a second unit positioned in the water column 2.5 metres above. A third unit was stationed on shore to continually log incident PAR. Five minute scan intervals were integrated and logged continuously. This configuration enabled high frequency attenuation data and *in situ* benthic photon flux data to be calculated. Photosynthetic characteristics from sediment cores collected throughout the logger deployments enabled high resolution oxygen budgets to be generated.

4.3. Results.

4.3.1. Physical parameters

Temperature

All sites showed a gradual rise in water temperature immediately overlying the sediments from September to late summer (Figs 11). Maximal temperatures reached were higher at Indented Head and at Werribee (25 - 28^{o}C) than at Carrum (22^{o}C). Bottom temperatures dropped to reach a minimum in July/August. Maximum bottom temperatures reached at Indented Head and Werribee were, in summer, higher at the shallower stations. Temperatures during other seasons were similar in both deep and shallow stations. At the Carrum site, there was negligible temperature difference between shallow and deep stations at any time for the year.

Light attenuation

The proportion of surface light (I_b) reaching the sediment is shown for shallow and deep stations at each of the sites in Fig 12. In general, vertical attenuation was quite variable, particularly at the shallow stations. Variability was greater at Werribee and Indented Head than at the Carrum site. At a depth of 1m, light penetration over the course of the study period varied from 0.2 to 0.8 of surface intensity at Carrum, 0.08 to 0.7 of surface intensity at Indented Head and from 0.05 to 0.4 of surface intensity at Werribee. A more detailed investigation of small scale temporal variability in vertical attenuation was carried out and is described in Section 4.4.

4.3.2. Seasonal changes in chlorophyll and pheophytin.

Ratio of chlorophylls a:b:c

Chlorophylls *a* and *c* were predominant at all sites and stations (Fig 13). Chl *a:c* ratios were within the range found in eucaryotic microalgae, suggesting a minimal role of cyanobacteria in the MPB populations. This is consistent with microscopic observations (data not shown) that the MPB populations were always dominated by diatoms. Chlorophyll *b* was found on a few occasions from stations at Carrum and Indented Head but was more common (though still a minor component) at Werribee, indicating the presence of a low level of chlorophyte algae in the MPB populations. There were no obvious seasonal or spatial trends in the proportions of the different chlorophylls.

Seasonal trends in chlorophyll a

Seasonal trends in MPB biomass, as indicated by areal based chlorophyll *a* values, are shown in Fig 14. Maximum values (approximately 145 mg chl *a* m^{-2}) were found at the shallow site at Werribee in March 1995. Values for shallow and mid-depth stations were, in general, more variable than those in deeper stations. At Carrum, chlorophyll *a* values tended to be greater at the mid and deep stations, whereas at Werribee the MPB populations were denser at the shallow and mid-depth stations and at Indented Head highest at the mid-depth station. There were no consistent seasonal trends in areal based chlorophyll biomass.

The seasonal and spatial variability was essentially the same when chlorophyll was expressed per gram dry weight of sediment (Fig 15). Absolute values were highest at Werribee (up to 20 μg g-1 dry wt) and lowest at Indented Head (maximum of 2 μg g-1 dry wt).

Seasonal trends in pheophytin

Pheophytin levels showed no consistent trends with depth on areal or concentration basis (Figs. 16 and 17). There were also no consistent seasonal trends, although the mid-depth sites at Carrum and Indented Head and the shallow site at Werribee exhibited a maximum in late summer. Pheophytin at Werribee was considerably higher than at the other two sites while Carrum had lowest values per m^2, and, because of the density of the substrate, Indented Head showed the lowest concentrations per gram sediment.

Functional Chl a *: total chlorophyll* a *ratio*

The ratio of functional chlorophyll *a* to total chlorophyll *a* (functional chl *a* + pheophytin) is shown for each of the three sites in Fig 18. Highest values were found at the shallow stations at Carrum and Indented Heads whilst this ratio never exceeded 0.6 at Werribee. There was a clear correlation between station depth and the ratio of functional chl *a* : total chlorophyll *a* at each site, deeper stations generally showing considerably lower values.

4.3.3. The effects of disturbance on MPB:

Another research task in the Bay Study involved the deployment of a SEDCAM frame (Black,1995). The opportunity was taken to attach a fluorimeter to this frame at 0.4m above the sediment surface. Readings were taken at two sites and the calculated chlorophyll *a* levels are shown in Fig 19. From this figure it is clear that both sites were subject to disturbance events leading to marked excursions in the chlorophyll *a* concentration above the sediment. The Werribee deployment showed higher and more variable chlorophyll *a* values than the Sandringham deployment as might be expected from the difference in depth. It is clear that disturbance events can lead to resuspension of chlorophyll as – containing particles (presumably MPB) into the water column.

Another indication of the importance of physical disturbance to MPB biomass is given by the “mixing index” data in Fig 20. This mixing index (MI) is defined as the ratio of chlorophyll in the 10-20mm stratum divided by that in the top 10mm. If the MPB are evenly distributed in the sediments this will lead to a maximum value for the MI of 1.0. Values for MI showed no seasonality and were fairly consistent throughout the year. The Carrum site tended to be more variable than Indented Head or Werribee. Overall, MI values at Carrum and Indented Head were higher than at Werribee indicating a higher degree of disturbance and mixing at those sites.

4.3.4. Photosynthetic characteristics of MPB.

Capacity for photosynthesis (Gross Pmax)

Rates of light saturated oxygen evolution from sediment cores during the study period are shown in Fig 21. Although there was a strong seasonality at Werribee and Indented Head, with values reaching a maximum over summer at both the shallow and deep stations of both sites, there was little variation throughout the same period at Carrum where gross photosynthetic rates were consistently <200 mg O_2. m^{-2}. h^{-1}. At Werribee, rates were much lower in cores from the deeper stations. Maximal rates from Werribee sediments reached >900 mg O_2. m^{-2}. h^{-1} in February, whereas the highest rates measured from cores from Indented Heads were approximately 400 mg O_2. m^{-2}. h^{-1}.

Assimilation number

When light saturated photosynthetic rates were corrected for the biomass of MPB and expressed as mg O_2 mg chl a^{-1}.h^{-1}, (i.e. assimilation number), a marked seasonality in the photoautotrophic capacity was seen in cores from Indented Head and Werribee (Fig 22). Assimilation numbers at these sites were higher in summer (> 10 mg O_2 mg chl a^{-1}. h^{-1}), dropping to values of 5 mg O_2 mg chl a^{-1}.h^{-1} or less during the rest of the year. In contrast, at the shallow station at the Carrum site assimilation numbers showed little trend, with values remaining between 5 and 10 mg O_2 mg chl a^{-1}.h^{-1} throughout the study period.

Theoretical saturating photon flux, Ik

The parameter Ik is an approximation of the photon flux at which photosynthesis becomes light saturated. Increases in Ik can be brought about either by an increase in maximum cellular rates of photosynthesis or by a decrease in the efficiency of light harvesting - usually brought about by an increase in cell content of light harvesting pigments (see Richardson *et al* (1983) for a review of light adaptation strategies in microalgae). Conversely, a decreased Ik is commonly associated with adaptation to low light availability. Ik values for shallow and deep MPB populations at the three study sites are presented in Figs 23 to 25.

As might be expected, Ik values were generally lower at the deeper stations at each site. This was particularly marked at Werribee where there was a two-fold difference between Ik values at shallow and deep stations (Fig. 23). The large peak in Ik at the Werribee shallow station in March was associated with a marked rise in bottom temperature, although neither gross areal photosynthetic capacity nor assimilation number exhibited a corresponding peak at the same period.

All sites showed a seasonality in Ik values, with markedly higher values in summer.

Photosynthetic quantum yield, α

Values for α (expressed as mg O_2 h^{-1}. μEin.s^{-1}) for the three sites are summarised in Fig 26. Values for α tended to be lower in summer and higher in winter as might be expected from populations that show acclamation to photon flux. Shallow sites showed higher values at Werribee and lower values at Indented Head, reflecting water column

attenuation. Deep sites showed lowest values of α at Carrum and highest values at Indented Head.

4.3.5. Benthic respiration

Respiration data for the benthic communities on shallow and deep sediments at the three sites are summarised in Fig 27. Respiration rates of the sediment community (fauna, bacteria, chemical demands of the sediment itself and MPB), at both the shallow and deep sites at Carrum were less than 100 mg O_2 m^{-2} h^{-1} and showed no seasonal variation. At Indented Head, respiratory rates were also ≤ 100 mg O_2 m^{-2} h^{-1} except during the summer, when values at the shallow station showed a slight increase from December to February. At the deep station at Indented Head values were consistently ≤ 100 mg O_2 m^{-2} h^{-1} except for a value of 300 mg O_2 m^{-2} h^{-1} during January. Respiration rates at the shallow station at Werribee were considerably higher than at the other two sites and, with the exception of the September 1994 sampling period, were generally higher in summer (December - March; ~250 mg O_2 m^{-2} h^{-1}) than at other times of the year. At the deep station off Werribee, respiration values were less than ≤ 100 mg O_2 m^{-2} h^{-1} except for a slightly higher value in January.

4.3.6. Daily *in situ* primary productivity

Values for modelled *in situ* primary productivity of MPB are shown in Figs 28 to30. Values were strongly affected by variation in water column attenuation (see Fig 12). Shallow sites always showed the higher *in situ* productivity. Within the shallow sites, Werribee showed the highest values (up to 8000 mg O_2 m^{-2}. day^{-1}) followed by Indented Head (up to 3000 mg O_2 m^{-2}. day^{-1}) and Carrum (up to 2000 mg O_2 m^{-2}. day^{-1}). Within deeper sites Indented Head showed the highest values (up to 4000 mg O_2 m^{-2}. day^{-1}), followed by Werribee and Carrum (up to approximately 1200 mg O_2 m^{-2}. day^{-1}). For comparison, values of benthic respiration and the ratio of production to respiration at all sites are also shown in Figs 28 to 30.

4.4. Discussion

4.4.1. MPB biomass

The functional chlorophyll *a* biomass of subtidal environments has been studied previously by Matheke and Horner (1974), Sournia (1976), Sundback (1984), Lukatelich and McComb (1986), Sundback and Jonsson (1988), Delgado (1989), Cahoon *et al* (1993), Plante-Cuny *et al* (1993), and Screiber and Pennock (1995). The mean functional chlorophyll *a* biomass recorded in Port Phillip Bay surface sediments at the three sites for the sampling period (33 mg m^{-2}; Table 5) is more or less comparable to that reported for temperate subtidal environments of similar water depth (combined mean 22 mg m^{-2}, Table 6). However, the functional chlorophyll *a* biomass reported by Matheke and Horner (1974) in arctic subtidal sediments (35-321 mg m^{-2}) and Sournia (1976) in tropical subtidal sediments (56-140 mg m^{-2}) is considerably higher than that found in Port Phillip Bay. Functional chlorophyll *a* biomass found in the present study is also lower than that reported by Sundback (1984) in a marine embayment on the Falsterbo Peninsula, SW Sweden, (23-258 mg m^{-2}) and Lukatelich and McComb (1986)

in the Peel-Harvey Estuary, SW Australia, (27-558 mg m^{-2}). Although sharing similar temperate latitudes, benthic microalgal biomasses in the Falsterbo Peninsula embayment and Peel-Harvey estuarine system were measured in relatively shallow waters (< 2m), whereas biomass values for Port Phillip Bay are from a mean water depth 11.3 m. Moreover, the Peel-Harvey Estuary is generally considered a eutrophic system (McComb *et al*., 1981) whereas Port Phillip Bay is relatively oligotrophic (Axelrad *et al*., 1981).

Table 5. Mean biomass and potential productivity at sites during the period September 1994 to September 1995. Values relate to the top 10 mm of sediment.

Parameter	Depth	Carrum		Indented Head		Werribee	
Mean chlorophyll a	Shallow	18.355	±1.092	23.070	±2.062	61.606	±9.186
(mg.m^{-2})	Mid	41.389	±7.687	46.793	±5.336	33.074	±2.844
	deep	32.331	±2.680	36.009	±1.594	14.326	±2.289
Mean chlorophyll a	Shallow	2.109	±0.125	0.662	±0.085	9.136	±1.362
(mg.g^{-1} dry wt sediment)	Mid	4.990	±0.927	1.202	±0.137	4.448	±0.382
	deep	3.531	±0.293	1.194	±0.053	2.051	±0.327
Mean gross Pmax	Shallow	129.82	±10.72	180.10	±28.28	328.06	±78.99
(mgC.m^{-2}. h^{-1})	Deep	111.66	±12.19	118.70	±28.02	97.98	±22.47

In the only previous assessment of benthic microalgal biomass in Port Phillip Bay, Axelrad *et al*., (1979) examined total chlorophyll *a* values uncorrected for pheopigments at two shallow water (1.5-2.5m) sites over an annual cycle. Axelrad *et al*. (1981) reported total chlorophyll *a* values (12-130 mg m^{-2}) which were generally lower than the range of values encountered in the present study (16-356 mg m^{-2}).

Table 6. Functional chlorophyll *a* biomass of sediments in temperate subtidal environments of similar water depths.

Location (Lat.)	Depth (m)	mg m^{-2} (mean, range)	sediment thickness (mm)	reference
Laholm Bay, Sweden (56° N)	2-20	13; 1-87	5	Sundback & Jonsson (1988)
Alfacs and Fanger Bays Spain (41° N)	2-6.5	15; 2-32	3	Delgado (1989)
Onslow Bay, USA (34° N)	13-23	32; 18-42	30	Cahoon et al. (1990)
Gulf of Main, USA (44° N)	21-27	40; 16-79	30	Cahoon et al. (1993)
Gulf of Fos, France (43° N)	4.5	14; 9-18	10	Plante-Cuny et al (1993)

4.4.2. Photosynthetic characteristics of MPB populations

Irrespective of site and water depth, significant correlations were found between Ik, gross Pmax and alpha. Hierarchical partitioning was then used to determine whether the relationship of Ik to gross Pmax and alpha represents multiple dependence on these variables or whether the variation in Ik can be largely attributed to a single variable.

Hierarchical partitioning does not aim to identify the best regression model as such but rather uses all models in a regression hierarchy to distinguish which variable has a high independent correlation with the dependent variable (Mac Nally 1996).

In terms of independent effects, Werribee shallow is the only site where there appears little discernible difference between the independent variables, alpha and Pmax, in explaining variation in Ik (Table 7).

Table 7. Percent distribution of the independent effects of alpha and Pmax on the dependent variable Ik at shallow and deep sites at Werribee, Indented Head and Carrum. Results obtained from hierarchical partitioning of linear models.

Site / depth	Percent distribution of independent effects on Ik	
	Alpha	Pmax
Werribee shallow	49.8	50.2
Werribee deep	54.9	45.1
Indented Head shallow	59.8	40.2
Indented Head deep	78.9	21.1
Carrum shallow	77.3	22.7
Carrum deep	71.8	28.2

At the remaining site/depths, most of the variation in Ik is attributable to alpha whereas Pmax appears to be of comparatively less importance. Excluding Werribee shallow, most of the explanatory power of alpha is unique to itself; the independent contributions of alpha are larger (10 - 58 %) than the contributions it has in common with Pmax.

Thus, excluding Werribee shallow, it appears that the variation in Ik is determined principally by variation in alpha. Results indicate that Ik is less causally related to gross Pmax.

This dependence of Ik on α reflects the acclamation of microalgae to photon flux (Richardson *et al* 1983) and indicates that the photosynthetic characteristics of MPB populations in Port Phillip Bay respond to the previous light history in the environment.

The theoretical saturating photon flux (I_k) of a benthic microalgal population is an approximation of the photon flux at which photosynthesis becomes light saturated and is a direct result of physiological processes. The relationships between I_k and the integrated eight day benthic photon flux, calculated from instantaneous water column attenuation at each time of sampling (I_b day^{-8} $_{(\text{monthly attn})}$) and mean water column attenuation for the twelve month sampling period (I_b day^{-8} $_{(\text{mean attn } y^{-1})}$) are presented in Figs 23 to 25. Irrespective of site and water depth, I_b day^{-8} $_{(\text{mean attn } y^{-1})}$ follows a strongly sinusoidal distribution exhibiting a summer maximum and a winter minimum whereas this seasonal signal periodically breaks down in the case of I_b day^{-8} $_{(\text{monthly attn})}$. Irrespective of site and water depth, I_k strongly mirrors I_b day^{-8} $_{(\text{mean attn } y^{-1})}$. Benthic microalgae provide a window into the light history to which these organisms have been exposed through the parameter I_k; benthic microalgae have the ability to integrate environmental effects, in this case benthic photon flux, over longer periods of time than we as biologists care to measure. The relationship between I_k and I_b day^{-8} $_{(\text{mean attn } y^{-1})}$ appears not as strong in the shallow sites, as compared to the deeper sites. This

observation may, in part, be due to abiotic factors other than benthic irradiance in these depths (eg. bottom shear) and offers subsequent modelling possibilities. The poor relationship between I_k and I_b day^{-8} $_{(monthly\ attn)}$, as compared to I_k and I_b day^{-8} $_{(mean\ attn\ y^{-1})}$, indicates the inaccuracy involved in using a single monthly vertical attenuation coefficient and assuming this parameter remains constant throughout the sampling interval. Clearly, highly attenuated water masses recover rapidly following resuspension or bloom events.

4.4.3. Primary productivity

Annual primary productivity at the three study sites

Studies of primary productivity of MPB in Port Phillip Bay are limited to the single investigation of Axelrad *et al* (1979) who reported values for gross productivity ranging from 290 to 1060 mg C m^{-2} day^{-1} (928 - 3392 mg O_2 m^{-2} day^{-1}), rates that represent the higher end of the range for global MPB populations presented by Beardall and Light (1994).

The values presented in Table 5 are based on maximal rates of photosynthesis at the three sites, and are thus not directly comparable to those of Axelrad (1979). However, values for modelled *in situ* gross productivity (Figs 28 to 30) frequently exceed the estimates obtained by Axelrad (1979) and confirm that MBP primary productivity in Port Phillip Bay is amongst the highest found globally.

The respiratory load within the sediments, however, frequently exceeds the gross photosynthetic rate. This is consistently the case in the deep sites as compared to the shallow sites. Consequently, net primary productivity within the sediment community only attains positive values during peaks periods of high incident light and/or low water column attenuation (Figs 28 to 30; lower graphs).

The mean daily rates for MPB primary productivity presented in Figs 28 to 30 may be converted, using continuous records of incoming irradiation, to annual estimates for production at the three sites. These are summarised in Table 8.

Table 8. Annual estimates of *in situ* productivity. Estimates based on Sept 1994 to Sept 1995 annual cycle, monthly P-I parameters and monthly vertical attenuation coefficients.

Site	Depth (metres)	GP ($g\ O_2\ m^{-2}\ y^{-1}$)	R ($g\ O_2\ m^{-2}\ y^{-1}$)	P:R ratio
Werribee	0.9	715.361	1306.941	0.5474
	9.5	140.323	630.687	0.2225
Indented Head	1.1	555.546	599.932	0.9260
	9.5	312.769	742.285	0.4214
Carrum	1.0	429.225	505.497	0.8491
	10	143.915	489.291	0.2941

Estimates of primary productivity based on high frequency sampling of water column attenuation

Daily box-plots for attenuation data calculated at five minute intervals between 09:00 and 15:00 hours for winter 1995 and summer 1996 are presented in Fig 31. Excluding a period of obvious sensor fouling in the summer 1996 deployment (22 Jan - 15 Feb), water column attenuation, Ib, gross production, benthic respiration and P to R ratio data are summarised in Table 9.

Table 9. Mean water column attenuation, Ib, gross production, benthic respiration and P to R ratio data for two in situ data logger deployment programmes (winter and summer) in Port Phillip Bay.

Season	mean attenuation coefficient	mean in situ benthic PFD (μEin m^{-2} d^{-1})	mean GP (mg O_2 m^{-2} d^{-1})	mean R (mg O_2 m^{-2} d^{-1})	P:R ratio
winter '95	0.17 ±0.002	2161.51	187.44	714.95	0.26
summer '96	0.293 ±0.006	4457.26	319.68	1209.91	0.26
W:S ratio	0.57	0.52	0.41	0.41	1.0

These data indicate that despite increased water column attenuation in summer, higher incident photon flux results in greater benthic photon flux density (PFD) and a consequent increase in *in situ* primary productivity by the MPB. The benthic respiration also increases in the same proportion, providing P:R ratios of 0.26 in both seasons, implying that the two process are tightly coupled (see below).

4.4.4. Benthic community respiration.

Significant correlations were found between benthic respiration, *in situ* gross production, bottom water temperature and the previous 8 day integrated benthic-irradiance history ($I_b day^{-8}$). Hierarchical partitioning was used, on this occasion, to elucidate whether variation in benthic community respiration was attributable to one or more of the independent variables measured.

Table 10. Partitioning of results from linear regressions of *in situ* gross production, bottom water temperature and $I_b day^{-8}$ on the dependent variable benthic respiration. Results are for complete data set

	Gross P	Temp	$I_b day^{-8}$	Total
linear regression effects				
Rc	0.5112	0.0686	0.0437	0.6235
Ic	0.4719	0.0319	0.0186	0.5224
Jc	0.0393	0.0367	0.0251	0.1011
percent distribution of effects				
Ic	90.33	6.11	3.56	100.00
Jc	38.87	36.30	24.83	100.00

[*Rc is the zero-order association between the dependent variable and the independent variable, Ic is the independent component of Rc, Jc is the joint component of Rc*]

Separate analyses have been computed for each site / water depth. Results reported in Table 10, for the complete data set, are indicative of trends occurring at all sites. In terms of independent effects, >90 percent of the variation in benthic community respiration is attributable to *in situ* gross production whereas bottom water temperature and $I_b day^{-8}$ appear to be comparatively unimportant. Most of the explanatory power of gross production is unique to itself; the independent contribution of gross production is much larger than the contribution it has in common with other variables. In contrast, both temperature and $I_b day^{-8}$ exhibit joint variation contributions that are much closer to and greater than their independent effects.

Benthic community respiration is closely linked to *in situ* gross production. Results suggest that benthic respiration is not causally related to bottom water temperature or to the previous 8 day integrated benthic-irradiance history.

5. ANNUAL BAY-WIDE ESTIMATES OF BENTHIC CHLOROPHYLL *A* STANDING STOCK AND PRIMARY PRODUCTION

5.1. Introduction and aims

The aims of this section was to use results described in Sections 2 and 4 to arrive at Bay-wide estimates of benthic chlorophyll *a* and primary production in Port Phillip Bay and to use these figures to estimate benthic microalgal N and P requirements in the Bay. These results are then discussed in relation to the energetics and overall nutrient pathways and budgets of the system.

5.2. Methods

The methodology employed in this task is based on results obtained in Sections 2 and 4. The synoptic distribution of surficial chlorophyll *a* (0-10mm sediment stratum) reported in Section 2 (Fig. 7) is the basis to which all estimates are made. For the purpose of this exercise, Port Phillip Bay was divided into three segments (Fig. 32). Each segment contained the depth stratified sites which were sampled as part of Section 4. The rationale for segment boundary location was based on existing data on vertical attenuation and a generalised view of phytoplankton spatial dynamics in Port Phillip Bay (see Beardall *et al*., 1996).

It was necessary to locate several reference position fixes common to the sampling periods for synoptic studies and the temporal sampling series (these were identified as Werribee mid and Carrum deep) and make an appropriate correction. A factor of 2.145 was thus applied to the Section 2 data to account for observed differences in chlorophyll *a* concentration, at a given site, from the synoptic study to that from the seasonal study. From this point, the dynamics of the three depth stratified fixed sampling sites in each segment were used to model the chlorophyll *a* dynamics of all sites within each respective segment. For each month, all new chlorophyll *a* values were combined in a single file, referenced to their respective easting and northing attributes, a new interpolation computed and a map generated. Thirteen chl *a* bins were used (Fig 33).

Using a Geographic Information System (GIS), a 5 bin bathymetry (0-5.0, 5.1-10.0, 10.1-15.0, 15.1-20.0, 20.1-25.0 metre) overlay (Fig. 32) in addition to the three segment boundary overlay was applied to each monthly interpolation and the segment x depth bin x chlorophyll *a* bin areal coverages were output to file.

Midpoint values were used in all depth bin and chlorophyll *a* bin calculations. Mean hourly *in situ* photon flux density (PFD) was calculated for each month x segment x depth bin combination based on a continuous record of incident PAR and monthly *in situ* vertical attenuation data. Mean monthly parameterised models describing chlorophyll *a* adjusted Gross P_{max} and irradiance at fixed sites, and therefore their respective segments, formed the final input to the model.

For each month, chlorophyll *a* biomass was calculated for each segment according to the equation:

$$\Sigma((a_1 \times b_1)+(a_2 \times b_2)+ .... (a_n \times b_n))$$

where: a = chlorophyll *a* bin and b = areal coverage (m^2).

For each month, assuming a 12hr light:12hr dark day, *in situ* gross production was calculated for each segment according to the equation:

$$\Sigma((a_1 \times b_1 \times c_1)+(a_2 \times b_2 \times c_2)+ .... (a_n \times b_n \times c_n)) \times 12 \times 30.417$$

where: a = chlorophyll *a* bin, b = areal coverage (m^2) and c = mean chlorophyll *a* adjusted *in situ* gross production (mg C m^{-2} hr^{-1}).

For each month, benthic respiration was calculated for each segment according to the equation:

$$(d \times e) \times 24 \times 30.417$$

where d = segment areal coverage (m^2) and e = mean benthic respiration (mg C m^{-2} hr^{-1})

5.3. Results and Discussion

5.3.1. Annual productivity of MPB and sediment communities.

Estimates for *in situ* gross production over an annual cycle in Port Phillip Bay have been made for an area totalling 1, 764 km^2. Two small segments totalling 168 km^2 were omitted from the final calculations due to poor field coverage during the sampling programme. A further area (water depth > 25 metres) of negligible size was also omitted. Values for the yearly annual production at the three study sites are shown in Table 11.

Table 11. Modelled annual production and respiration rates of sediments in segments of Port Phillip Bay. GP = gross production, R = respiration, NP = net production.

Segment	Area (m^2)	GP (g C y^{-1})	R (g C y^{-1})	NP (g C y^{-1})
Werribee	7.20×10^8	64.369×10^9	217.977×10^9	-153.608×10^9
Indented Head	5.75×10^8	43.063×10^9	120.590×10^9	-77.527×10^9
Carrum	4.69×10^8	11.843×10^9	72.899×10^9	-61.056×10^9
Total	17.64×10^8	119.275×10^9	411.466×10^9	-292.191×10^9

Despite high gross production rates of benthic microalgae in Port Phillip Bay, the net production rates of the benthic community as a whole indicates a net loss of carbon

from the system. It is important to emphasise that the respiratory requirements of the sediment is a community parameter and represents consumption by the entire benthos (faunal, bacterial, any chemical demand by the sediment itself) including the benthic microalgae. It is pointless to discuss net benthic microalgal production because we know nothing about the respiratory requirements of the benthic microalgae. It is more appropriate to discuss sediment energetics in terms of net benthic community production or benthic microalgal gross production. Thus, under *in situ* photon flux, benthic microalgae supplied approximately 30 percent of the total organic carbon respired by the sediment over the course of an annual cycle.

Production/respiration ratios of 10 have been established for phytoplankton. As an exercise to examine the potential importance of benthic microalgal production to the energetics of the Port Phillip Bay system, a benthic microalgal respiration rate equating to 10 percent of gross benthic microalgal Pmax can be applied to the data and the estimates re-calculated (Table 12).

Table 12. Modelled annual production and respiration rates for benthic microalgae in segments of Port Phillip Bay. Benthic microalgal respiration rates assume a P:R ratio of 10. GP = gross production, R = respiration, NP = net production.

Segment	GP (g C y-1)	R (g C y-1)	NP (g C y-1)
Werribee	64.369×10^9	22.718×10^9	41.651×10^9
Indented Head	43.063×10^9	8.968×10^9	34.095×10^9
Carrum	11.843×10^9	6.140×10^9	5.703×10^9
Total	119.275×10^9	37.826×10^9	81.449×10^9

These budgets indicate that up to 70 percent of the organic carbon fixed annually by benthic microalgae (81.449×10^9 g C) is available as a source of carbon to the Port Phillip Bay system.

Assuming a C to chlorophyll *a* ratio of 50 (de Jonge 1980), these data may be used to estimate mean turnover times for the MPB populations in the Bay (Table 13).

Table 13. Modelled annual productivity, biomass and turn-over rates for benthic microalgae in Port Phillip Bay. Carbon equivalents for chlorophyll *a* assumes a carbon:chlorophyll *a* ratio of 50.

Segment	GP (g C y^{-1})	Biomass (g Chl a y^{-1})	Biomass (g C y^{-1})	Turn-over (fix biomass^{-1} y^{-1})
Werribee	64.369×10^9	21.6×10^6	1080.0×10^6	59.6
Indented Head	43.063×10^9	19.7×10^6	985.0×10^6	43.7
Carrum	11.843×10^9	7.4×10^6	369.0×10^6	32.0
Total	119.275×10^9	48.7×10^6	2434.0×10^6	49.0

The data in Table 13 indicate that the MPB populations turn over at a rate of once every 6 to 11 days. Werribee populations showed the most rapid turnover with those at Carrum exhibiting the slowest.

5.3.2. Nutrient cycling

The MPB in Port Phillip Bay have high nutrient requirements. Using Redfield stoichiometry, the Bay-wide carbon fixation rate equates to benthic microalgal N and P requirements of 21 x 10^9 and 2.9 x 10^9 g y^{-1} respectively (Table 14). By comparison, annual external N and P loads to the Bay are in the vicinity of 5.5 x 10^9 and 1.4 x 10^9 g y^{-1} respectively. High turn-over rates (Table 13) imply rapid nutrient regeneration rates, putting these annual N and P requirements into perspective. Benthic microalgae are also located at the sediment-water interface, which is the site of maximum nutrient regeneration.

Table 14. Modelled annual gross production and nutrient requirements for benthic microalgae in segments of Port Phillip Bay. Total N and P requirements are based on Redfield stoichiometry.

Segment	GP (g C y^{-1})	N - use (g y^{-1})	P - use (g y^{-1})
Werribee	64.369 x 10^9	11.335 x 10^9	1.569 x 10^9
Indented Head	43.063 x 10^9	7.583 x 10^9	1.049 x 10^9
Carrum	11.843 x 10^9	2.086 x 10^9	0.289 x 10^9
Total	119.275 x 10^9	21.004 x 10^9	2.907 x 10^9

Nutrient uptake at the sediment surface in conjunction with high turn-over and rapid regeneration rates has important implications for the cycling of these nutrients, particularly nitrogen, in the Port Phillip Bay system. Nitrogen assimilation at the sediment surface is of direct importance to denitrification rates measured in Port Phillip Bay. These rates have been estimated as the difference between predicted (from oxygen/carbon dioxide fluxes) and observed nitrogen fluxes (Nicholson *et al*., 1996). In the light of nitrogen requirements of benthic microalgae reported here, denitrification rates measured by Nicholson *et al*. (1996) might be over-estimated. Some of the nitrogen difference between predicted and observed will be attributable to MPB nutrient assimilation.

In addition to direct assimilation, MPB can influence nutrient fluxes from the sediment by regulating oxygen conditions at the sediment water interface as well as nutrient exchange processes. Specifically, benthic microalgae can, on a diurnal basis, increase the oxic microlayer at the sediment surface where bacterial action mineralises particulate organic nitrogen to ammonia (Sundback *et al*., 1991). If the ammonia is not assimilated directly by MPB at the sediment surface it can be oxidised to nitrate by nitrifying bacteria in the diurnal oxic microlayer created by benthic microalgal photosynthesis (Rysgaard *et al*., 1993). Similarly, benthic microalgal respiration may lead to diurnal anoxia at the sediment interface enabling nitrate to be reduced by denitrifying bacteria to nitrogen gas which is lost from the system (Rysgaard *et al*., 1995). By regulating the oxygen conditions at the sediment surface via photosynthesis, benthic microalgae can also physically control the release and retention of phosphates (Masini 1987). Benthic microalgal mediated nutrient fluxes between the sediment and overlying water column is currently the subject of on-going research at Monash University.

5.3.3. Comparison of MPB Production with other Primary Producers in Port Phillip Bay

Irrespective of phototrophic group, primary productivity data pertaining to Port Phillip Bay are scant. Several comparisons have been sought from the literature. Different methods have been used to measure productivity in each instance, however, the estimates are reported here for comparative purposes. Excluding phytoplankton, it is also important to emphasise that benthic microalgae occupy the dominant habitat in Port Phillip Bay (ie., bare sand either colonised or uncolonised by macrophytes; see MPB distribution). By comparison, seagrass and benthic macrophytes (soft and hard substrate) occupy limited areas of Port Phillip Bay.

Data on benthic microalgal and phytoplankton biomass and productivity at Werribee, Port Phillip Bay, are summarised in Table 15. Both benthic microalgae and phytoplankton exhibit a winter minimum in primary productivity at Werribee. Despite the marked difference in habitat volume (1m x 1m x 0.05m = benthic microalgae cf. 1m x 1m x 8.5m = phytoplankton), benthic microalgae show a three-fold increase in biomass compared to phytoplankton. *In situ* daily net production rates indicate a large carbon deficit in the case of benthic microalgae, which is an artefact of benthic community respiratory processes. However, using a P:R ratio of 10, *in situ* daily net production of benthic microalgae increases to approximately half that of the total overlying water column production. In terms of light quantity, benthic microalgae receive far less than their water column counter-parts.

Table 15. Comparison between sediment and water column biomass and production at Werribee, Port Phillip Bay.

	Sediment	Water column
Sampling date	Aug 1995	Aug 1993, Aug 1994
mean water depth	9.5 m	8.5 m
plant biomass (mg C m^{-2})	384.5 ± 26.0	108.2 ± 34.2
Production (mg C m^{-2} day^{-1})		
daily gross	185.5 ± 50.1	500.0
daily net	-527.5 ± 50.0	400.0
	150.0 (P:R = 10)	
turn-over	0.49	4.60
source of data	this study	Beardall et al 1996

Biomass and productivity data for benthic microalgae and the dominant seagrass *Heterozostera tasmanica* in the Indented Head region of Port Phillip Bay are summarised in Table 16. Both benthic microalgae and *H. tasmanica* show a summer maxima in primary production in this region. Despite a 40-fold difference in biomass, benthic microalgae exhibit greater daily production on either a gross or estimated net basis when compared to this seagrass species. Specific growth rates indicate that although the benthic microalgal biomass is low, turn-over rate is some 40-fold faster than *H. tasmanica*.

Table 16. Comparison between sediment and seagrass system biomass and production at Indented Head, Port Phillip Bay.

	Sediment	Heterozostera tasmanica
Sampling date	Feb 1975	Feb 1979
mean water depth	1.0 m	0.6 m
plant biomass (mg C m^{-2})	1.30 ± 0.25	43.0 ± 5.0
Production (mg C m^{-2} day^{-1})		
daily gross	1.45	1.08
daily net	0.75	0.72
	1.16 (P:R = 10)	
turn-over	1.12	0.025
source of data	this study	Bulthuis & Woelkerling (1983)

Comparative biomass and productivity data for a mixed reef macroalgal assemblage and benthic microalgae at Werribee, Port Phillip Bay are presented in Table 17. This macroalgal assemblage is composed of fast growing annual species (*Ulva*, *Enteromorphora*, *Cladophora*) which are recognised as important contributors to aquatic primary productivity. These taxa grow rapidly and respond positively to nutrient enrichment (Brown *et al*., 1980). Despite this widely accepted view, benthic microalgae compete surprisingly well; under *in situ* photon flux they fix approximately 25 percent as much carbon as the fast-growing annual reef macroalgae, on an aerial basis, and more per unit biomass. These results are based on reef areas being 100 percent vegetated which they are invariably not.; Port Phillip Bay harbours a notable absence of hard substrate (Womersley 1966), compared to soft substrate harbouring benthic microalgae.

Table 17. Comparison between sediment and mixed macroalgal reef biomass and production at Werribee, Port Phillip Bay.

	Sediment	Mixed reef macroalgae
Sampling date	1994/1995	1979
mean water depth	1 m	1 m
plant biomass (mg C m^{-2})	3.08 ± 0.46	17.5
Production (mg C m^{-2} day^{-1})		
daily gross	1.19	4.68
daily net	0.06	3.02
	0.95 (P:R = 10)	
turn-over	0.38	0.27
source of data	this study	Brown et al., (1980)

It can therefore be concluded that benthic microalgae play a significant role in terms of primary production in Port Phillip Bay. Compared to some of the more traditional and conspicuous phototrophic compartments benthic microalgae must be considered as important contributors to the flow of organic carbon and the overall energetics of the Port Phillip Bay system.

6. ACKNOWLEDGMENTS

Melbourne Water Corporation as part of the Port Phillip Bay Environmental Study funded this work.

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8. FIGURES

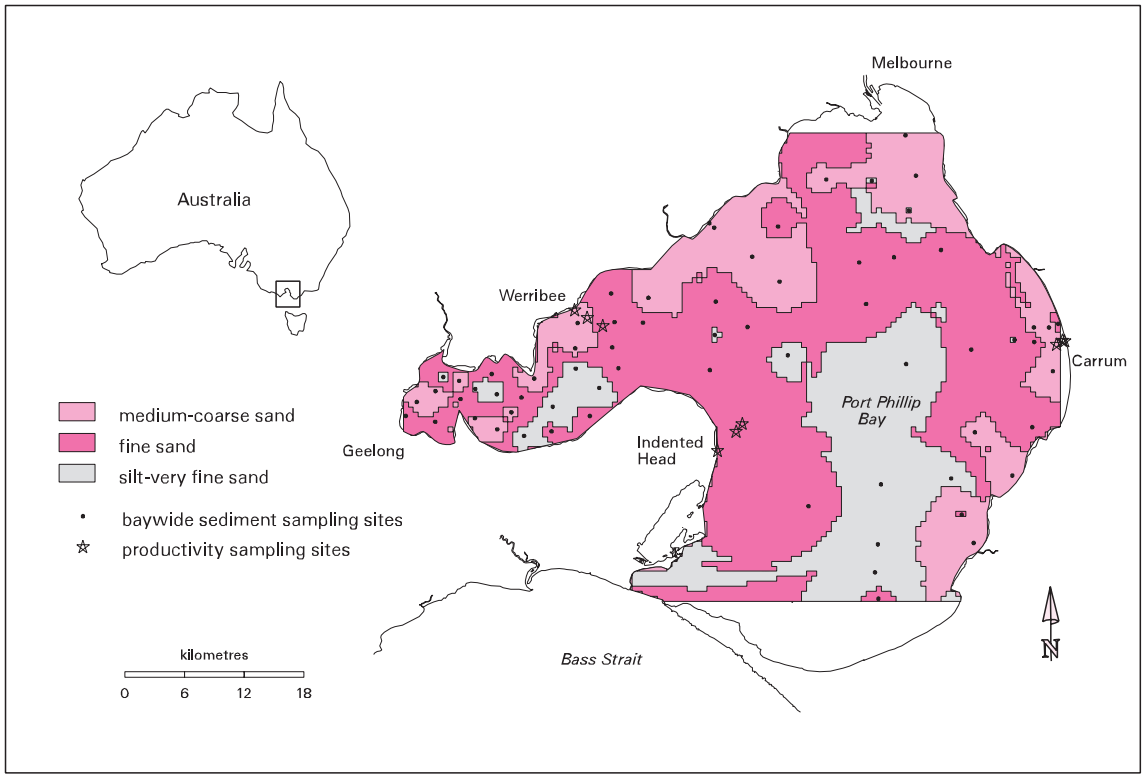


Fig. 1. Location map of Port Phillip Bay showing sampling sites for Bay-wide chlorophyll *a* distribution and fixed site biomass and primary productivity sampling programmes. Interpolated distribution of three broad sediment types in Port Phillip Bay.

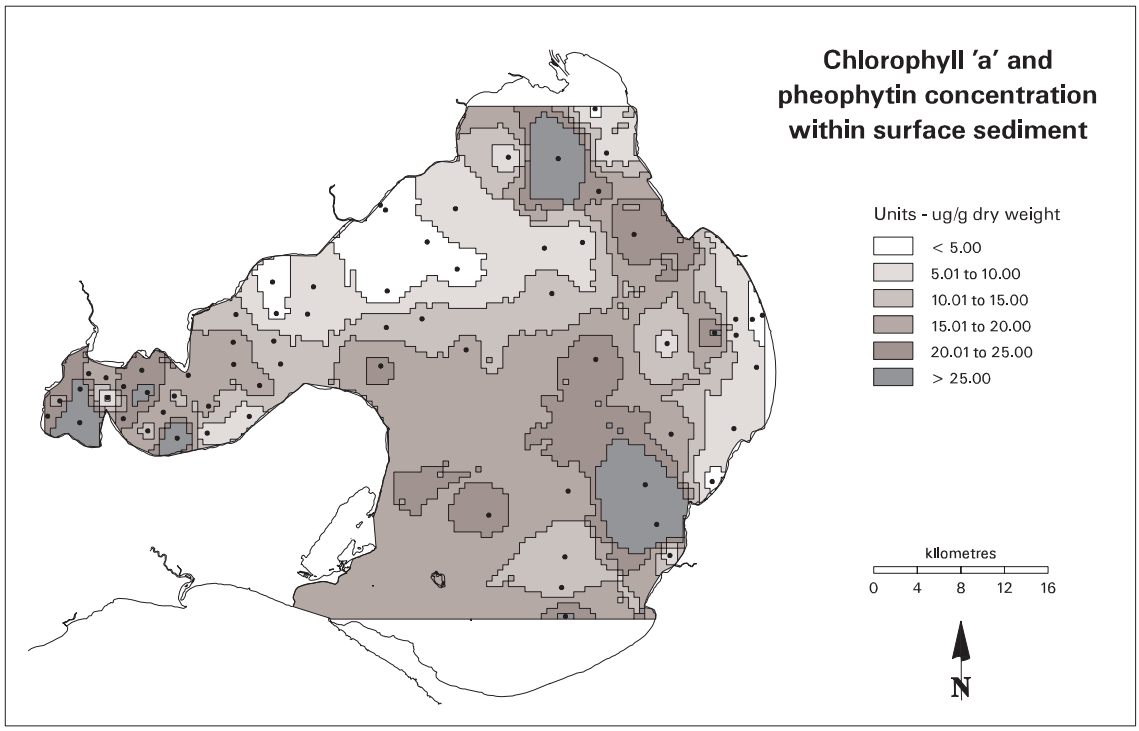


Fig. 2. Interpolated distribution (µg/g) of total chlorophyll *a* (functional chlorophyll + pheophytin) concentration in Port Phillip Bay surficial sediments (0-10mm).

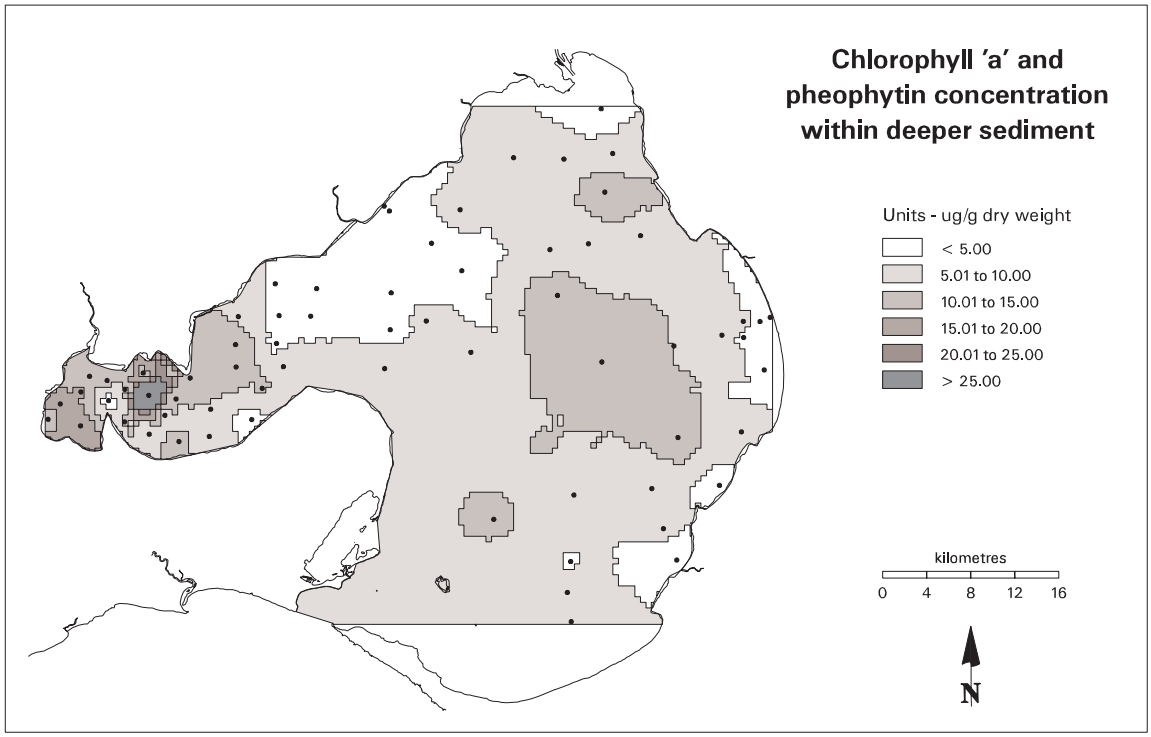


Fig. 3. Interpolated distribution (µg/g) of total chlorophyll *a* (functional chlorophyll + pheophytin) concentration in Port Phillip Bay deeper sediments (10-20mm).

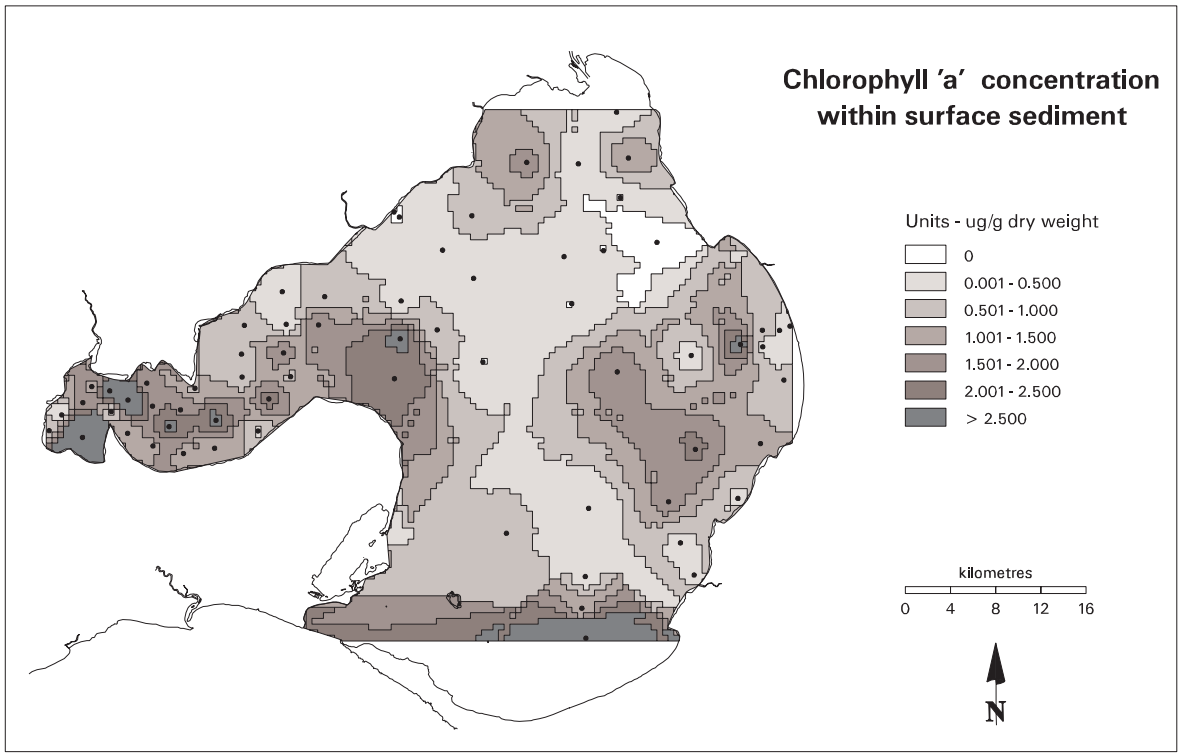


Fig. 4. Interpolated distribution (µg/g) of functional chlorophyll *a* concentration in Port Phillip Bay surficial sediments (0-10mm).

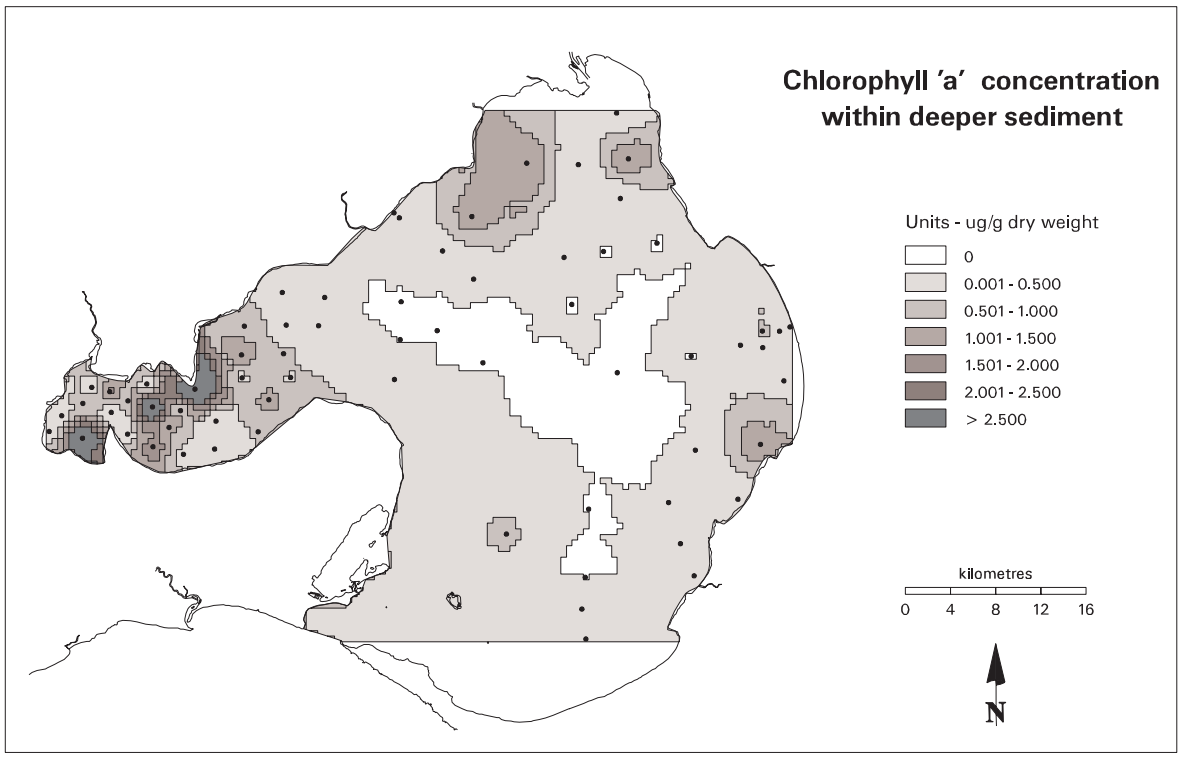


Fig. 5. Interpolated distribution (µg/g) of functional chlorophyll *a* concentration in Port Phillip Bay lower sediments (10-20mm).

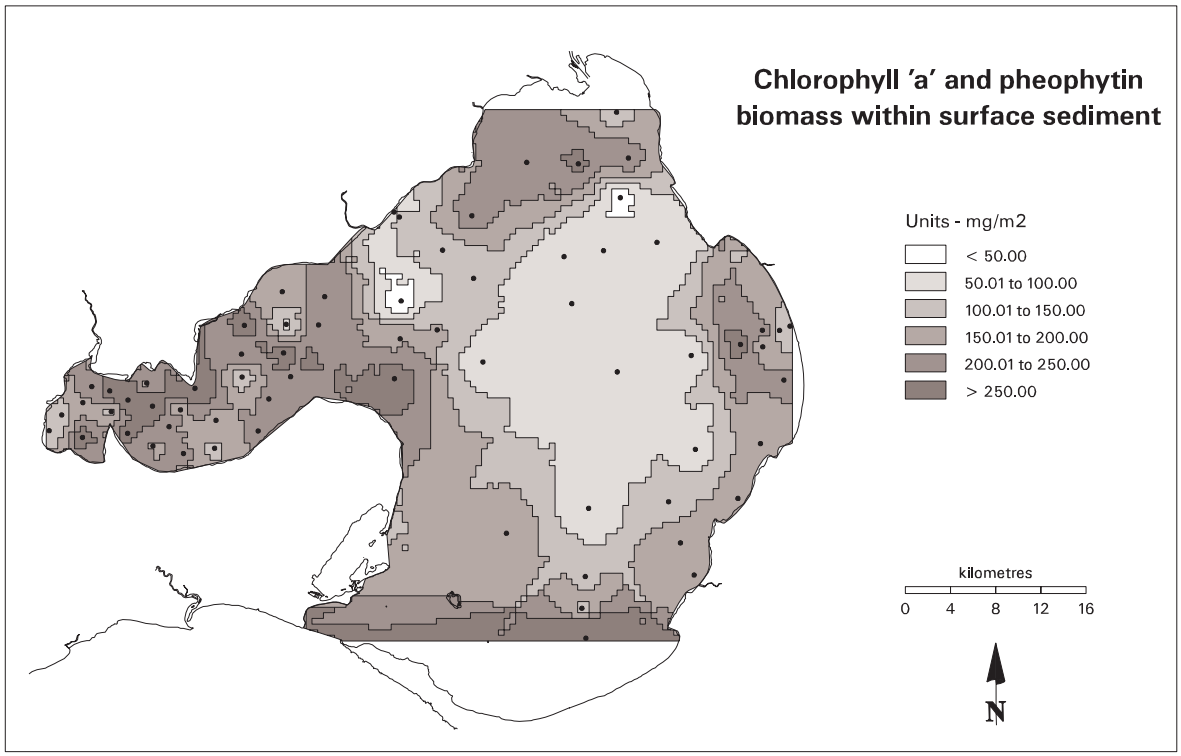


Fig. 6. Interpolated distribution (mg/m^2) of total chlorophyll *a* (functional chlorophyll + pheophytin) biomass in Port Phillip Bay surficial sediments (0-10mm).

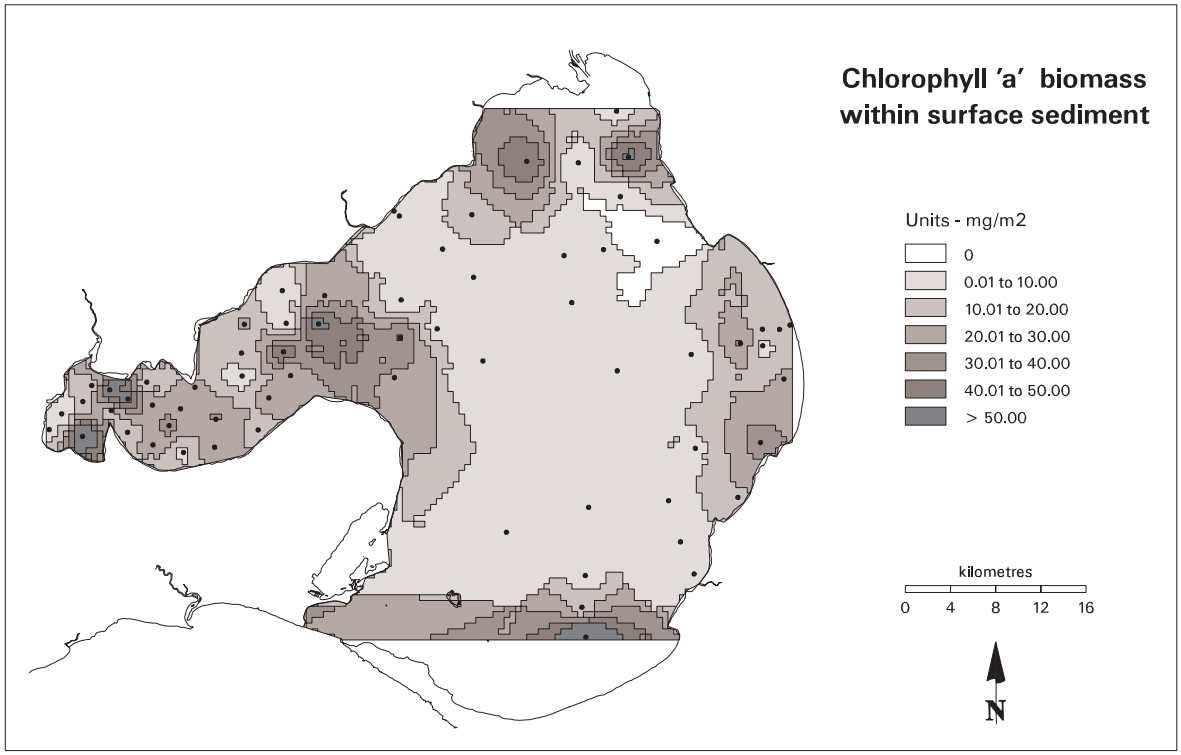


Fig. 7. Interpolated distribution (mg/m^2) of functional chlorophyll *a* biomass in Port Phillip Bay surficial sediments (0-10mm).

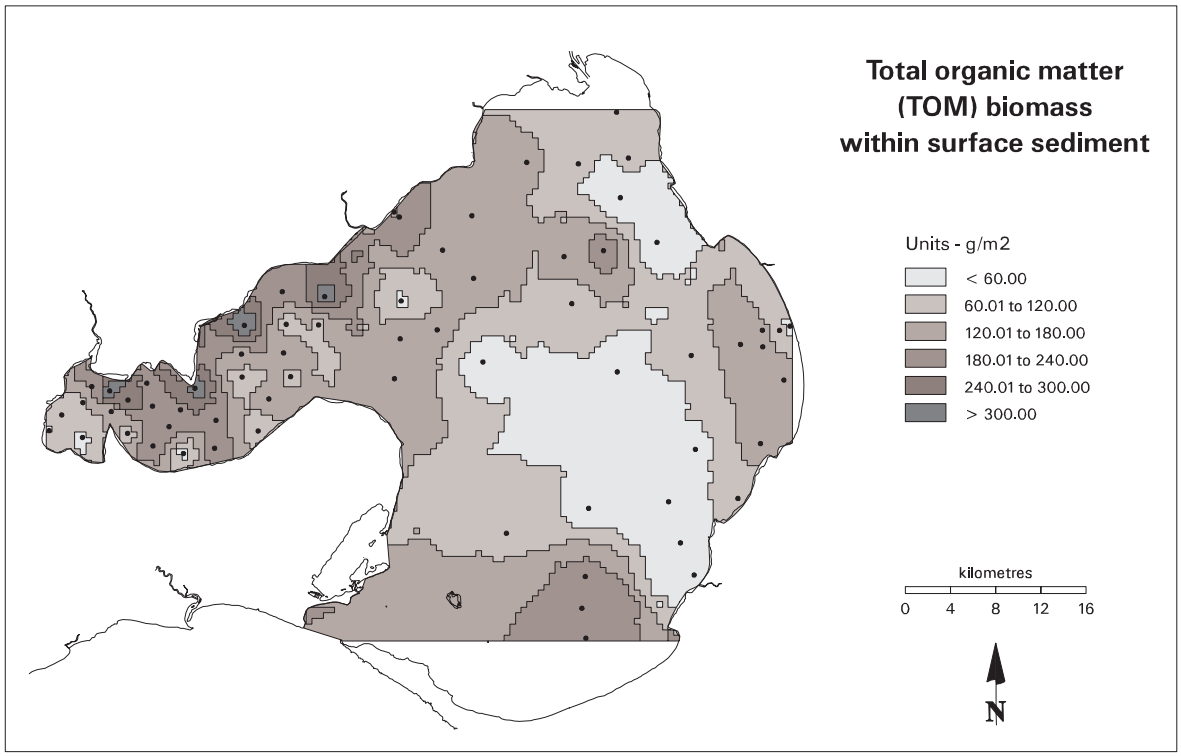


Fig. 8. Interpolated distribution (g/m^2) of total organic matter biomass in Port Phillip Bay surficial sediments (0-10mm).

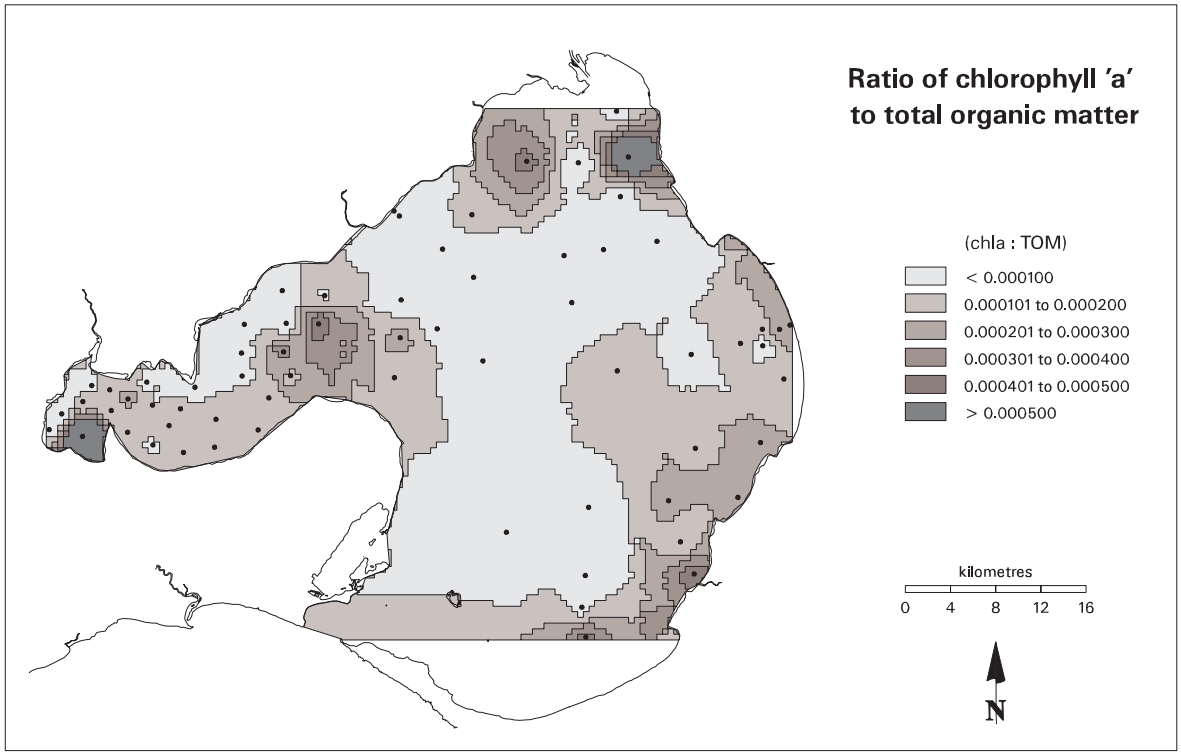


Fig. 9. Interpolated distribution of autotrophic index in Port Phillip Bay surficial sediments (0-10mm).

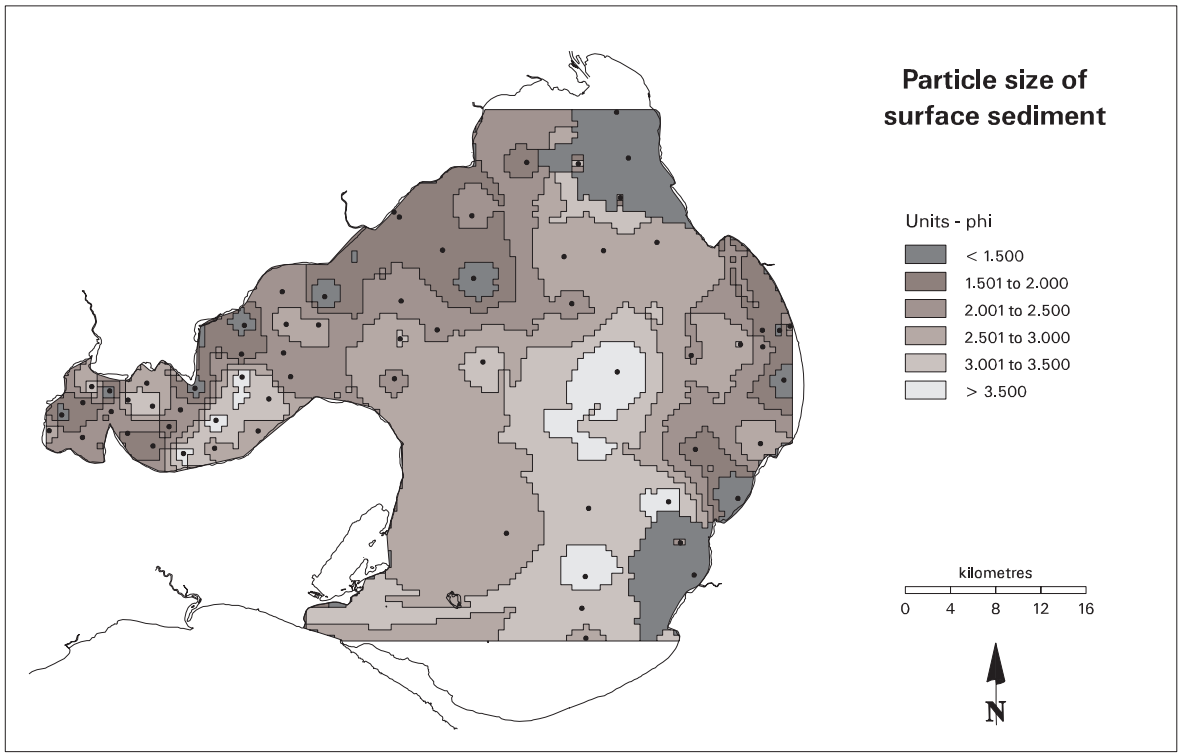


Fig. 10. Interpolated distribution of particle size (phi units) in Port Phillip Bay.

Fig. 11. Bottom water temperatures at the Werribee, Indented Head and Carrum shallow and deep water sites over the 12-month sampling period.

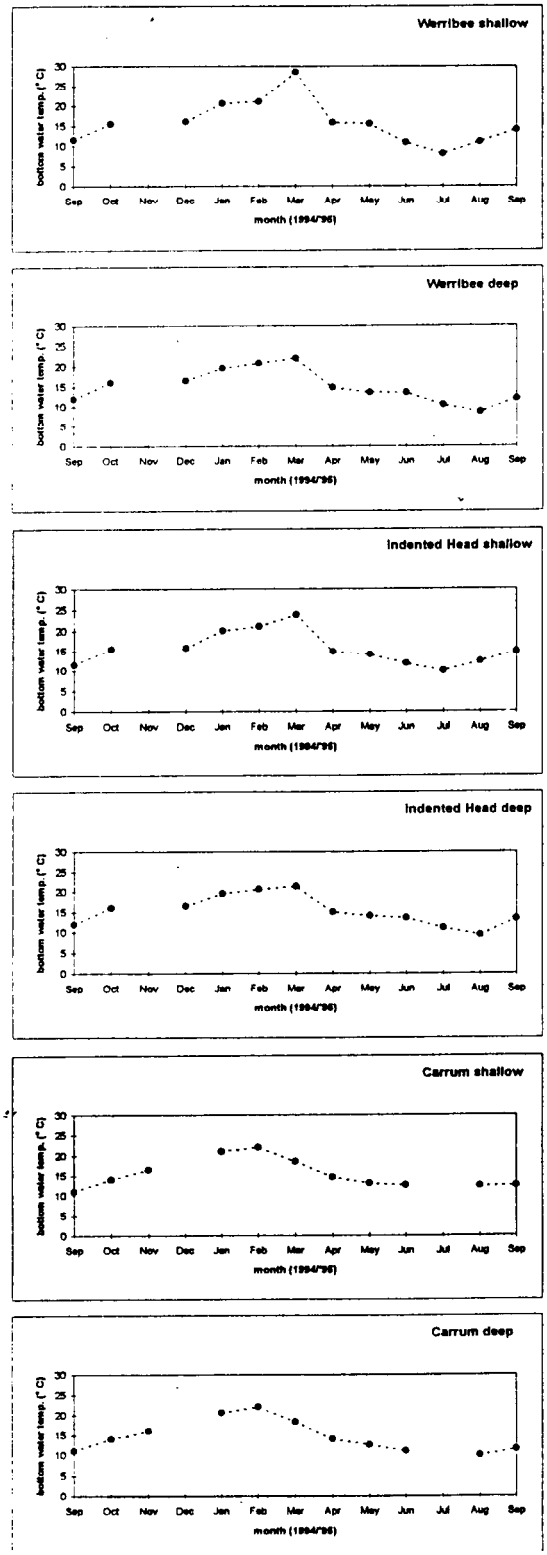


Fig. 12. Proportion of incident PAR reaching the bottom at the Werribee, Indented Head and Carrum shallow and deep water sites over the 12-month sampling period.

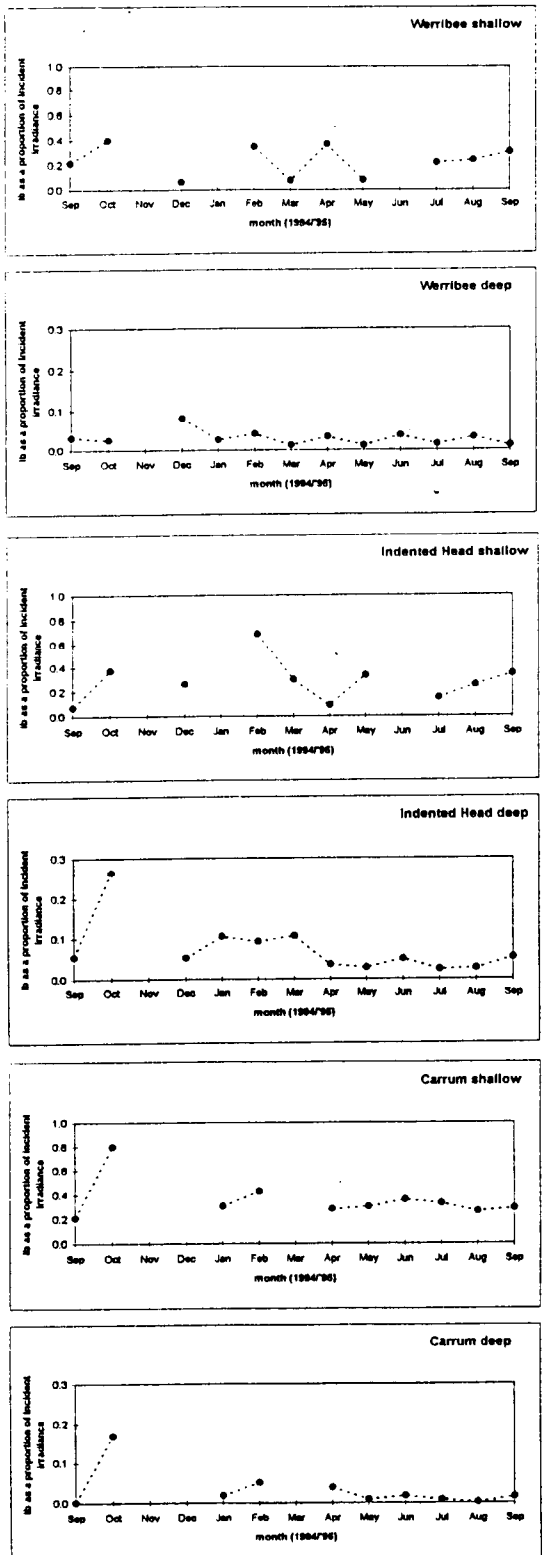


Fig. 13. Relative proportion of chlorophylls *a*, *b* and *c* comprising the microphytobenthos at the Werribee, Indented Head and Carrum shallow and deep water sites over the 12-month sampling period.

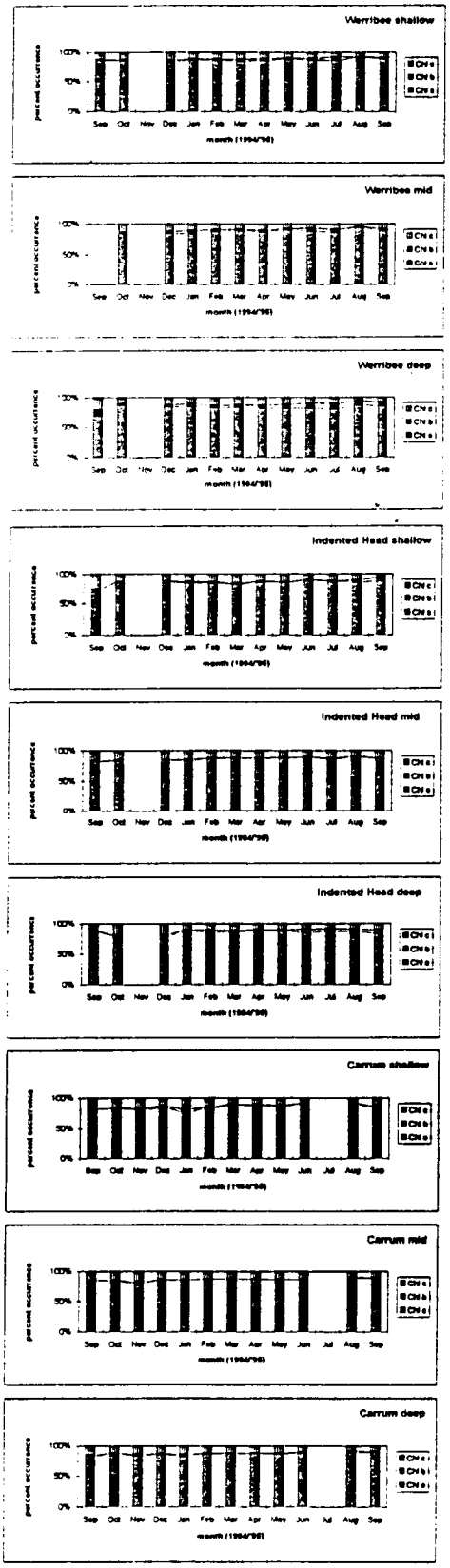


Fig. 14. Chlorophyll *a* biomass (mg/m^{-2}) in the upper 5mm of sediment at the Werribee, Indented Head and Carrum shallow mid and deep water sites over the 12-month sampling period. Values are the mean ±1 SE (n=12).

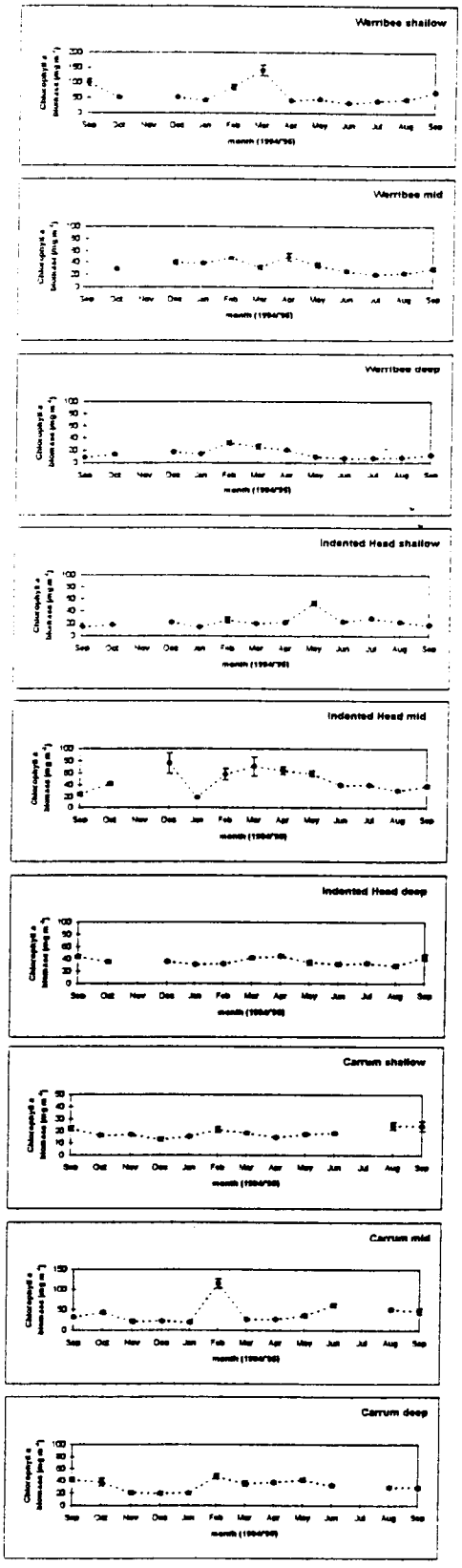


Fig. 15. Chlorophyll *a* concentration ($\mu g/g^{-1}$ Du) in the upper 5mm of sediment at the Werribee, Indented Head and Carrum shallow and deep water sites over the 12-month sampling period. Values are the mean ±1 SE (n=12).

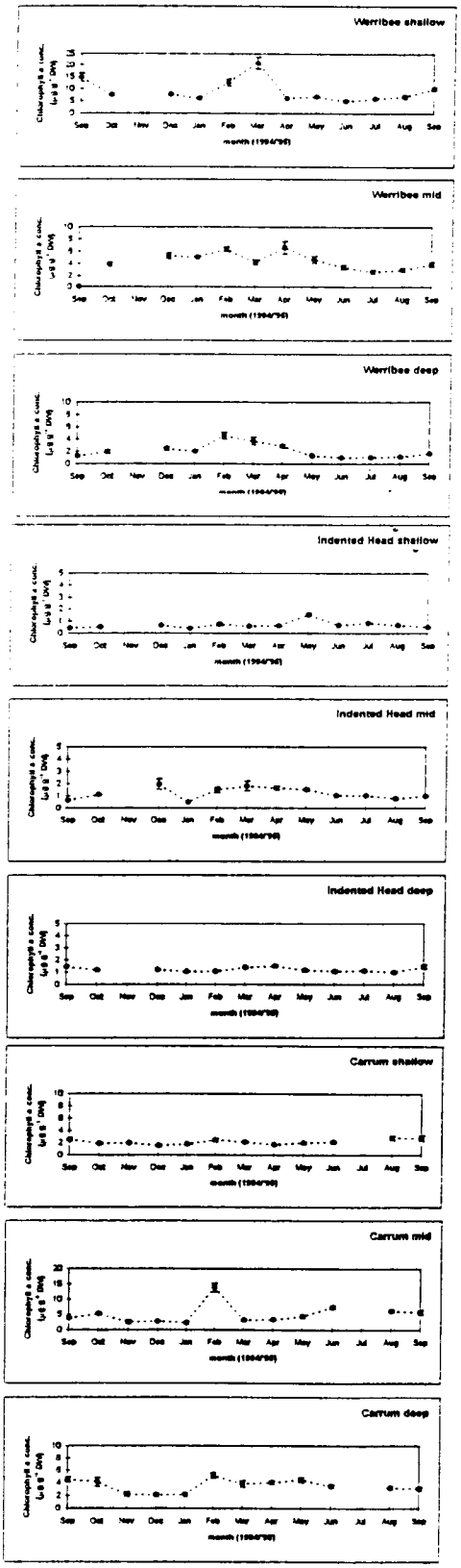


Fig. 16. Pheophytin *a* biomass (mg/m^2) in the upper 5mm of sediment at at the Werribee, Indented Head and Carrum shallow and deep water sites over the 12-month sampling period. Values are the mean ±1 SE (n=12).

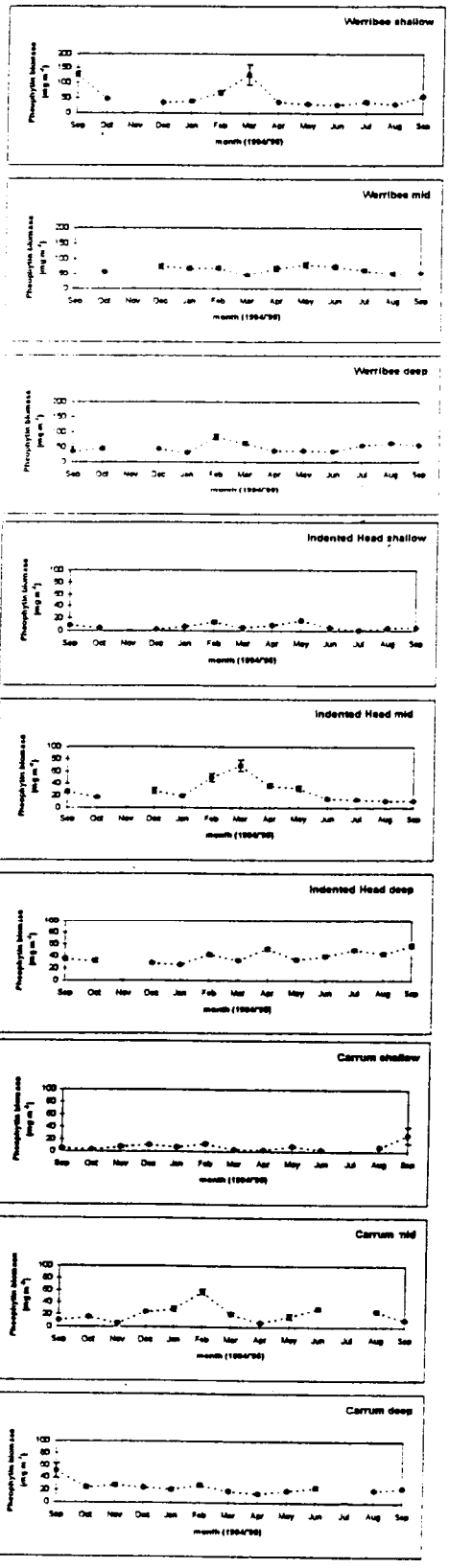


Fig. 17. Pheophytin *a* concentration ($\mu g/g^{-1}$ Du) in the upper 5mm of sediment at at the Werribee, Indented Head and Carrum shallow, mid and deep water sites over the 12-month sampling period. Values are the mean ±1 SE (n=12).

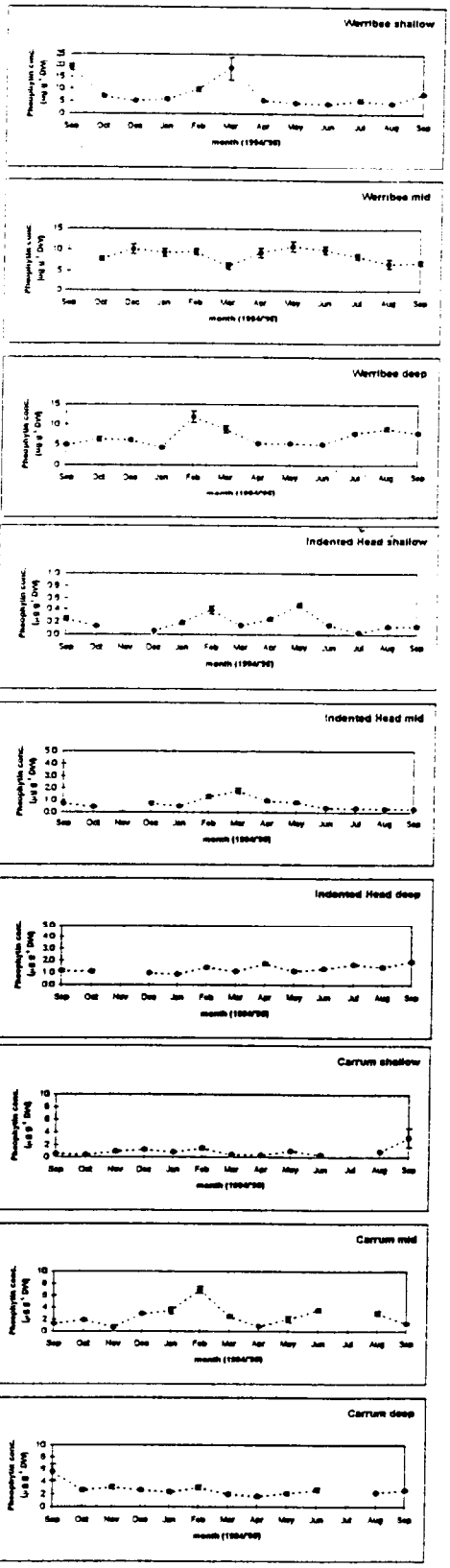


Fig. 18. The ratio of functional chlorophyll *a* to total chlorophyll *a* in the upper 5mm of sediment at at the Werribee, Indented Head and Carrum shallow, mid and deep water sites over the 12-month sampling period. Values are the mean ±1 SE (n=12).

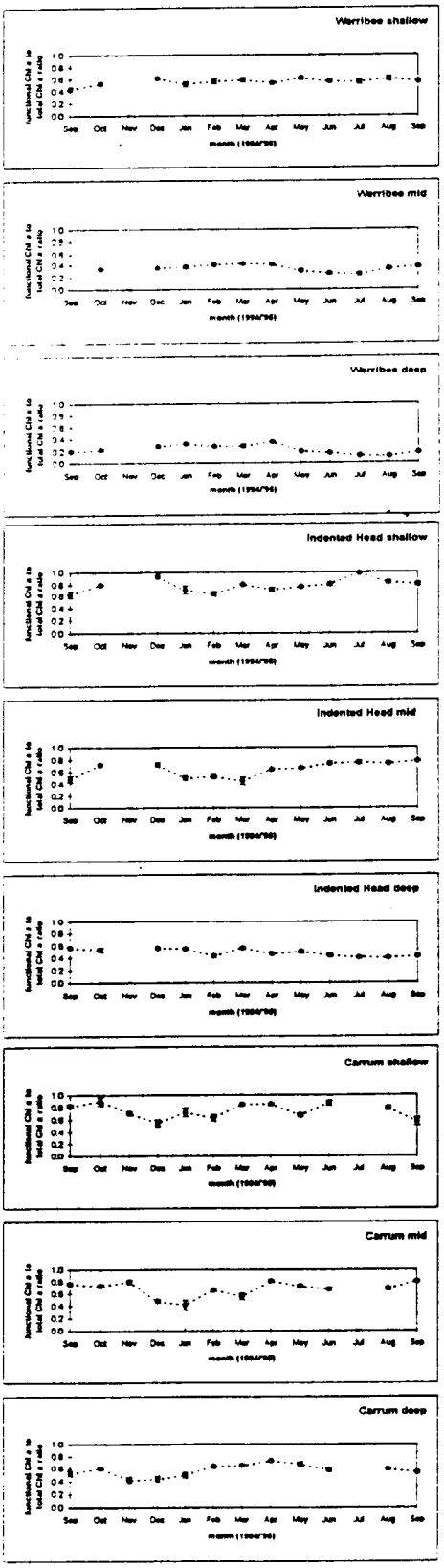
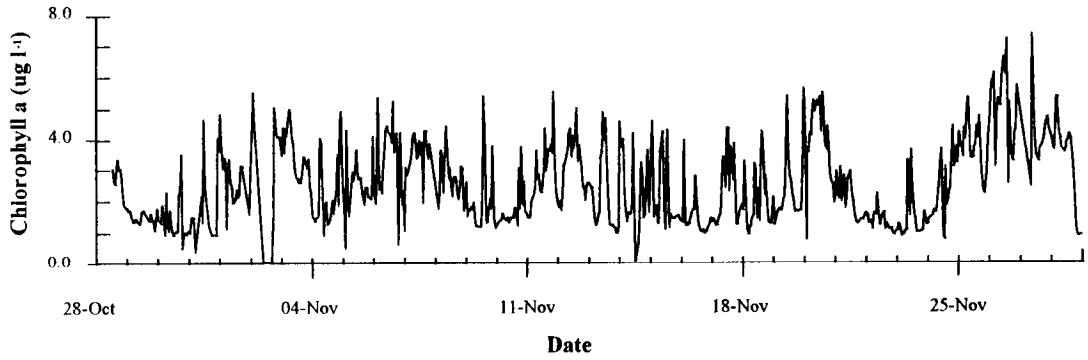


Fig. 19. Chlorophyll *a* fluorescence detected during a SEDCAM deployment at Werribee (water depth=6m) and at Sandringham (water depth=15m). The Seatech fluorometer was situated 0.4m above the benthos.

Sedcam deployment #3 - 1994
Site: Werribee
Height above benthos: 40 cm
Water depth: 6 m



Sedcam deployment #2 - 1994
Site: Sandringham
Height above benthos: 40 cm
Water depth: 15 m

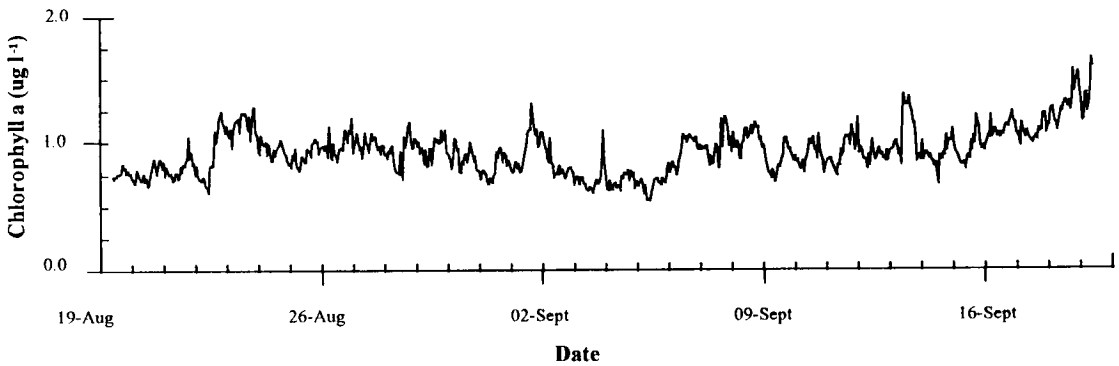


Fig. 20. The index of mixing or strata heterogeneity with respect to functional chlorophyll *a* at the Werribee, Indented Head and Carrum shallow and deep water sites over the 12-month sampling period. Values are the mean ±1 SE (n=12).

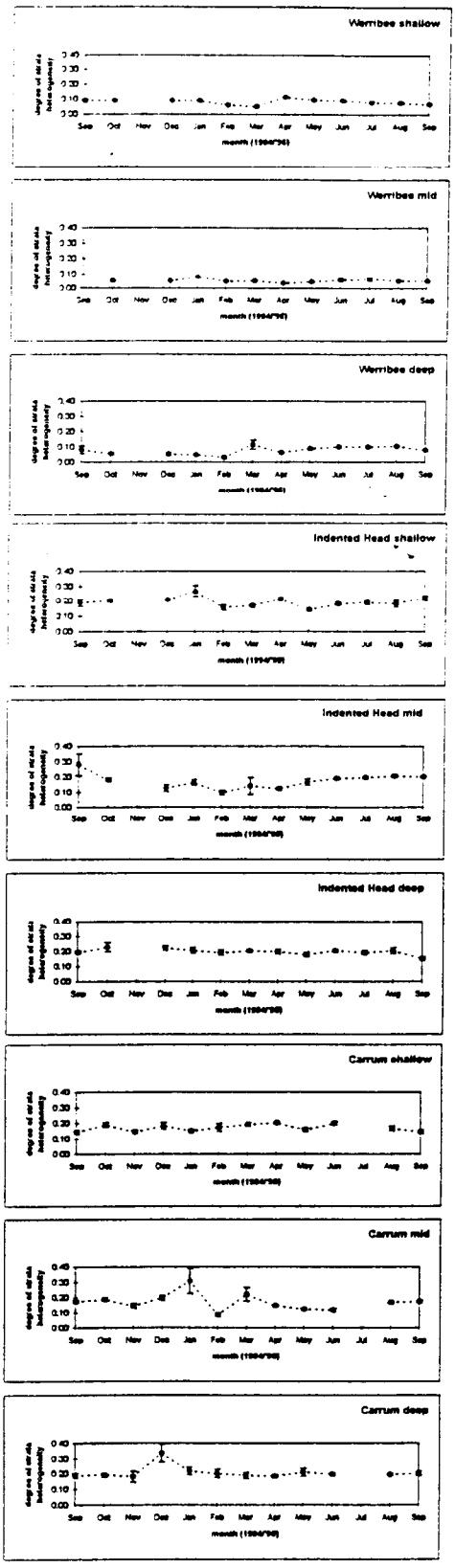


Fig. 21. Gross photosynthetic capacity (as mg $O_2/m^2/hr$) of MPB at the Werribee Indented Head and Carrrum shallow and deep water sites over the 12-month sampling period. Values are the mean ±1 SE (n=3).

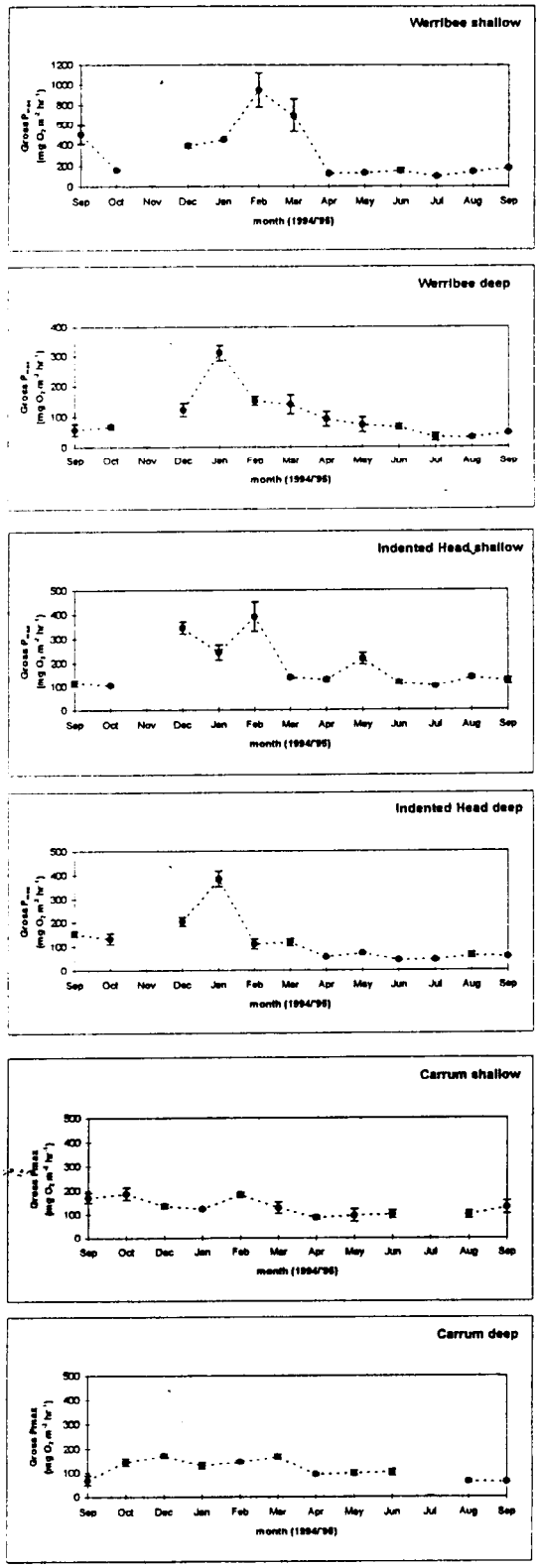


Fig. 22. Assimilation number of MPB at the Werribee, Indented Head and Carrum shallow and deep water sites over the 12-month sampling period. Values are the mean ±1 SE (n=3).

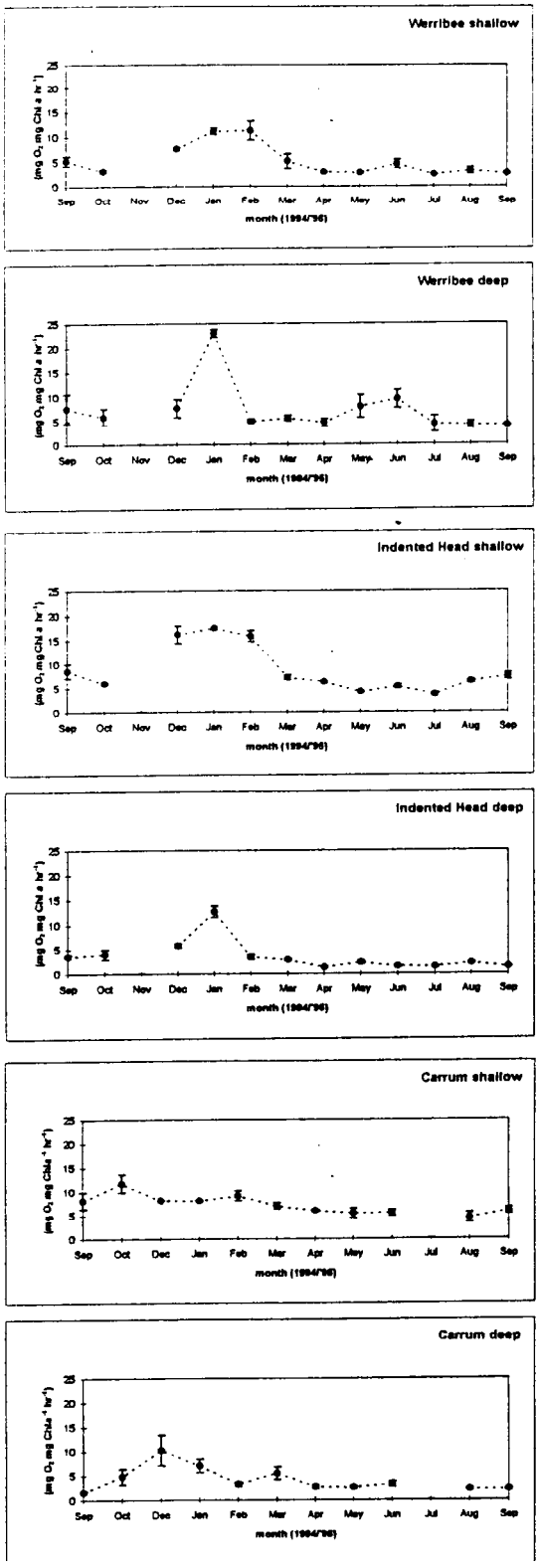


Fig. 23. The theoretical saturating irradiance (*Ik*) in relation to benthic irradiance (monthly attenuation) and benthic irradiance (mean attenuation) of MPB at the Werribee shallow and deep water sites over the 12-month sampling period. Values are the mean ±1 SE (n=3).

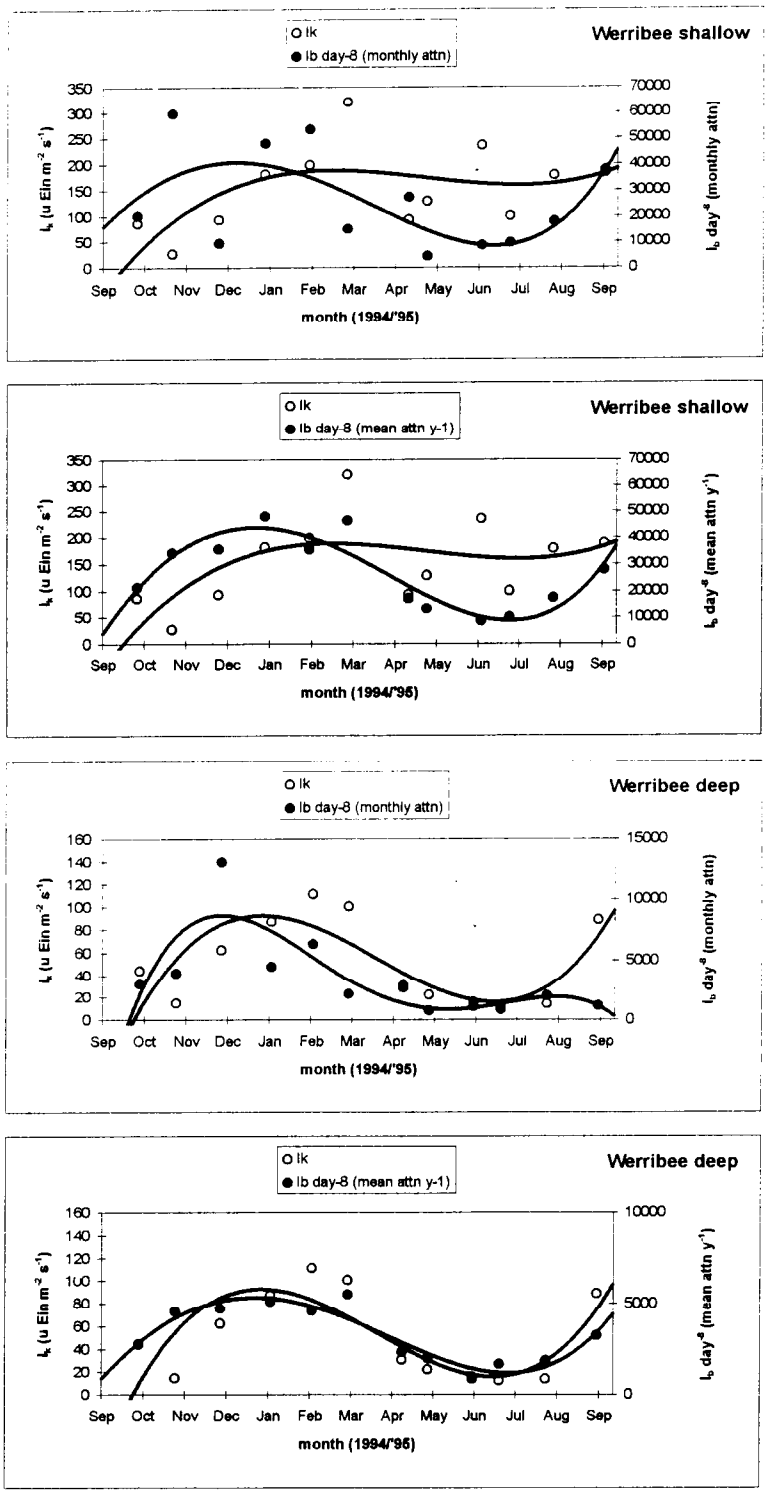


Fig. 24. The theoretical saturating irradiance (*Ik*) in relation to benthic irradiance (monthly attenuation) and benthic irradiance (mean attenuation) (see text) of MPB at the Indented Head shallow and deep water sites over the 12-month sampling period. Values are the mean ±1 SE (n=3).

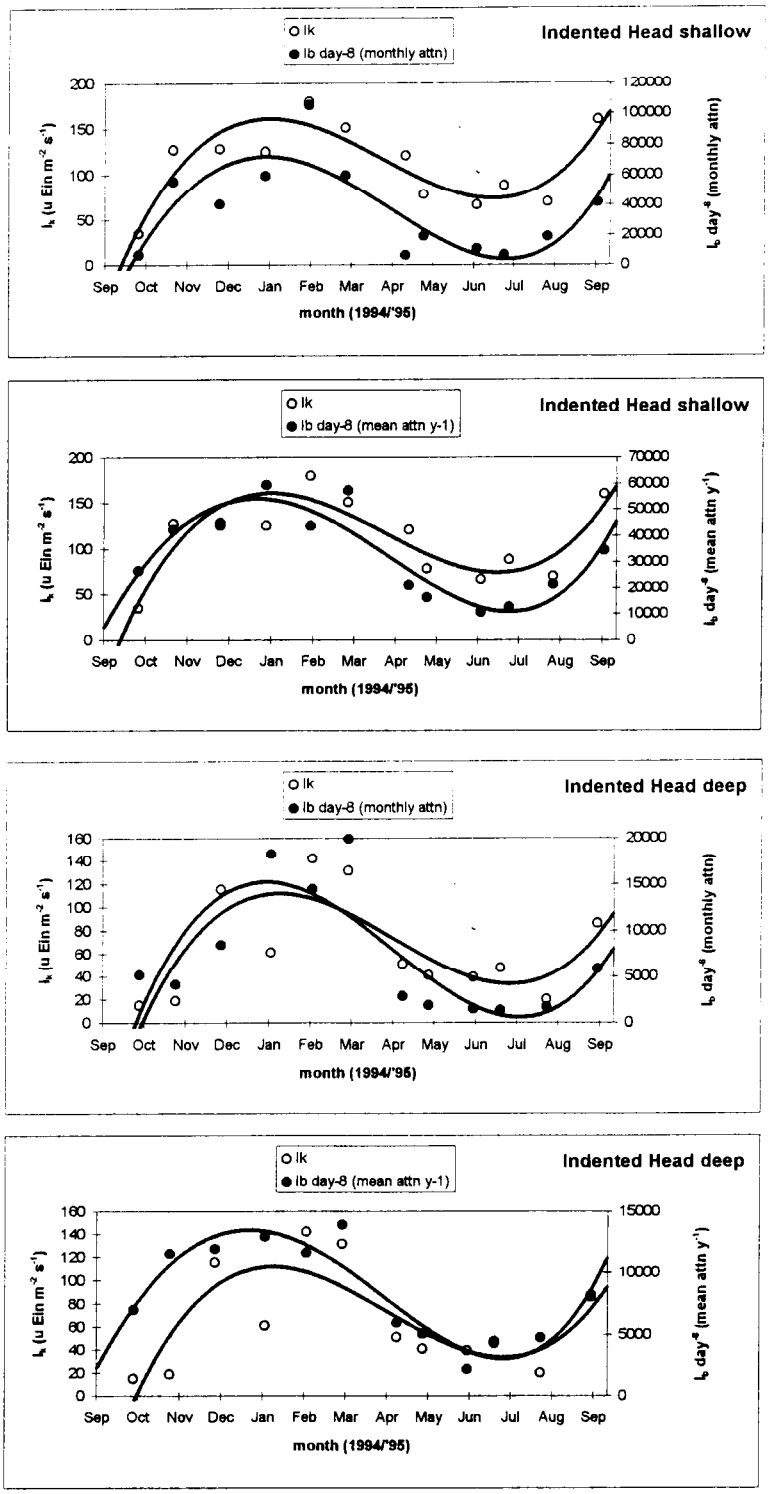


Fig. 25. The theoretical saturating irradiance (*Ik*) in relation to benthic irradiance (monthly attenuation) and benthic irradiance (mean attenuation) (see text) of MPB at the Carrum shallow and deep water sites over the 12-month sampling period. Values are the mean ±1 SE (n=3).

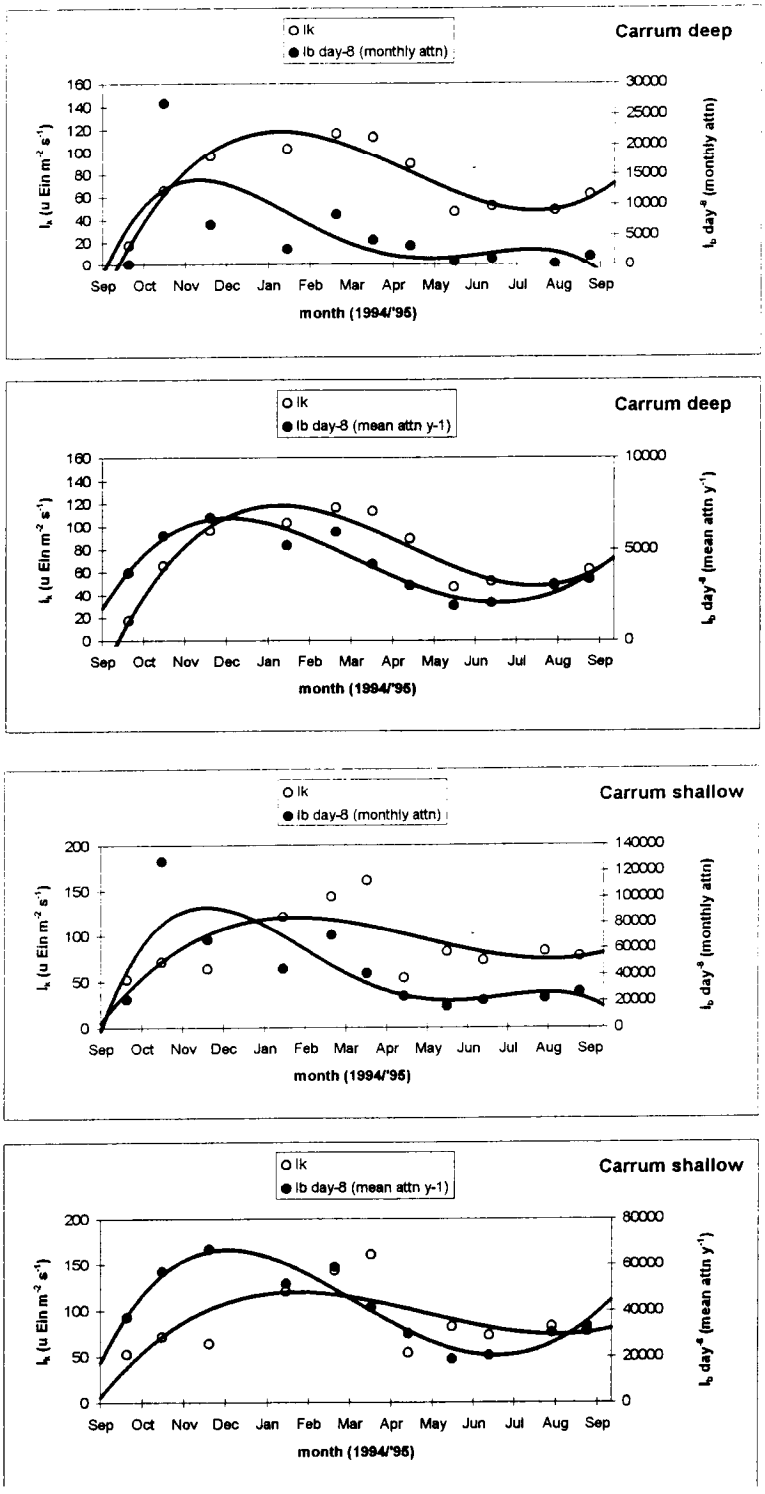


Fig. 26. The photosynthetic quantum yield (α) (expressed as mg O_2 h^{-1}. μEin.s^{-1}) of MPB at the Werribee, Indented Head and Carrum shallow and deep water sites over the 12-month sampling period. Values are the mean ±1 SE (n=3).

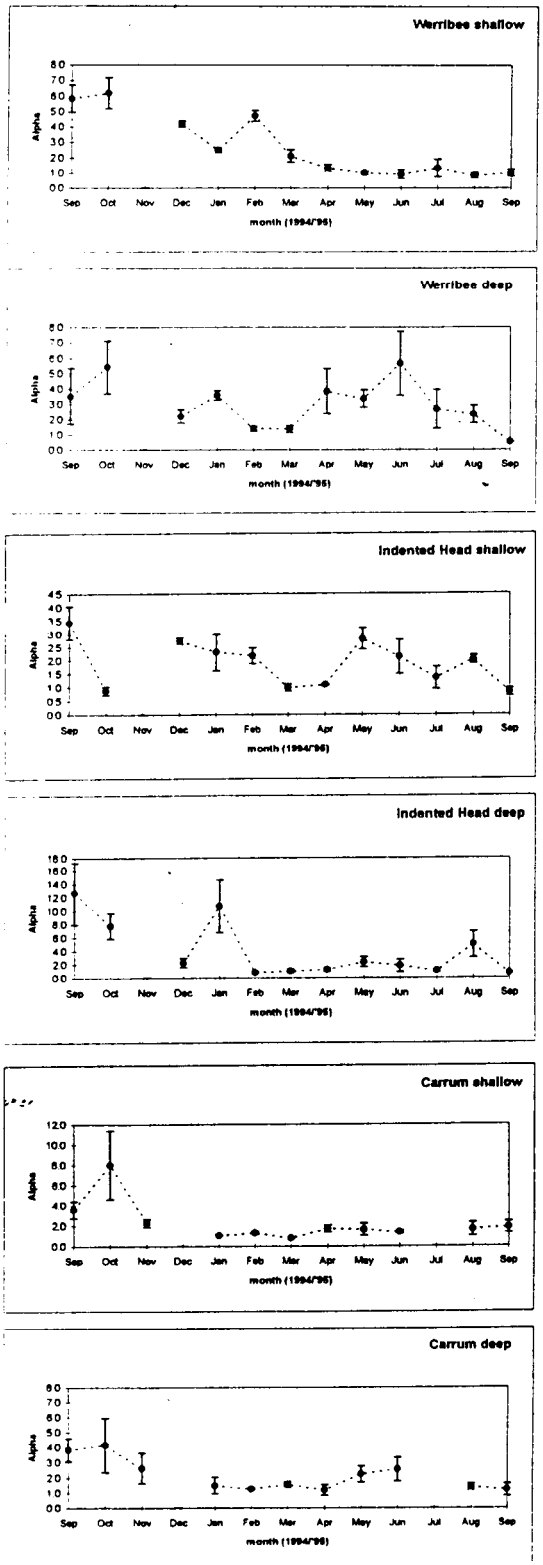


Fig. 27. Benthic community respiration (as mg $O_2/m^2/hr$) at the Werribee, Indented Head and Carrum shallow and deep water sites over the 12-month sampling period. Values are the mean ±1 SE (n=3).

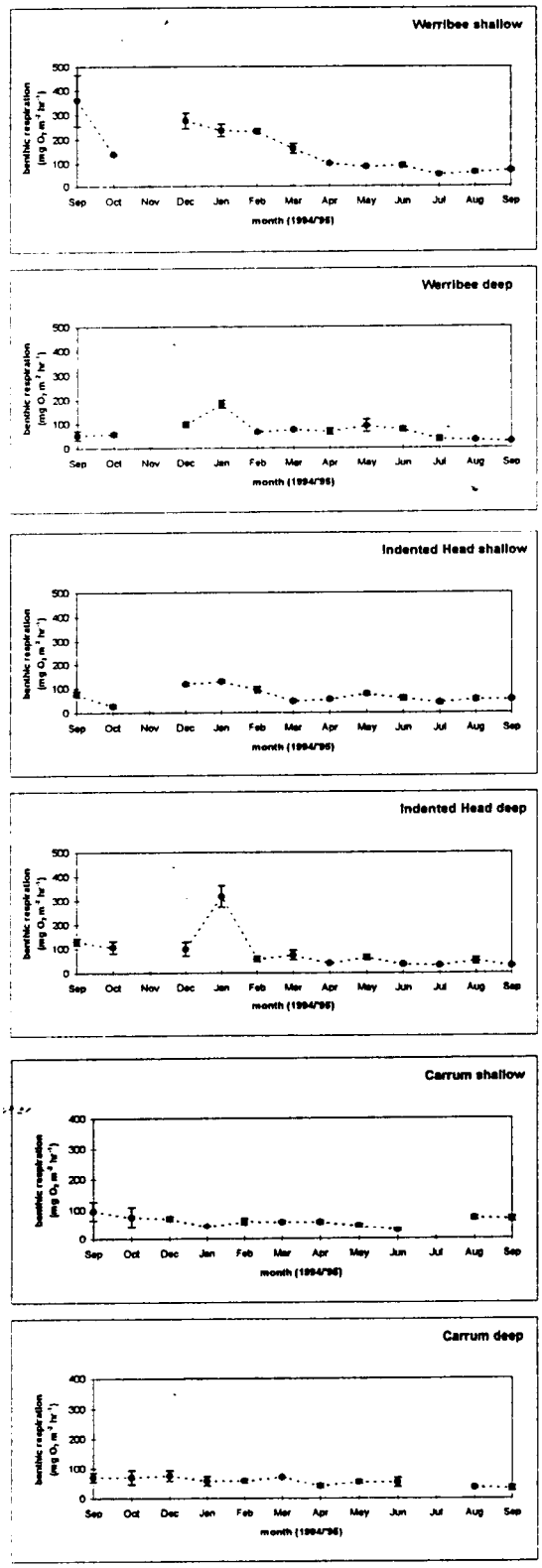


Fig. 28. Daily in situ gross production and benthic respiration (as mg $O_2/m^2/hr$) and the ratio of gross production to benthic respiration at Werribee sites over the 12-month sampling period.

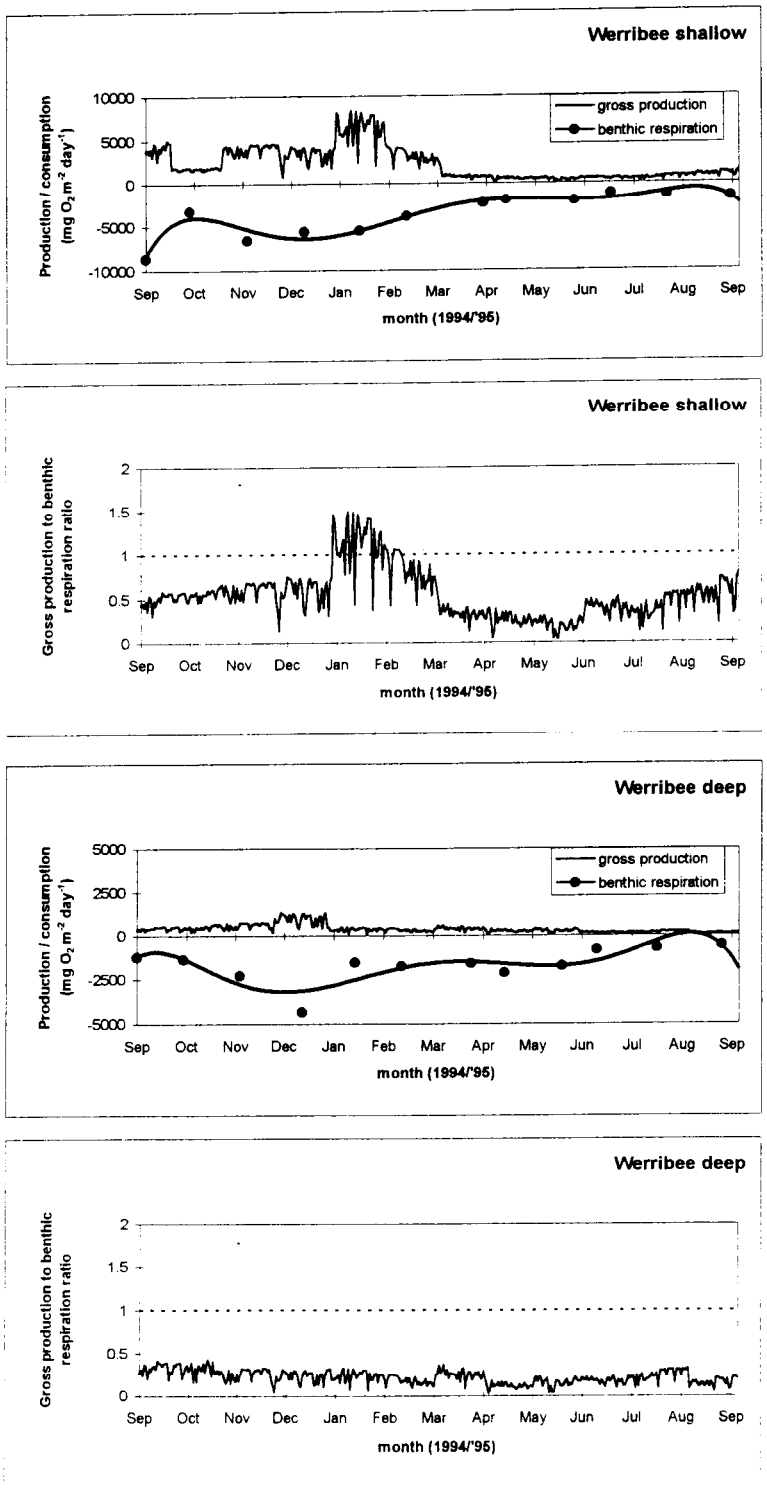


Fig. 29. Daily in situ gross production, benthic respiration (as mg $O_2/m^2/hr$) and the ratio of gross production to benthic respiration at Indented Head sites over the 12-month sampling period.

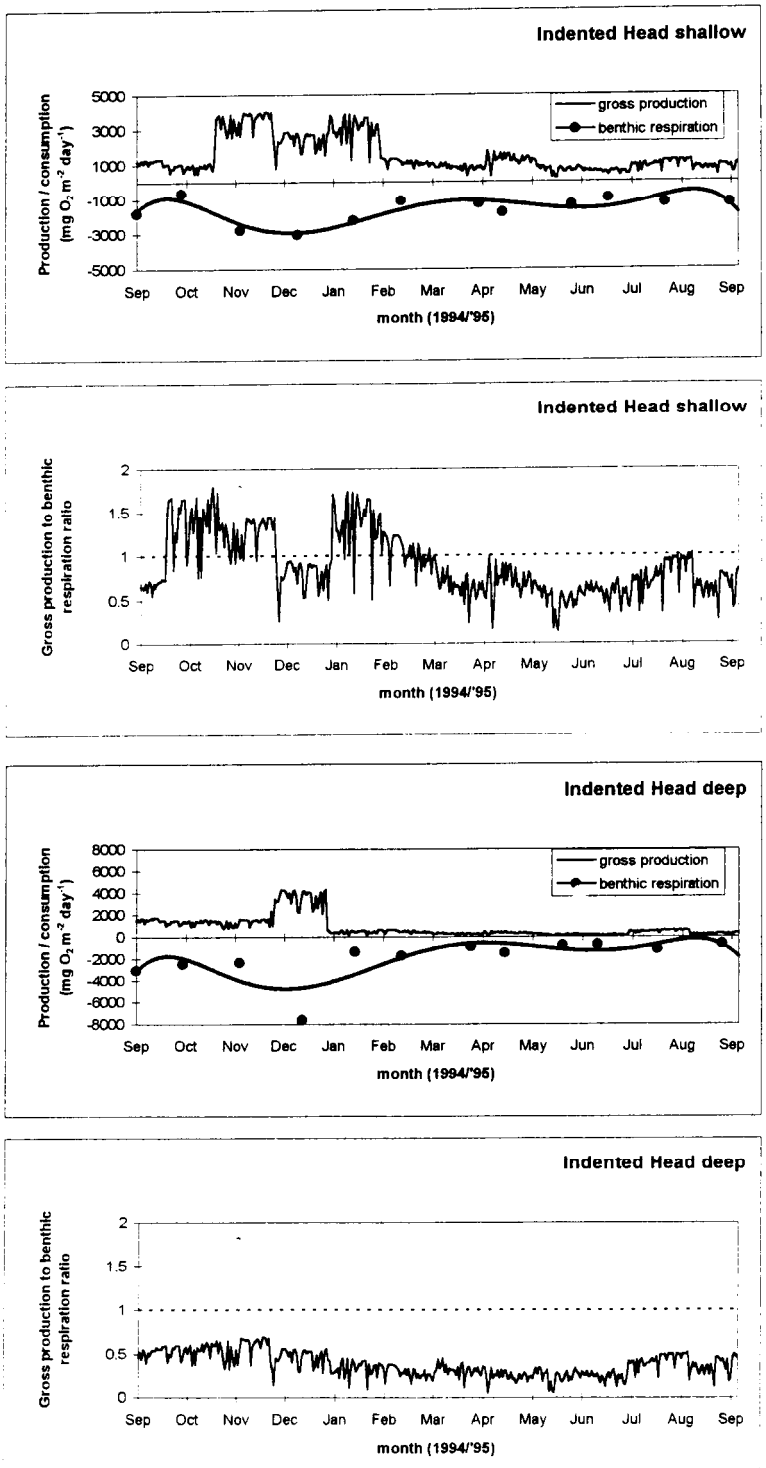
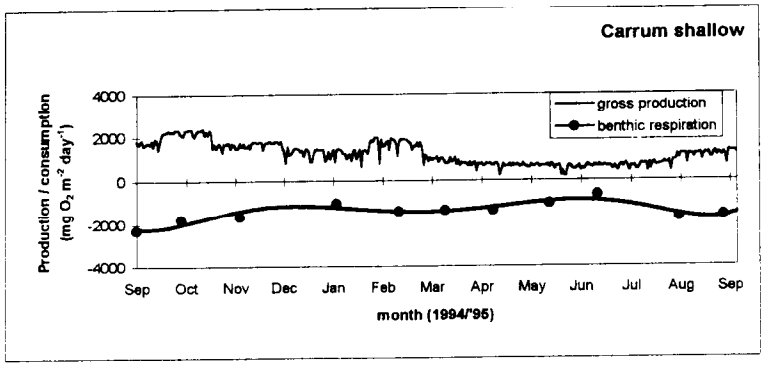
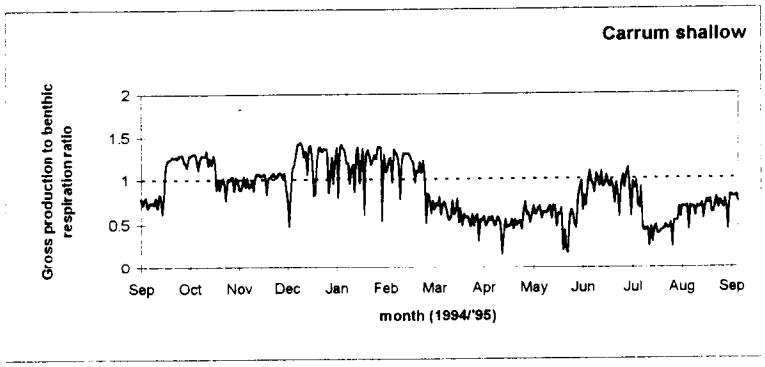
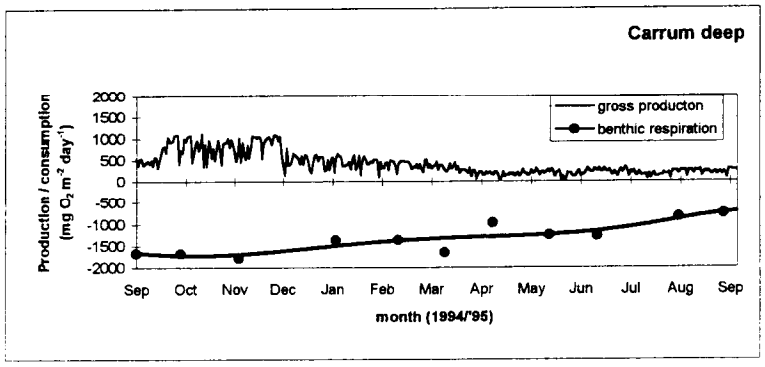


Fig. 30. Daily in situ gross production, benthic respiration (as mg $O_2/m^2/hr$) and the ratio of gross production to benthic respiration at Carrum sites over the 12-month sampling period.







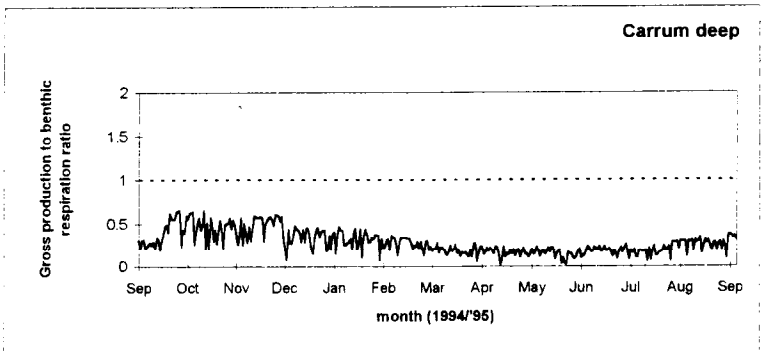
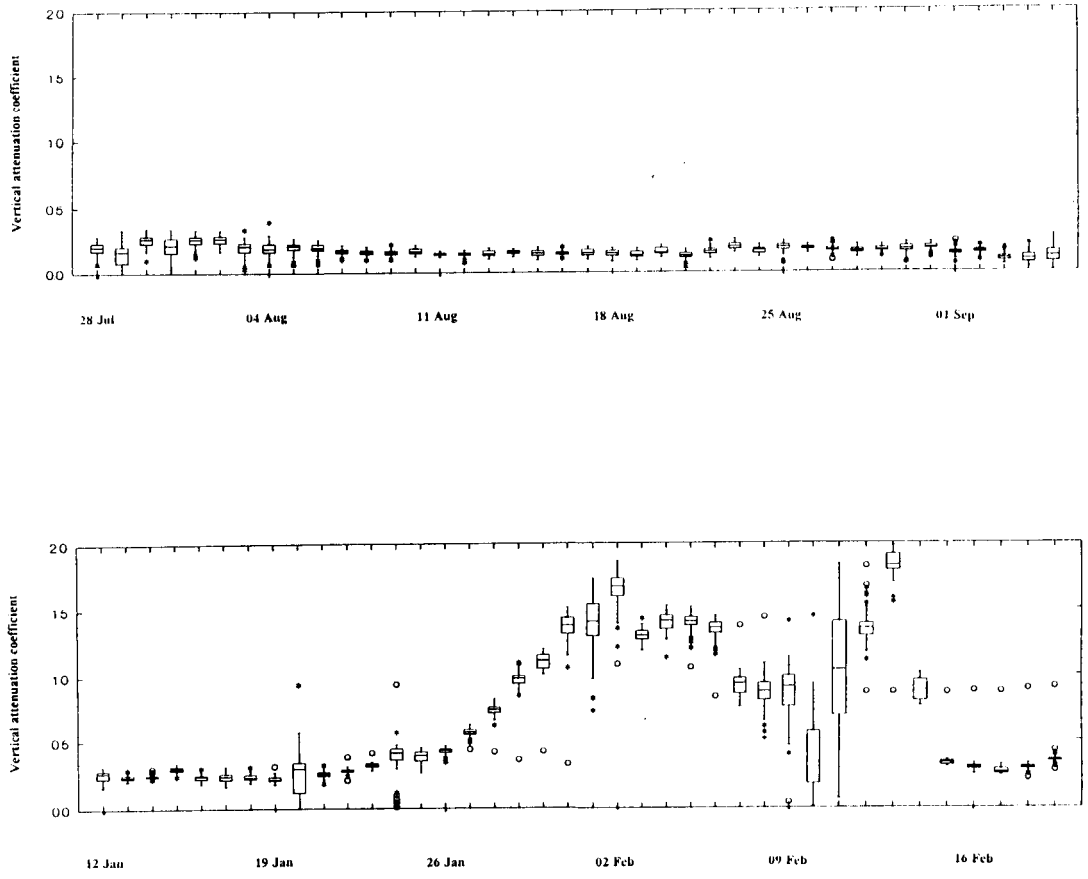


Fig. 31. Box-plot of 5 minute water column attenuation data (9:00-15:00 hrs) versus day for winter 1995 and for summer 1996.



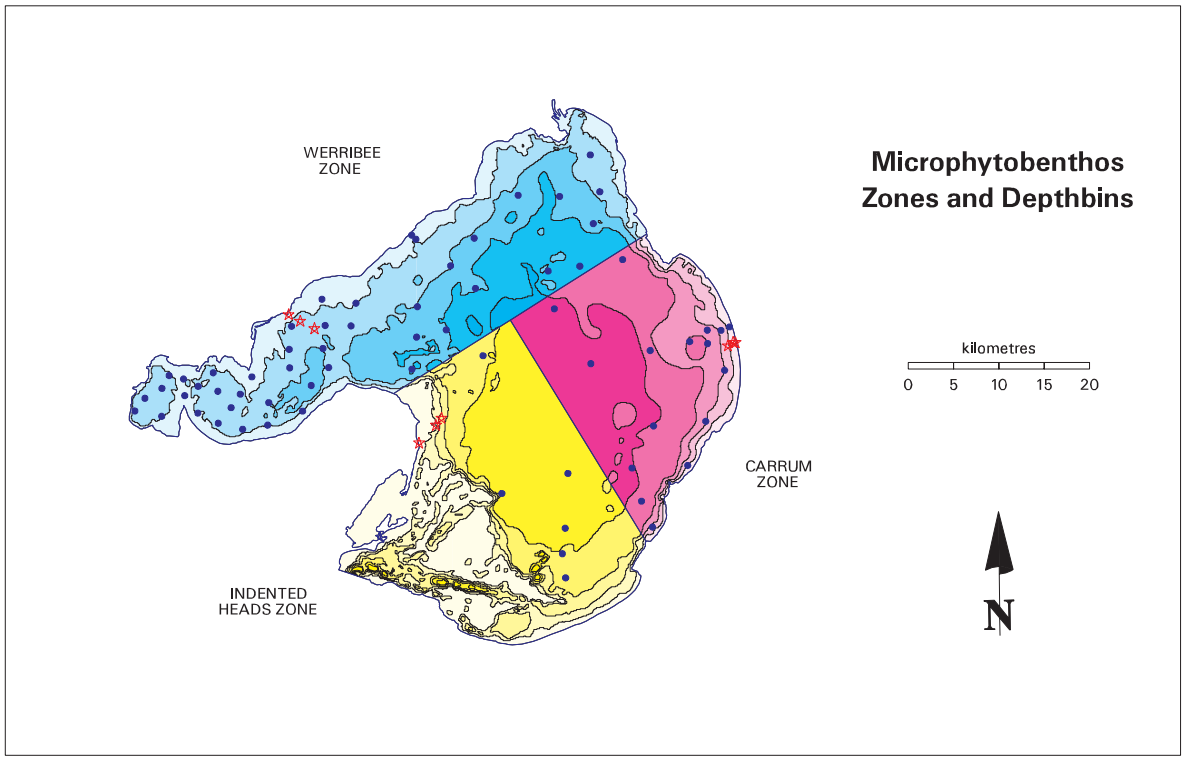


Fig. 32. Segment boundaries and depth bins for modelled MPB biomass and primary production estimates.

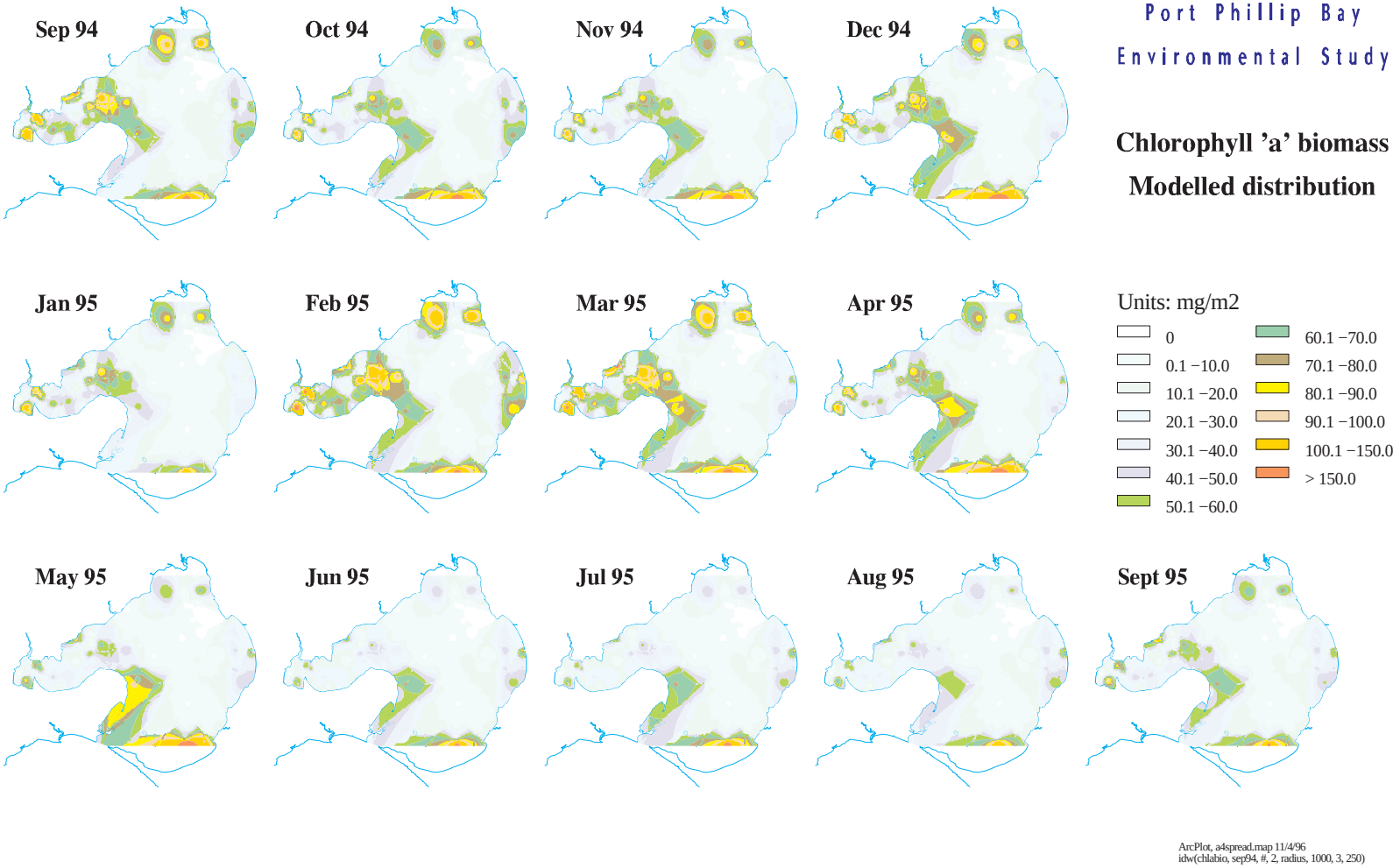


Fig. 33. Interpolated distributions of MPB biomass based on modelled estimates. Separate interpolations were computed for each month (see text).