STUDIES ON THE SEASONAL PRIMARY PRODUCTION OF CAPE PENINSULA LITTORAL AND SUBLITTORAL SEAWEEDS

by

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ABSTRACT

The seasonal primary production of five species of littoral seaweeds and three species of sublittoral understorey seaweeds has been investigated. Measurement of the primary production of littoral seaweeds was performed *ex situ* using manometric techniques and infra-red gas analysis, while that of sublittoral seaweeds was performed *in situ* using dissolved oxygen methods.

Highest levels of primary production in submersed intertidal seaweeds were observed mainly in spring (September), and lowest levels in late summer, autumn and winter. Potential rates of maximum net production were in the region of 2.45-9.51mg C fixed.g $dw^{-1}.hr^{-1}$ (maxima) and 0.81-2.91mg C fixed.g $dw^{-1}.hr^{-1}$ (minima). The thin sheet-like thallus forms, *Ulva rigida* and *Porphyra capensis*, displayed the greatest rates of net photosynthesis, while the coarsely branched forms (*Splachnidium rugosum* and *Bifurcaria brassicaeformis*) displayed the lowest net photosynthetic rates. No distinct seasonal variation in adaptation to seasonal changes in irradiance are apparent in the intertidal seaweeds, while levels of water content in these species varied seasonally, with summer maxima and autumn-winter-spring minima. *Porphyra capensis* is better able to resist desiccation stress than other intertidal species which grow lower on the shore, photosynthesis by *Porphyra capensis* under exposed conditions being greater at equivalent levels of thallus desiccation than in other species. Two species, *Porphyra capensis* and *Gigartina radula*, are able to maintain positive rates of net

photosynthesis for up to six hours while exposed. Rates of desiccation of all species are similar.

Seasonal variation in nitrogen content was apparent in four of the five intertidal species investigated, with summer minima and winter maxima. These four species displayed no seasonal patterns in percentage carbon, whilst the only species not to display a seasonal pattern in nitrogen content, *Bifurcaria brassicaeformis*, displayed a seasonal pattern in carbon content.

Annual turnover rates of the intertidal species (calculated from the total annual amount of net photosynthesis and average carbon content) show a highest value of 33 times p. a. for *Ulva rigida* and a lowest value of 12 times p. a. for *Porphyra capensis*. Turnover rates for *Gigartina radula*, *Splachnidium rugosum* and *Bifurcaria brassicaeformis* are similar at *ca.* 23 times p. a. The highest annual gross production is shown by *Gigartina radula*, with 1.0892kg C fixed per running metre of shore per annum. This is double the annual production rate of the next most productive species, *Ulva rigida*, which has a total annual gross production of 0.5272kg C fixed per running metre of shore per annum. Despite the ability of *Porphyra capensis* to photosynthesize while exposed, the long duration of the exposure period of this species contributes to its much lower annual gross production of 0.1915kg C fixed per running metre of shore.

Gigartina radula, *Botryocarpa prolifera* and *Epymenia obtusa* contribute substantially to the total understorey biomass of Cape Peninsula kelp beds, existing in an environment with a seasonal pattern of irradiance (high in summer, low in

winter) and variable temperature regime (cooler in summer than in winter). All three species show distinct seasonal patterns of photosynthesis, with maxima in spring and minima in winter. *Botryocarpa prolifera* was the most productive understorey species (with figures of 2.39mg C fixed.g $dw^{-1}.hr^{-1}$ in spring and 0.15mg C fixed.g $dw^{-1}.hr^{-1}$ in winter). Spring and winter values of 1.14 and 0.03mg C fixed.g $dw^{-1}.hr^{-1}$ for *Epymenia obtusa* and 1.82 and 0.24mg C fixed.g $dw^{-1}.hr^{-1}$ for *Gigartina radula* were recorded. Respiration rates of these species followed the same seasonal pattern, with spring maxima and winter minima. Summer and winter P-I curves show that *Botryocarpa prolifera* and *Epymenia obtusa* have higher P_{max} values in summer than in winter, the opposite being observed in *Gigartina radula*. Summer I_k values are higher in all three species than in winter. *Botryocarpa prolifera* and *Epymenia obtusa* are shade-adapted species with fairly low I_k values being observed. *Gigartina radula* shows I_k values similar to those of intertidal plants of the same (and other) species. This indicates that this species is adapted for high irradiance environments, but is capable of colonising the shallow sublittoral where irradiance attenuation is not too great. C:N ratios of these sublittoral species are generally low, with only *Botryocarpa prolifera* displaying a significant seasonal pattern (low in summer, high in winter). The ratio of net photosynthesis to respiration (Pn:R) is fairly constant for *Botryocarpa prolifera* and *Epymenia obtusa*, and this implies that the photosynthetic processes of these species are governed more by seasonal variations in irradiance rather than instantaneous light availability. The

Pn:R ratio in *Gigartina radula* is variable, thus implying that this species is more responsive to fluctuations in irradiance and may therefore be adapted for rapid growth during periods of high irradiance. Turnover rates of the sublittoral seaweeds are lower than the intertidal seaweeds, with rates of 11 and 13 times p. a. respectively for *Botryocarpa prolifera* and *Gigartina radula* and 8 times p. a. for *Epymenia obtusa*. *Gigartina radula* is the most productive sublittoral species with a total annual gross production of 0. 8990kg C fixed per running metre of shoreline. *Epymenia obtusa* and *Botryocarpa prolifera* also show substantial total annual gross production with figures of 0. 6766 and 0. 6435kg C fixed per running metre of shoreline respectively. Comparison with the intertidal figures reveals that *Gigartina radula* is the most productive species and is adapted to both the littoral and sublittoral environment, but is much more productive in the intertidal. On a running metre of shoreline basis, the intertidal seaweeds are substantially more productive than the understorey seaweeds with an average of 5. 990kg C fixed. running metre of $shore^{-1}.yr^{-1}$ for the three most abundant intertidal species, as opposed to an average of 0. 740kg C fixed. running metre of $shore^{-1}.yr^{-1}$ for the three sublittoral species investigated. The intertidal and understorey productivity figures are, however, relatively insignificant when compared to an estimated South-Western Cape kelp bed productivity figure of 0. 35 tonnes C fixed per running metre of shoreline .

CHAPTER 1. GENERAL INTRODUCTION

The determination of the photosynthetic rate of marine macrophytes is not a new field of scientific endeavour, having been carried on since the end of the 19th century as an aspect of either ecological or physiological research. Measurement of the production of organic matter by marine plants can be carried out by the measurement of the rate of photosynthesis by the aquatic plant communities under investigation (Ryther, 1956). Some of the organic matter produced by the photosynthetic process in a plant is respired to provide the energy for its own metabolism (Westlake, 1963), while the rest accumulates in the plant thallus. Ultimately, the unrespired portion (the net photosynthesis) becomes available for transfer to higher trophic levels either before or after the death of the plant. As a result, the process of photosynthesis by either marine phytoplankton or marine macrophytes is the primary source of energy on which nearly all forms of life in the oceans are dependent.

The magnitude of this photosynthetic primary production, together with the factors influencing it, is extremely important as it is one of the main factors ultimately controlling the rate of increase in both size and number of the organisms in a community. Also, the productivity of commercially important species is of interest since new methods may make more of a resource available, and it is important to know the rate at which a resource is produced for successful management of any harvesting that may occur. Furthermore, although some plant species themselves may not

be commercially important, commercially important animals may depend on these plant species both directly (grazers) or indirectly (further up the food chain). As well as the direct importance of the organic material produced by the photosynthetic process, the influence on the environment of the act of fixing this organic material may also be important. For example, the liberation of oxygen as a by-product of photosynthesis can be important in the supply of oxygen for respiration, especially in polluted waters.

Primary productivity can be defined as the rate of primary production, and the measurement of primary production can be in terms of standing crop, yield or biomass (Westlake, 1963). Reviews of marine primary production have been published from time to time (e.g. Blinks, 1955; Ryther, 1956; Westlake, 1963; Chapman, 1974; Mann, 1982). Measurement of productivity is best expressed as a rate, because primary production is not a static process - it is an active, dynamic process subject to both seasonal and short-term, physically-induced variations. Variation in dry mass over time is the most widely used method for rate comparisons of primary production (Westlake, 1963). The actual method used determines in what units the initial data is collected in a particular study. However, recent publications (e.g. Westlake, 1963; Littler, 1979; Littler and Arnold, 1980) have commonly settled on the measurement of primary production as photosynthetic rate expressed in milligrams carbon fixed per gram dry weight per hour (mg C.g $dw^{-1}.hr^{-1}$), and any measurements in different units (e.g. oxygen) should be converted to these units. When oxygen is measured, the conversion to carbon needs to be made for

comparison purposes with other studies, as well as for the calculation of turnover rates which are commonly based upon the organic carbon content of the species being investigated. The ratio between oxygen evolution and carbon dioxide uptake is commonly termed the photosynthetic quotient (PQ). A photosynthetic quotient greater than 1.0 is commonly used because the elaborate synthesis of proteins and fats affects the ratio between oxygen release and carbon dioxide consumption. According to Westlake (1963) the average PQ for natural macrophyte communities is 1.2 (1.3-1.4 when growth is rapid in the presence of nitrate). Assuming a PQ of 1.2 the conversion required is grams oxygen x 0.278 = grams carbon. It is the preferred convention that productivity is expressed in terms of the rate of carbon incorporation because:

i) the formation of organic matter depends on the properties of the carbon atom;

ii) the photosynthetic process is dependent on the fixation of carbon dioxide.

Plants with a high proportion of carbon tend to have a greater energy of combustion than those with a lower carbon content (Westlake, 1963). Energy is the most fundamental driving force behind all ecosytems, and a knowledge of energy contents allows the relation of photosynthesis to the efficiency of incorporation of the energy derived from the sun.

In global studies of the measurement of overall primary production, the seasonal variation in primary production of representative members (dominant species) of both the intertidal and subtidal communities of a particular region

together has received very little attention. This is unfortunate as an integrated study examining representative members of both the littoral and sublittoral communities of a particular region is probably one of the most important means of determining the extent of the primary source of ecosystem energy (primary production). Furthermore, seasonal measurements of primary production will give an indication of possible variations in this source of ecosystem energy. The limitations of, and problems associated with, aspects of the methodology of measuring primary production have been well documented by various authors (Ryther, 1954; Ryther, 1956; Carpenter, 1965; Carritt and Carpenter, 1966; Dromgoole, 1978; Littler, 1973; Hatcher, 1977; Littler, 1979; Littler and Arnold, 1980; Berger and Bate, 1986; Murthy *et al*, 1986).

Inshore and nearshore marine environments which are characterized by the presence of kelp beds have been shown to be areas of unusually high productivity (Mann, 1973; Chapman, 1974). Mann (1982) described coastal waters as one of the world's most productive plant systems, the majority of the primary production being provided by kelps in areas where kelp beds are present. Along the South African west coast extensive kelp beds occur, and associated with these beds is an extensive flora of understorey seaweeds of considerable biomass (Field *et al*, 1980). These kelp-dominated communities are associated with shallow subtidal rock surfaces and extend along the coast of southern Africa from an as yet unidentified locality in northern Namibia to a few kilometres west of Cape Agulhas (34·49.5'S, 20·03.3'E) in the south. The west coast is an extremely exposed

coastline with strong south-west swells reaching five to seven metres in height (with a period of eight to twelve seconds) being common (Field *et al*, 1980). In the summer, prevailing south-easterly winds are responsible for the upwelling of cool, nutrient-rich water. Upwelling is particularly strong at various foci along the coast where the wind is funneled between mountain ranges (Andrews & Cram, 1969). As a result of their localized high biomass (Field *et al*, 1980), macroalgae are potentially important consumers of these nutrients and conceivably could exert a substantial influence on the nutrient utilization patterns of the west coast region. Nutrient uptake by the South African kelp *Ecklonia maxima* (Osbeck) Papenfuss could well be exerting a significant influence on the pattern of west coast nutrient utilization - the amount of nitrogen uptake by this kelp being linearly related to the ambient nitrogen concentration, saturation point not being reached at concentrations greater than 20µg-at N. l^{-1} (Probyn and McQuaid, 1985). According to Probyn and McQuaid (1985), nitrate imported by upwelling is the chief source of nitrogen utilised within the kelp bed. Water temperatures in the kelp beds in summer range from 8-14·C, while in winter the prevailing north-westerly onshore winds result in warmer surface water of up to 17·C reaching the coast (Field *et al*, 1980).

Internationally, the productivity of kelps has been intensively studied (e. g. Mann, 1972b, 1973; Towle and Pearse, 1973; Hatcher, 1977; Hatcher *et al*, 1977; Mann and Kirkman, 1981; Smith *et al*, 1983). Locally in the Cape Peninsula, kelp bed biomass (Field *et al*, 1980); growth rates of the

kelp *Laminaria pallida* (Greville) ex J. Agardh (Dieckmann, 1978, 1980); the productivity of the kelp *Ecklonia maxima* (Mann *et al*, 1979) and estimates of total Cape Peninsula kelp primary productivity (Jarman and Carter, 1981), have been performed. However, not as much attention has been paid locally to the smaller seaweed members of kelp dominated ecosystems which, according to Smith (1981), are one of the least understood components of continental shelf ecosystems. Some studies on primary production of smaller sublittoral macrophytes have been performed elsewhere (e.g Tschudy, 1934; Johnston, 1969; Brinkhuis and Jones, 1974; Mathieson and Norall, 1975; Arnold and Murray, 1980; Heine, 1983). Generally, smaller seaweeds growing in or near kelp-dominated ecosystems can be divided into two distinct ecological categories:

i) The sublittoral understorey seaweeds which are shade-adapted for survival in the light-limited environment beneath the kelp beds;

ii) The intertidal seaweeds which, although not directly physically associated with the kelp beds, exist in close proximity and share the same water and nutrient environment and whose contribution must be significant because they are dominant seaweeds with a large biomass (McQuaid, 1985).

Globally, there has been extensive study of primary production in intertidal macrophytes (e.g. Littler and Murray, 1974; Mathieson and Norall, 1975a; King and Schramm, 1976; Brinkhuis, 1977a, b; Buesa, 1977; Littler *et al*, 1979; Littler, 1980; Oates, 1986). Locally, only a small amount of information is available on intertidal seaweeds in the Cape

Peninsula as the result of student investigations (e.g. Probyn, 1975; Fielding, 1979), so an in depth investigation of local intertidal seaweeds is necessary to provide accurate and up to date information. The intertidal seaweeds are also interesting because, in order to survive the shore environment, they must be able to tolerate rapidly fluctuating extremes of strong wave action and harsh desiccation. There have been no local investigations into seaweed photosynthesis while exposed to the air, or into desiccation resistance while exposed, but there have been a number of international studies into this aspect (e.g. Johnson *et al*, 1974; Brinkhuis *et al*, 1976; Dawes *et al*, 1978; Schonbeck and Norton, 1978, 1979a, b, c; Quadir *et al*, 1979; Dromgoole, 1980). Thus any measurement of the primary production of local intertidal seaweed species would be extremely useful, especially in view of the fact that, in the near future, the intertidal region is likely to bear the brunt of any commercial exploitation of both marine seaweeds and animals dependent upon marine seaweeds. The total primary production of intertidal seaweeds is difficult to assess since the relative rates of photosynthesis while both submersed at high tide and exposed at low tide must be taken into account.

The process of photosynthesis is classically represented by the summary equation of photosynthesis:

$CO_2 + 2H_2O + 472.8kJ \rightarrow [CH_2O] + O_2 + H_2O$ (Šeštāk *et al*, 1971)

From this equation, it may be deduced that one of the possible ways of measuring photosynthesis in emersed plants is by measuring the influx of carbon dioxide (CO_2). The

influx of carbon dioxide is a measure of photosynthetic rate, and together with the oxygen efflux measurement, is the method most frequently used in determining plant photosynthesis (Šeštāk *et al*, 1971). The oxygen method is most common with submerged plants, because the solubility of oxygen in water is very low and oxygen determination is not complicated by problems associated with CO_2 and its different equilibrium states when dissolved in water. The photosynthetic quotient (PQ) (i.e. the ratio of O_2 evolution to CO_2 uptake) generally has a value close to one, so any preference for either of the two methods of determining photosynthesis is largely governed by technical considerations and by the type of plant being investigated. For these reasons, photosynthesis in submerged intertidal and sublittoral macrophytes is best measured using the oxygen evolution method (such as by the use of a Gilson respirometer or measurement of the change in oxygen levels by the Winkler method), while in emersed intertidal macrophytes the carbon dioxide uptake method is preferable because the high concentration of oxygen in air requires a very sensitive method to detect the small changes in oxygen concentration due to photosynthesis (relative to the air oxygen concentration). The most frequently used instrument for the measurement of carbon dioxide uptake by photosynthesizing emersed whole plants is the infra-red gas analyser, and this instrument was used in this study.

Kelps form the the major portion of the plant material in Cape Peninsula kelp bed communities (Field *et al*, 1977), and the eroded detritus from the kelp fronds forms the major part of the diet of filter and detritus feeding animals (e.g

Choromytilus meridionalis Krauss) which dominate the small invertebrate fauna. To illustrate a typical commercially important Cape Peninsula food chain, an important predator of these small invertebrates is the rock lobster *Jasus lalandii* (M. Edw.) which attains a high biomass and is in turn preyed upon by carnivores such as dogfish, seals and cormorants. In the Cape Peninsula (especially False Bay), large numbers of the Cape fur seal (*Arctocephalus pusillus* subsp. *pusillus* Schreber) are present and these are mainly preyed upon by a large population of the great white shark *Carcharodon carcharius* Linnaeus. Thus it can be seen that attached plants form the basis of this food chain, and their importance is more than just academic - the rock lobster catch being 3727 tons in the 1984/85 season (Anon., 1985). The relative contribution of the small seaweeds to this detritus driven food chain is probably small compared to the kelps because of the huge kelp biomass of half a million tons along the Cape coast (Jarman and Carter, . 1981). Nevertheless, the contribution of small seaweeds to the ecosytem is important and their rate of production needs to be investigated so that it can be compared with that of the kelps *Ecklonia maxima* and *Laminaria pallida* which together fix a total of 36 220 tons of carbon per annum (Jarman and Carter, 1981) over a length of coastline of 98.5Km (Field *et al*, 1980 from South Head (33·06.1'S, 18·57.0'E) to Cape Point (34·21.2'S, 18·29.7'E)). Methods for the measurement of primary production in large kelps have been developed by Mann (1972), and applied to the Southern African kelp *Ecklonia maxima* by Mann *et al* (1979). Worldwide, kelp beds have a high rate of primary production of 1000-2000g

C. m^{-2}. yr^{-1} (Velimirov *et al*, 1977), while South African *Ecklonia* beds have a production rate of 5.56g C. m^{-2}. day^{-1} (Mann *et al*, 1979), which is 2030.79g C. m^{-2}. yr^{-1}. Such a high rate of production cannot be expected on a unit area basis for understorey seaweeds simply because they have a much lower biomass per unit area due to their smaller size and patchy distribution. Furthermore, it is common for large areas under kelp beds to be without understorey seaweeds - two seemingly relatively stable understorey situations being common in kelp beds worldwide. One is characterized by an abundant understorey flora common to the particular region, the other by large populations of sea urchins which seem to preclude understorey seaweed growth (Johnson and Mann, in press). In the Cape Peninsula region, sea urchins are only common in kelp beds in False Bay. On the west coast of the peninsula, understorey seaweeds are dominant down to depths of 15-20m after which animals such as crinoids predominate. It is quite possible that similar rates of production to the kelps (per unit biomass) may be achieved by the understorey seaweeds. High rates of production of both subtidal and intertidal seaweeds in the Cape Peninsula may be expected since the region is characterized by nutrient-rich upwelled water. In the summer, south-east winds drive the surface waters offshore, resulting in extensive upwelling of cold, nutrient-rich water along the Cape west coast. Nutrient concentrations in Cape Peninsula upwelled water are high (20µg-at. l^{-1} for nitrate and 1-1.5ug-at. l^{-1} for phosphate (Andrews, 1974)), and rates of upwelling are exceptionally high, up to 30m. day^{-1} vertical upward water movement has been observed (Bang and Andrews, 1974). Large swells are

common in the Cape Peninsula inshore region, and the kelps act as large (and very effective) breakwaters which dissipate the energy of incoming swells and allow both understorey and intertidal seaweeds (as well as the kelp bed fauna) to occupy areas which may otherwise have been too exposed for them to inhabit. In the case of understorey seaweeds, the kelp bed almost certainly provides the protection from wave action that these plants seem to require. Velimirov *et al* (1977) found that understorey seaweeds occur mainly in the inshore to intermediate depth offshore kelp beds, and much less abundantly in the offshore (deep water) kelp beds, the inshore region providing progressively more protection from swells and also more available light for photosynthesis, due to the shallower water.

Thus, the aim of this study is to investigate the seasonal rates of primary production of some representative sublittoral seaweeds and to compare the results obtained with those from similar studies in other regions. Finally, an annual amount of production for the littoral and sublittoral species investigated will be calculated, as well as estimates made of seasonal gross production and turnover rates of these species. These figures will be used to compare the primary production of littoral and sublittoral Cape Peninsula seaweed communities with both the local kelp population and the results of similar studies elsewhere.

CHAPTER 2. PRIMARY PRODUCTION IN INTERTIDAL SEAWEEDS

INTRODUCTION

Local investigations into the primary production of Cape Peninsula seaweeds have so far been limited to one-off light and dark bottle incubations using either the radioactive carbon ($NaH^{14}CO_3$) technique (Fielding, 1979), or the direct measurement of oxygen evolution/uptake (Probyn, 1975). While these studies suffice to give instantaneous productivity estimates, the estimation of seasonal primary production requires frequent sampling to determine whether any seasonal variations in photosynthesis are taking place. Furthermore, any investigation into the extent of seasonal primary production of intertidal seaweeds should take into account whether photosynthesis takes place while a plant species is exposed as well as when it is submersed. Consequently, any calculations of total seasonal primary production have to include the relative exposure times of the various species investigated at different levels on the shore.

In this study, the measurement of seasonal primary production of five species of intertidal seaweed was conducted *ex situ*, mainly because it was felt that more accurate data could be obtained in this manner. For example, the data from *in situ* experiments is more prone to variation induced by daily variability in environmental factors such as irradiance and temperature. As a result of such variability, data from an *in situ* shore study may result in any seasonal patterns of production being masked by plant physiological responses to daily environmental variation.

Also, sources of experimental error are more easily minimized in an *ex situ* study, and the data obtained from an *ex situ* study is more accurate than an *in situ* study.

Kanwisher (1966) considered the algal frond as a "population" (sic) of photosynthetic cells in a structural matrix. As a result, on a dry weight basis, large forms which contain relatively higher ratios of structural to photosynthetic components have a lower capacity for photosynthesis than thinner forms. The data of Ramus (1978) supported this postulation - Ramus (1978) finding that the relative internal light trapping capabilities of two species with a different structural morphology (*Codium* and *Ulva*) are adapted to low and high irradiance environments respectively.

Littler and Murray (1974) published the first detailed data concerning the relationship between primary production and seaweed thallus morphology. They observed that sheet-like forms were the most productive. In a further study, Littler (1980) sought to test this functional-form hypothesis. He observed that the various forms showed distinct levels of photosynthesis, the ranking (in decreasing rate of production) being as follows:

i) thin sheet-like forms;

ii) finely branched forms;

iii) coarsely branched forms;

iv) articulated coralline forms;

v) saccate cushion-like forms;

vi) thick sheet-like forms;

vii) saxicolous prostrate forms.

The traditional method of algal productivity measurement has been to study and discuss the photosynthetic performance of selected species under various experimental environmental factors such as irradiance and temperature (e.g. Mathieson and Norall, 1975; Brinkhuis, 1977). The methods of the traditional approach were used in this study. However, some discussion relevant to the functional-form hypothesis is also important as it adds to our ability to generalize and make predictions concerning processes that determine photosynthetic properties. For example, the relationship between algal morphology and photosynthesis (productivity) may reveal interesting plant evolutionary strategies such as discussed by Littler *et al* (1983). Littler *et al* (1983) hypothesized that persistent forms which allocate resources for environmental resistance, interference competition and antiherbivory defences, do so at the cost of lower rates of primary production.

Fitting of light-saturation curves to laboratory photosynthesis data has been carried out in the past using three major mathematical functions. These are the right rectangular hyperbola $P = P_{max}I/(I+I_K)$ of Wethey and Porter (1976), the exponential function $P = P_{max}(1-e^{-I/I_K})$ of Graus and Macintyre (1976) and the hyperbolic tangent function $P = P_{max}\tanh(I/I_K)$ of Chalker (1980, 1981). The hyperbolic tangent function was preferred for the purpose of this study because it is more accurate than the right rectangular hyperbola (as measured by co-efficients of determination) - the right rectangular hyperbola producing consistent overestimates of P_{max} of 13-44% (Chalker, 1981). Light saturation curves plotting the rate of photosynthesis (P)

versus irradiance (I) have the following shape. Initially, the rate of photosynthesis is directly proportional to irradiance. Thereafter, the photosynthetic rate approaches a horizontal asymptote which is the maximum capacity for photosynthesis (P_{max}). The irradiance at which the initial slope of the curve (α) intercepts the horizontal asymptote is I_k (Talling, 1957). According to Steeman Nielsen (1975), I_k is a commonly used measure of the adaptation of a plant to its light regime. The importance of choosing the correct model (function) has been elaborated upon by Chalker (1981). Most importantly, the model must accurately simulate the experimental data and should include biologically meaningful parameters if the answers obtained are to ecologically relevant. For these reasons, the hyperbolic tangent function seems to be the most useful function for simulating light-saturation curves for photosynthesis and must be considered for studies on primary production by benthic seaweeds.

A number of studies (e.g. Kanwisher, 1966; Quadir *et al*, 1979) have examined the relationship between desiccation and photosynthesis, but this has not been investigated locally. Algal shore zonation is partly determined by species tolerance to the duration and extent of exposure that occurs at different tidal heights. Studies have shown (e.g. Johnson *et al*, 1974) that intertidal algae growing lower on the shore have a reduced photosynthetic capacity in air compared to their submerged rate, while middle and upper shore species display enhanced photosynthesis after some desiccation. Brinkhuis *et al* (1976) observed a pronounced effect of desiccation on exposed salt-marsh fucoids. They observed that photosynthesis increased slightly between 0%

and 25% water loss, levelled off, and decreased sharply at levels of water loss greater than 50%. Investigations by Chapman (1965) showed that the photosynthesis of intertidal algae exposed to the atmosphere was either equal to, or less than, photosynthesis under submerged conditions. However, what is also important is the ability to recover full photosynthetic ability once re-submersed after suffering extreme desiccation stress (Dring, 1982).

It is important to account for the amount of photosynthesis occurring under emersed conditions as well as submersed conditions, since the photosynthetic responses of marine seaweeds to environmental parameters such as irradiance and temperature under exposed conditions may be different than under submersed conditions.

The measurement of photosynthesis in algae collected from different shore zones is of interest because variations in the ability of shore species to tolerate tissue dehydration can be assessed. Schonbeck and Norton (1979a) demonstrated that tolerance to desiccation (drought hardening) developed in *Fucus spiralis* L. in response to non-lethal desiccation stress. Conversely, de-hardening took place in plants of the same species moved to physiologically less stressed conditions. Levitt (1972) defined drought tolerance as the ability of a plant to undergo tissue dehydration and subsequently function normally, so the present study must assess the degree to which drought tolerance (as measured by their ability to continue photosynthesis while severely desiccated) is displayed by Cape Peninsula intertidal seaweeds.

According to Branch and Branch (1981) there are four distinct recognisable zones on South African coasts. On the west coast, the algal zonation is often as follows. The highest zone (termed the littorina zone because of the dominance of the tiny snail *Littorina africana* Phil.) is occupied by the alga *Porphyra capensis* Kuetzing. Slightly lower down, in the Upper Balanoid zone (so termed because of the dominance of barnacles among the fauna), the most abundant seaweed is *Ulva* sp. Still lower on the shore, in a zone termed the lower balanoid, more fleshy seaweeds such as *Gigartina radula* (Esper) J. Agardh, *Gigartina stiriata* (Turner) J. Agardh, *Aeodes orbitosa* (Suhr) Schmitz, *Iridaea capensis* J. Agardh and *Splachnidium rugosum* (Linnaeus) Greville are abundant. Finally, bordering on the sublittoral fringe of the lowest recognised intertidal zone (the cochlear zone - named after the dominant limpet *Patella cochlear* Born.), algae such as *Bifurcaria brassicaeformis* (Kuetzing) Barton are present.

The aim of this study was therefore to measure the photosynthetic rates of intertidal seaweeds in both exposed and submerged conditions, and to compare the rates of photosynthesis observed. The observed rates of photosynthesis will be discussed according to the functional-form grouping of each species, and also according to shore zonation patterns and desiccation resistance of each species. Any apparent seasonal patterns of photosynthesis and other parameters measured will be discussed and comparisons with figures from other studies will be drawn.

MATERIALS AND METHODS

Plants were collected at Dalebrook (34·07.4'S, 18·27.4'E - fig. 1, plate 1) in False Bay which bounds the eastern shore of the Cape Peninsula. The intertidal region of this shore consists of gently sloping ledges of Table Mountain sandstone which is exposed to moderately strong wave action. McQuaid (1985), in a quantitative study of the factors determining the intertidal biotas of the Cape Peninsula, identified 24 species of macroalgae as being present on this shore, and five of these were chosen for this investigation because they are amongst the most abundant (McQuaid, 1980), and also because they represent different functional plant forms (i.e. thin, sheet-like thallus, thick cartilaginous thallus, coarsely branched thallus). The species chosen were as follows:

i) *Porphyra capensis* (Rhodophyta: Bangiales) (thin, sheet-like form);

ii) *Ulva rigida* C. Agardh (Chlorophyta: Ulvales) (thin, sheet-like form);

iii) *Gigartina radula* (Rhodophyta: Gigartinales) (thick cartilaginous form);

iv) *Splachnidium rugosum* (Phaeophyta: Ectocarpales) (coarsely branched form);

v) *Bifurcaria brassicaeformis* (Phaeophyta: Fucales) (coarsely branched form).

The investigation took the form of measuring the rate of photosynthesis of both submersed and emersed plants of the five species investigated. The investigation into photosynthesis of submersed algae was the major component of

the study, concentrating on seasonal patterns of photosynthetic potential. Measurement of seasonal photosynthesis for the five species being studied took place during the following periods: June 1984, September 1984, November 1984 (*Gigartina radula* and *Bifurcaria brassicaeformis* only due to technical problems), February 1985, April 1985, June 1985, August 1985 and November 1985. At these times samples of each species were collected and taken back to the laboratory for determination of photosynthetic light curves using a Gilson respirometer model GP8 (Gilson Medical Electronics Inc., Middleton, Wisconsin, USA). Tissue segments were incubated at 15·C in Gilson flasks in a buffered (0.1M $NaHCO_3$) nutrient enriched seawater solution (Provasoli, 1968). Eight sample flasks were incubated simultaneously, together with a control. Light was provided by incandescent white lights (General Electric reflector 2 X 100W, 8 X 30W). A temperature of 15·C was chosen because this is the middle of the mean annual temperature range of False Bay (14-16·C) described by Bolton (1986). Segments were incubated after a one hour equilibration period for six separate ten minute periods at each level of irradiance. Observations were converted to milligrams carbon fixed per gram dry weight per hour using the following equation (adapted from the Gilson GP8 instruction manual):

$$(i-f) \times \frac{(273.15) \times (P_b - 3 - P_w)}{(t+273.15) \times (760)} \times \frac{1}{dw} \times \frac{60}{T} \times \frac{1}{1000} \times \frac{16.0}{11.2} \times pq$$

Where: i = initial gilson respirometer reading (µl O_2)

f = final gilson respirometer reading (µl O_2)

P_b = operating (barometric) pressure (mmHg)

P_W = vapour pressure of incubation solution (mmHg)

t = temperature of water bath (·C)

dw = dry weight of sample (g)

T = incubation period (minutes)

pq = photosynthetic quotient

Explanation of constants:

273.15 - conversion to absolute temperature

760 - standard atmospheric pressure (mmHg)

60 - number of minutes in one hour

$\frac{1}{1000}$ - conversion from micro to milli units

$\frac{16.0}{11.2}$ - conversion factor from mlO_2 to mgO_2

(1ml $O_2 . l^{-1}$ = 11.2 mg-at $O_2 . l^{-1}$)

(1mg $O_2 . l^{-1}$ = 16.0 mg-at $O_2 . l^{-1}$)

Dark respiration rates were also measured in the Gilson respirometer. For every P-I curve determined, six replicate samples of the species being investigated were measured for dark respiration. Light was excluded by wrapping the Gilson flasks in tin foil, covering the respirometer with black plastic and operating the respirometer in a darkened, light-proof room.

Data was fitted to the light curve equation $P=P_{max} \cdot \tanh(I/I_K)$ of Chalker (1980, 1981); where P = photosynthetic production at irradiance I, P_{max} = maximum photosynthetic production reached at irradiance I_K. Fitting was performed using the non-linear curve-fitting program BMDP AR (see appendix I for BMDP runstream).

For the measurement of photosynthesis of emersed seaweeds (during September and October, 1985), seven whole plants of

each species were collected at mid-high tide while they were still immersed early in the morning of the day of each experiment and were transported to the laboratory (immersed). Each plant species was collected from the middle of zone on the shore it normally occupies. In the case of *Ulva rigida*, plants were collected from rock pools because these were more healthy and of a larger size than *Ulva rigida* plants found on the shore which are not rock pool residents. The collected plants were exposed to air at the time of their normal exposure during the tidal cycle so as not to disturb any innate rhythms that may have been present. The fresh weight of each plant was recorded at the time of exposure. The plants were desiccated under bright incandescent lights at an irradiance as close to that experienced on the shore as was possible to emulate at a constant temperature of 25·C ($\pm 1200 \mu\epsilon . m^{-2} . sec^{-1}$). A temperature of 25·C was chosen because this is mid-way between the summer and winter daylight temperature extremes experienced in the Cape Peninsula (35-15·C). The measurement of photosynthesis was carried out at 0.5, 1, 2, 3, 4, 5, and 6 hours after emersion on separate plants, each plant having its fresh weight measured at 0 hours after emersion and also directly after measurement of its photosynthetic rate. Each plant was thereafter dried to constant weight at 60·C, this being the most preferable temperature to avoid the loss of volatile constituents (Westlake, 1963). Measurement of photosynthesis was carried out using an ADC 225 MK3 infra-red gas analyser (IRGA) (Analytical Development Company Ltd, Hoddesdon, England). A closed system of measurement was used, it being simple and most suitable since it requires

little previous experience of gas-analysis techniques. It also does not require an extremely sensitive IRGA. In this closed system air is drawn from an incubation chamber enclosing the alga into the IRGA for analysis (in absolute mode), and then is recycled from the IRGA back to the chamber. As the plant enclosed in the chamber photosynthesizes, the carbon dioxide concentration declines until the compensation point of photosynthesis is reached. Measurement of the change in carbon dioxide concentration over time is used to calculate the rate of photosynthetic carbon dioxide assimilation per unit dry weight. With this instrument, the outside (reference) air acts as a control. In the experiment in the IRGA chamber, the sample plants were so placed as to try and emulate as close as possible the natural adaptation to resist water loss displayed by those species which fold over upon themselves as they desiccate (e.g. *Porphyra capensis*). This was done by placing the plants so that they lay naturally in the chamber.

Primary production of the emersed algae was calculated according to the following formula (adapted from Sēstāk *et al*, 1971):

$$\text{mg } CO_2 \text{ fixed.g } dw^{-1}.hr^{-1} = \frac{(ref - ana \times 0.000002) \times FR \times 60}{DW}$$

where:

ref = IRGA atmospheric CO_2 reference reading (ppm)

ana = experimental CO_2 photosynthetic reading (ppm)

0.000002 = constant to convert ppm to mg $CO_2.cm^{-3}$ air

FR = flow rate of air through IRGA ($cm^3.min^{-1}$)

60 = conversion from minutes to hours

DW = dry weight of plant (g)

The result, in mg CO_2 fixed, was then converted to mg C fixed by multiplying by 12 and dividing by 44 (the mass ratio of C in the CO_2 molecule).

Percentage desiccation of the plants after measurement in the IRGA was calculated as follows:

Percentage desiccation = (IWW-AWW) x (100/(IWW-DW))

where:

IWW = initial wet weight of plant

AWW = wet weight after IRGA analysis

DW = dry weight of plant after drying to constant weight.

This formula means that 100% desiccation = dry weight. In addition, four plants of each species were collected each month from July 1984 to May 1985 to determine their percentage water levels in the immersed state, and whether these levels varied seasonally. These plants were collected at low tide and allowed to soak in seawater for six hours. Thereafter they were blotted dry and weighed to determine actual wet weight. Then they were dried to constant weight at 60·C and reweighed. Percentage water was calculated as follows:

$$\text{Percentage water} = \frac{\text{wet weight - dry weight}}{\text{wet weight}} \times 100$$

Five fresh plants of each species were collected every month and freeze dried in a freeze drier model B67 (New Brunswick Scientific Co. Inc, New Brunswick, New Jersey, USA) and analyzed for total percentage carbon and total percentage nitrogen by an Heraeus Universal Combustion Analyzer model CHN-RAPID using the method of Monar (1972). Because of the expense of CHN-analysis, these five replicate plants of each

species were combined into one sample for each species. Freeze dried samples were also analysed for percentage inorganic matter and calorific value using a DDR CP500 macro bomb calorimeter.

All plants selected for these investigations were non-juvenile, non-senescent plants, preference being given to the collection of healthy, minimally grazed and, if possible, non-fertile individuals. Where tissue segments were utilised, only healthy, non-reproductive thalli free of epiphytes were used.

RESULTS

Seasonal water content

Table I shows the monthly variation in water content for the five species of intertidal seaweeds investigated from July 1984 through to May 1985. It can be seen that the thin sheet-like forms (*Porphyra capensis* and *Ulva rigida*) contain less water than the thicker more leathery or coarsely branched forms (significant at the 1% level, one way ANOVA $F = 94.61 > F_{0.01,1,53} = 7.08$). Of these two sheet-like species *Porphyra capensis* has the lower water content and this is significantly different from that of *Ulva rigida* at the 1% level ($F = 32.15 > F_{0.01,1,20} = 8.10$). Further one way ANOVA analysis of the water content of the other plant species investigated reveals that all are signficantly different from one another at the 1% level (*Ulva rigida* vs *Gigartina radula* $F = 14.82 > F_{0.01,1,20} = 8.10$; *Gigartina radula* vs *Bifurcaria brassicaeformis* $F = 12.00 > F_{0.01,1,20} = 8.10$; *Bifurcaria brassicaeformis* vs *Splachnidium rugosum* $F = 16.80 > F_{0.01,1,20} = 8.10$; *Splachnidium rugosum* vs *Gigartina radula* $F = 79.63 > F_{0.01,1,20} = 8.10$). On a seasonal basis, one way ANOVA tests conducted on each replicate of each species for each month reveals that *Porphyra capensis* is the only plant whose water content does not vary significantly on a monthly basis ($F = 0.62 < F_{0.05,10,33} = 2.14$). All the other species have water contents that do vary significantly on a monthly basis at the 1% level (*Ulva rigida* $F = 18.31 > F_{0.01,10,33} = 2.93$; *Gigartina radula* $F = 2.35 > F_{0.01,10,33} = 2.93$; *Splachnidium rugosum* $F = 8.06 > F_{0.01,10,33} = 2.93$; *Bifurcaria*

TABLE I: Seasonal % water levels of five intertidal seaweeds

	Porphyra	*Ulva*	*Gigartina*	*Splachnidium*	*Bifurcaria*
Jul 84	74.9729	78.9377	83.0749	89.5773	86.1008
Aug 84	74.5913	77.8431	83.1153	90.5151	88.2107
Sep 84	72.9799	78.0294	80.9605	91.6641	88.5463
Oct 84	79.1097	79.4727	84.5450	91.9522	85.9762
Nov 84	76.2937	80.6793	85.1541	91.1910	85.8029
Dec 84	76.4492	85.4736	82.7508	89.9132	85.7224
Jan 85	75.0301	79.7336	84.7064	86.5172	82.4836
Feb 85	74.9750	80.0436	81.6748	86.6916	82.8704
Mar 85	75.7024	83.6618	83.3408	90.7406	90.2183
Apr 85	75.1481	79.5799	85.1401	91.5934	87.6034
May 85	76.9182	81.2250	85.1224	92.4901	87.5815

TABLE II: Percentage inorganic matter and energy content of five intertidal seaweeds

	Inorganic matter (%)	kJ. g^{-1} dw
Porphyra capensis	8.40	15.71
Ulva rigida	23.01	10.19
Gigartina radula	26.71	10.46
Splachnidium rugosum	27.22	10.41
Bifurcaria brassicaeformis	23.03	10.21

brassicaeformis $F = 10.44 > F_{0.01,10,33} = 2.93$). For *Ulva rigida*, water content reaches a noticeable peak during the summer months (November to March) and is at a minimum during autumn, winter and early spring (April - July - September). *Gigartina radula* and *Splachnidium rugosum* display water content peaks during spring (October - November) and autumn (April and May) and have low points during early spring (September) and late summer (February). *Bifurcaria brassicaeformis* has peaks in late autumn (March to May) and late winter to early spring (August and September), with a definite minimum in mid to late summer (January and February).

Percentage Carbon, Percentage Nitrogen and C:N Ratios

Figure 2a-c shows the percentage carbon, percentage nitrogen and C:N ratios of the five intertidal species investigated from June 1984 through to August 1985. One way analysis of variance analysis was used on this monthly data to compare means between seasons. June, July and August were regarded as winter; September, October and November as spring; December, January and February as summer; and March, April and May as autumn. For percentage carbon (fig. 2a), only *Bifurcaria brassicaeformis* showed significant seasonal variation in percentage carbon levels at the 5% level ($F = 4.11 > F_{.05,3,11} = 3.59$). Conversely, *Bifurcaria brassicaeformis* was the only plant not to show any significant seasonal variation in percentage nitrogen (fig. 2b). The other four species all showed significant seasonal variation in percentage nitrogen at the 5% level (*Ulva rigida* $F = 4.17 > F_{.05,3,11} = 3.59$; *Porphyra capensis* $F = 8.26 > F_{.05,3,11} = 3.59$;, *Gigartina radula* $F = 7.39 >$

Fig. 2a: Seasonal variation in percentage carbon of five intertidal seaweeds at Dalebrook.

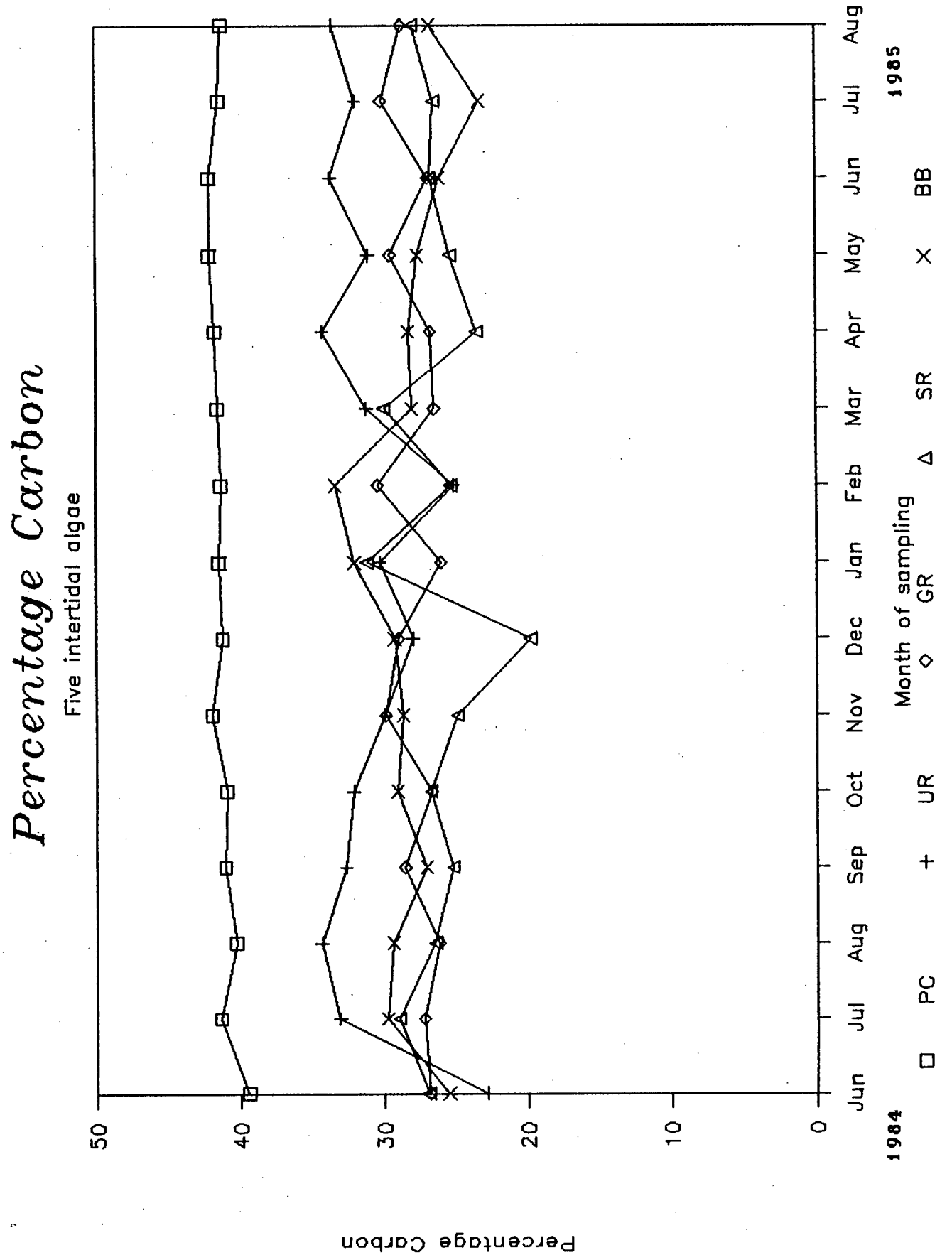


Fig. 2b: Seasonal variation in percentage nitrogen of five intertidal seaweeds at Dalebrook.

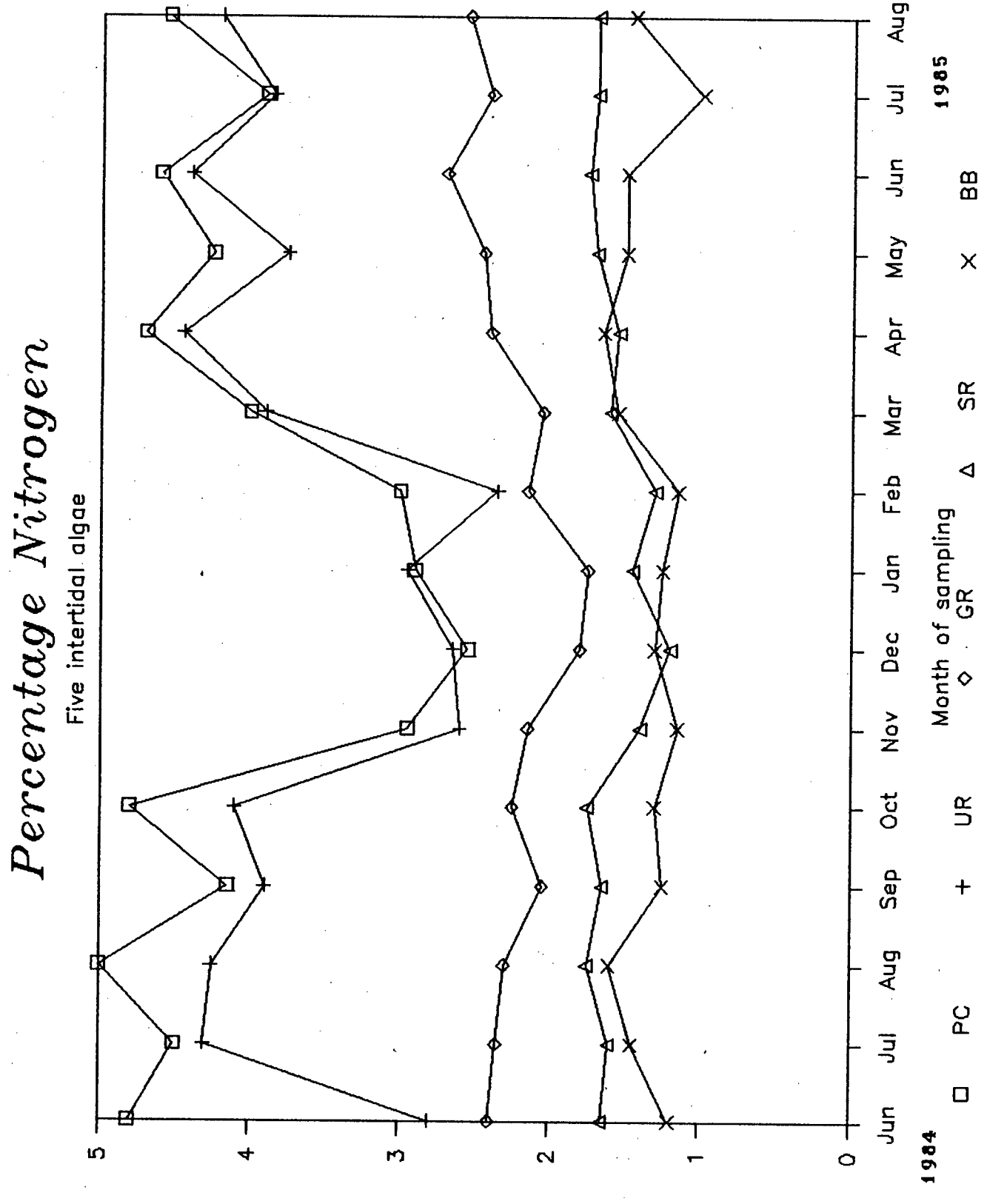
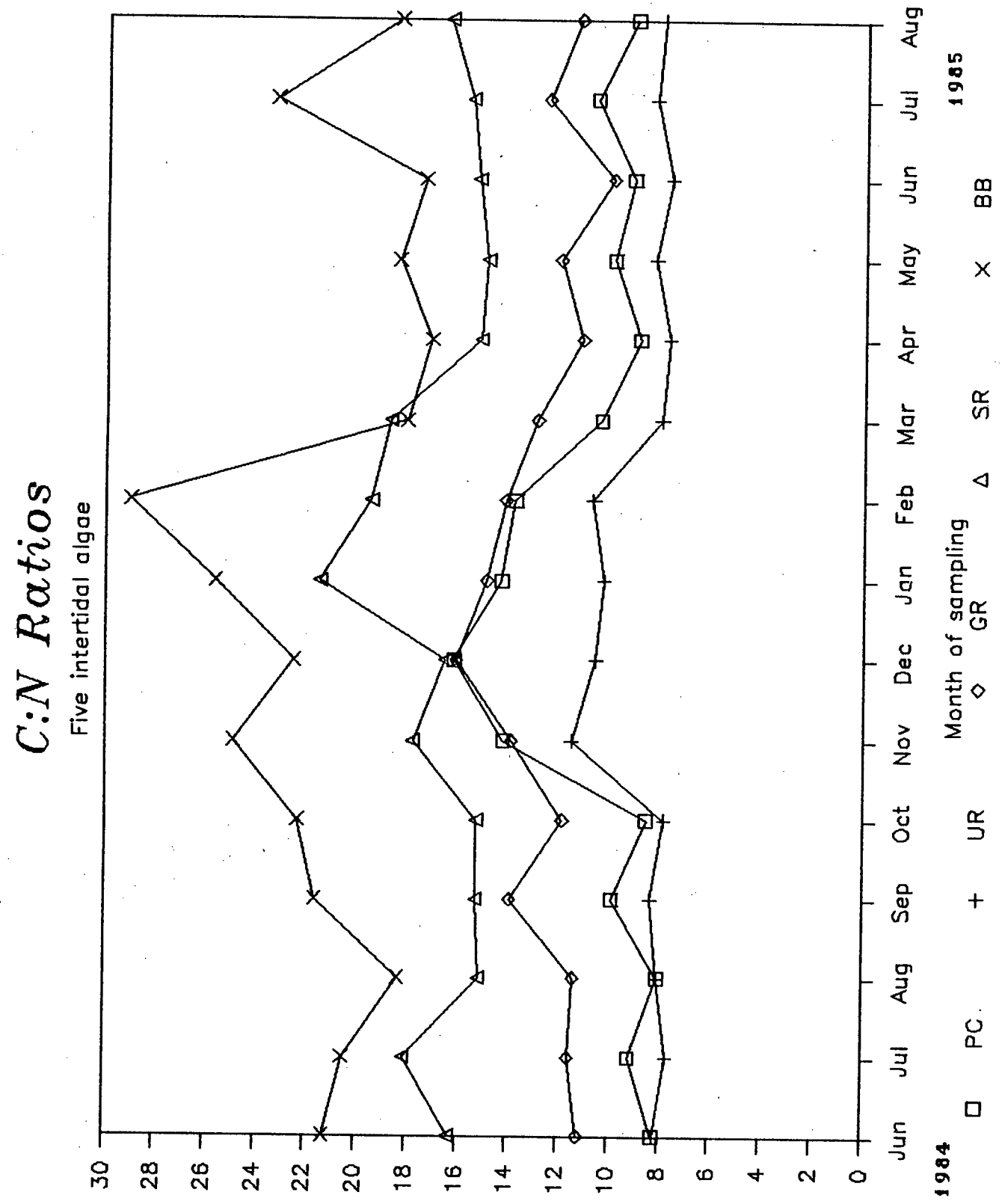


Fig. 2c: Seasonal variation in C:N ratios of five intertidal seaweeds at Dalebrook.



$F_{.05,3,11}$ = 3.59; *Splachnidium rugosum* F = 8.42 > $F_{.05,3,11}$ = 3.59). Seasonal variation in C:N ratio (fig. 2c) was not significant for *Splachnidium rugosum*, but was significant at the 1% level for the other four species investigated (*Porphyra capensis* F = 9.58 > $F_{.01,3,11}$ = 6.22; *Ulva rigida* F = 6.59 > $F_{.01,3,11}$ = 6.22; *Gigartina radula* F = 11.10 > $F_{.01,3,11}$ = 6.22; *Bifurcaria brassicaeformis* F = 7.98 > $F_{.01,3,11}$ = 6.22). The significant seasonal variation in percentage carbon for *Bifurcaria brassicaeformis* showed a summer maximum and a winter minimum. This pattern was reversed for the four species which showed a significant seasonal variation in percentage nitrogen, this being particularly evident in the case of *Porphyra capensis* and *Ulva rigida* (fig. 2b). These species had a summer minimum and a winter maximum in levels of percentage nitrogen. A summer maximum and winter minimum in C:N ratio (fig. 2c) was shown by the four species which displayed a significant seasonal variation in C:N ratio (*Porphyra capensis*, *Ulva rigida*, *Gigartina radula* and *Bifurcaria brassicaeformis*). *Splachnidium rugosum*, although not statistically significant, also showed a somewhat higher C:N ratio in summer than in winter.

Energy Content and Inorganic Matter

Table II shows the amount of inorganic matter as a percentage of total matter as well as the calorific values (in kiloJoules per gram dry weight) of the five species of intertidal seaweed investigated in this study. Four of the five species have fairly similar percentage inorganic matter levels (ranging from 23.01% to 27.22%), the exception being *Porphyra capensis* with an exceptionally low level of only

8.40%. Similarly, the same four species (*Ulva rigida*, *Gigartina radula*, *Splachnidium rugosum* and *Bifurcaria brassicaeformis*) display very similar calorific values (ranging from 10.19 kJ. g^{-1} to 10.46 kJ. g^{-1}). *Porphyra capensis* is again the exception with a comparatively much higher energy content of 15.71 kJ. g^{-1}.

Immersed Primary Production

Photosynthetic light curves (P-I curves) obtained seasonally for the five species of intertidal algae investigated are illustrated in appendix III. The P_{max} and I_K values obtained for each of these light curves are shown in table III and plotted in figures 3 and 4. *Porphyra capensis* shows a very high level of potential maximum production (fig. 3) with highest P_{max} levels being observed in late winter to early spring (August 1985 and September 1984 P_{max} = 4.68 and 6.77mg C fixed per gram dry weight per hour respectively) and lowest levels in autumn (April 1985 P_{max} = 2.25mg C fixed. g dw^{-1}. hr^{-1}). The average P_{max} value during the period investigated was 4.13mg C fixed. g dw^{-1}. hr^{-1}.

Similarly *Ulva rigida* (fig. 3) displays a late winter to early spring peak in P_{max} (August 1985 and September 1984 P_{max} = 5.30 and 9.51mg C fixed. g dw^{-1}. hr^{-1}), but has a late summer minimum in February 1985 (P_{max} = 2.91mg C fixed. g dw^{-1}. hr^{-1}), with an average P_{max} of 4.53mg C fixed. g dw^{-1}. hr^{-1}. *Porphyra capensis* and *Ulva rigida* are the two species with the highest net photosynthetic potential (greatest P_{max} values) of all the intertidal species investigated. The plant with the next highestnet potential primary production is *Gigartina radula* (fig. 3) with a peak P_{max} value in spring (September 1984 P_{max} = 4.60mg C fixed. g

TABLE III: Seasonal Pmax & Ik values for five submersed intertidal algae

	Jun 84		Sep 84		Nov 84		Feb 85	
	Pmax	Ik	Pmax	Ik	Pmax	Ik	Pmax	Ik
Porphyra	5.39	541	6.77	220	no data		3.11	218
Ulva	5.09	239	9.51	92	no data		2.91	298
Gigartina	2.36	253	4.60	150	0.81	82	1.17	248
Splachnidium	2.57	474	2.78	352	no data		1.32	661
Bifurcaria	0.82	66	1.66	114	2.05	323	0.90	208

Apr 85		Jun 85		Aug 85		Oct 85		Average	
Pmax	Ik	Pmax	Ik	Pmax	Ik	Pmax	Ik	Pmax	Ik
2.25	131	4.05	186	4.68	287	2.68	90	4.13	239
3.68	122	3.32	117	5.30	103	1.88	53	4.53	146
1.07	222	3.22	245	1.79	423	2.19	303	2.15	241
2.85	311	2.77	319	3.13	341	1.69	91	2.45	364
2.58	367	no data		1.99	238	1.85	77	1.69	199

TABLE IV: Respiration rates of five submersed intertidal seaweeds

	Rate (mg C respired. g dw^{-1}. hr^{-1} ± S.E.)	Percentage of P_{max}
Porphyra capensis	0.43 ±0.06	10.4%
Ulva rigida	0.60 ±0.11	13.2%
Gigartina radula	0.26 ±0.04	12.1%
Splachnidium rugosum	0.37 ±0.09	14.1%
Bifurcaria brassicaeformis	0.27 ±0.08	16.0%
Average respiration	0.39 ±0.10	13.0%

Fig. 3: Seasonal P_{max} values of five intertidal seaweeds at Dalebrook.

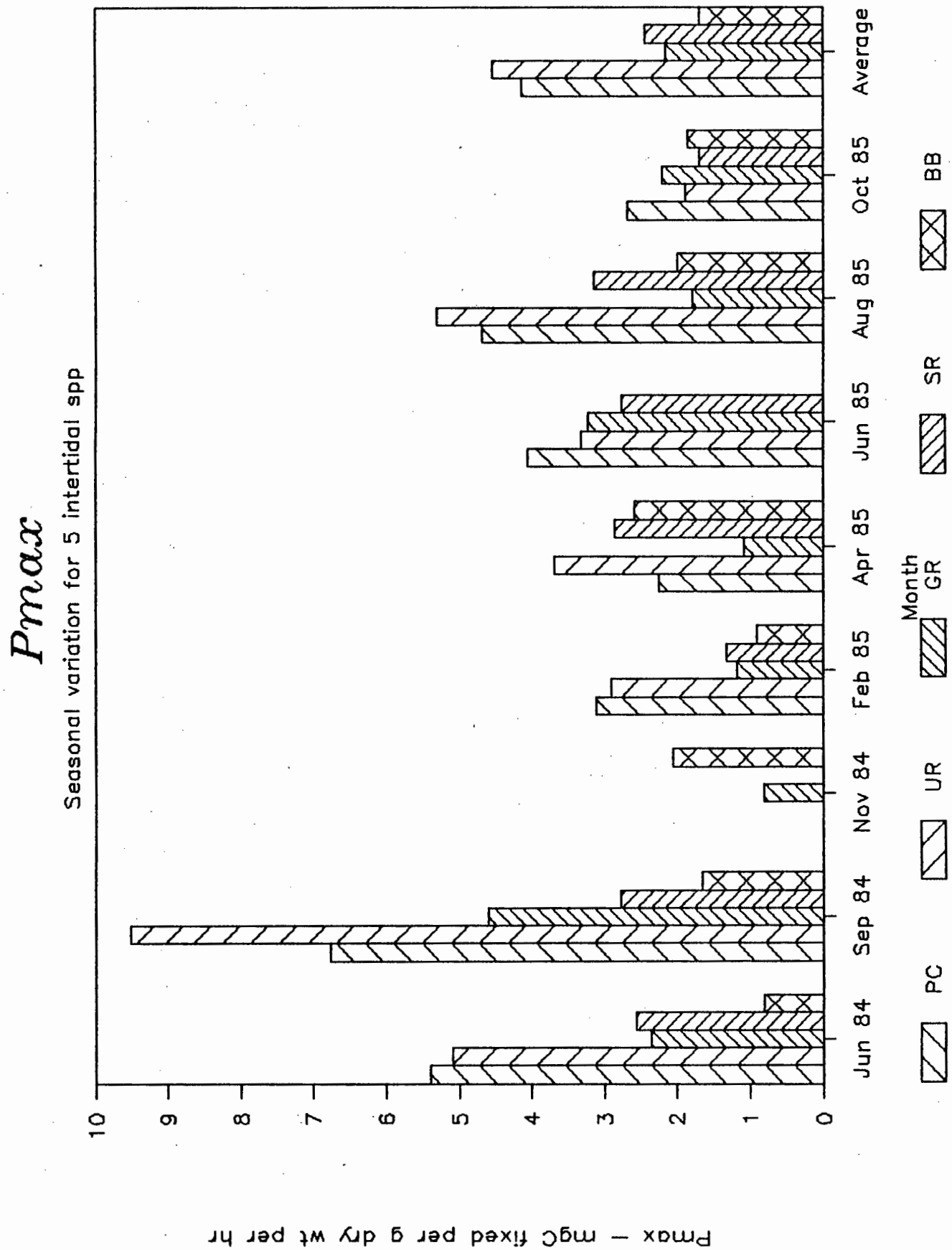
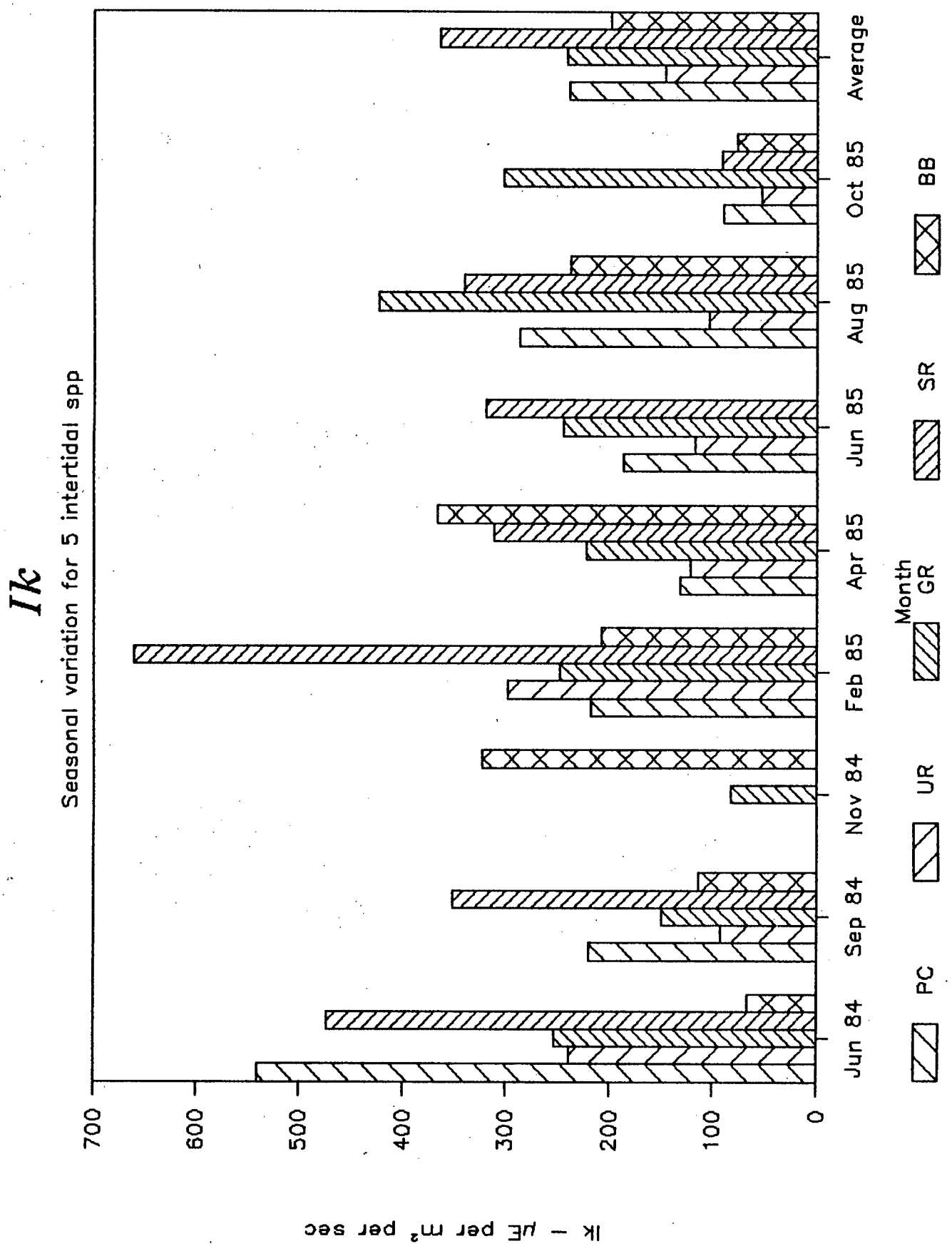


Fig. 4: Seasonal I_K values of five intertidal seaweeds at Dalebrook.



$dw^{-1}.hr^{-1}$) and a summer low in P_{max} of 0.81mg C fixed.g $dw^{-1}.hr^{-1}$ in November 1984. The average P_{max} of this species was 2.15mg C fixed.g $dw^{-1}.hr^{-1}$. A similar average figure was shown by *Splachnidium rugosum* (fig. 3) with an observed value of 2.45mg C fixed.g $dw^{-1}.hr^{-1}$. This species displayed a minimum P_{max} in summer (February 1985 P_{max} = 1.32mg C fixed.g $dw^{-1}.hr^{-1}$), but had no distinct seasonal maximum, the figures for June 1984, September 1984, April 1985, June 1985 and August 1985 being similar (August being the highest). In contrast to this, the greatest P_{max} for *Bifurcaria brassicaeformis* (fig. 3) is quite distinct in April 1985 (P_{max} = 2.58mg C fixed.g $dw^{-1}.hr^{-1}$), but the timing of the minimum P_{max} value is unclear with two similar values of 0.82 and 0.90mg C fixed.g $dw^{-1}.hr^{-1}$ being observed in June 1984 and February 1985 respectively. The average P_{max} for this species was 1.69mg C fixed.g $dw^{-1}.hr^{-1}$.

The I_k values of the five intertidal species are shown in fig. 4. *Splachnidium rugosum* has the highest average I_k with a value of 364$\mu\epsilon.m^{-2}.sec^{-1}$, followed by *Gigartina radula* and *Porphyra capensis* with 241 and 231$\mu\epsilon.m^{-2}.sec^{-1}$ respectively. *Bifurcaria brassicaeformis* and *Ulva rigida* have the lowest I_k values with respective measurements of 199 and 146$\mu\epsilon.m^{-2}.sec^{-1}$. Examination of the I_k values obtained for each species reveal no distinct seasonal variation patterns of I_k for any of the five species investigated. The average dark respiration rate of each species is shown in table IV. The respiration is shown as a rate in column one, and as a percentage of P_{max} in column two. Those species with the highest net production display the highest respiration rates (*Porphyra capensis* and *Ulva rigida*). However, when expressed

as a percentage of P_{max} it can be seen that the respiration rates of the five species are fairly similar with respect to the relative amount of photosynthesis occurring in each species. It is observeable that the species' with the higher P_{max}, whilst showing the highest rate of respiration, have lower respiration when expressed as a percentage of average P_{max}.

Emersed Primary Production

Figure 5 shows the primary production of each intertidal species at 0.5, 1, 2, 3, 4, 5 and 6 hours after emersion, while the percentage desiccation of each species at each time is shown in fig.6. It can be seen that the rate of carbon fixation declines as the time after emersion and percentage desiccation increase. *Porphyra capensis* shows the highest levels of primary production, followed in decreasing order by *Gigartina radula*, *Ulva rigida*, *Splachnidium rugosum* and *Bifurcaria brassicaeformis*. The production of *Porphyra capensis* declines the least rapidly as desiccation increases when compared to the other four species, a positive net photosynthetic rate being maintained throughout the experimental period - even at a desiccation level as high as 93%. *Gigartina radula* is the plant next most resistant to desiccation stress, it being able to maintain a positive net photosynthetic rate up to 94% desiccation throughout the duration of the experiment. Both *Ulva rigida* and *Splachnidium rugosum* show similar characteristics in their production versus desiccation curves. While *Ulva rigida* produces slightly more than *Splachnidium rugosum*, the rate of decrease of production in both species is similar with marked decreases in production as desiccation increases

Fig. 5: Net primary production versus time exposed of five exposed intertidal seaweeds at Dalebrook (September-October, 1985).

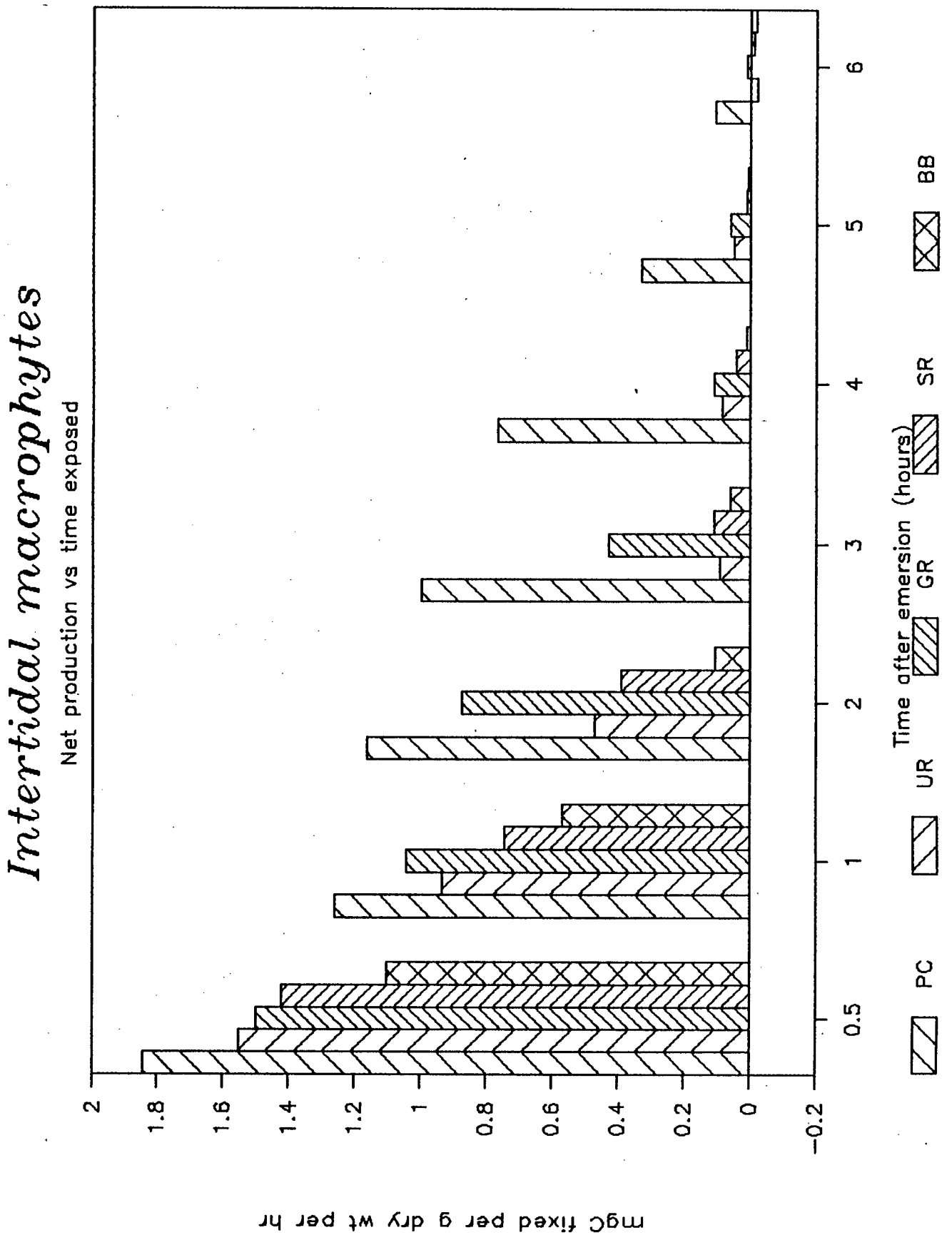
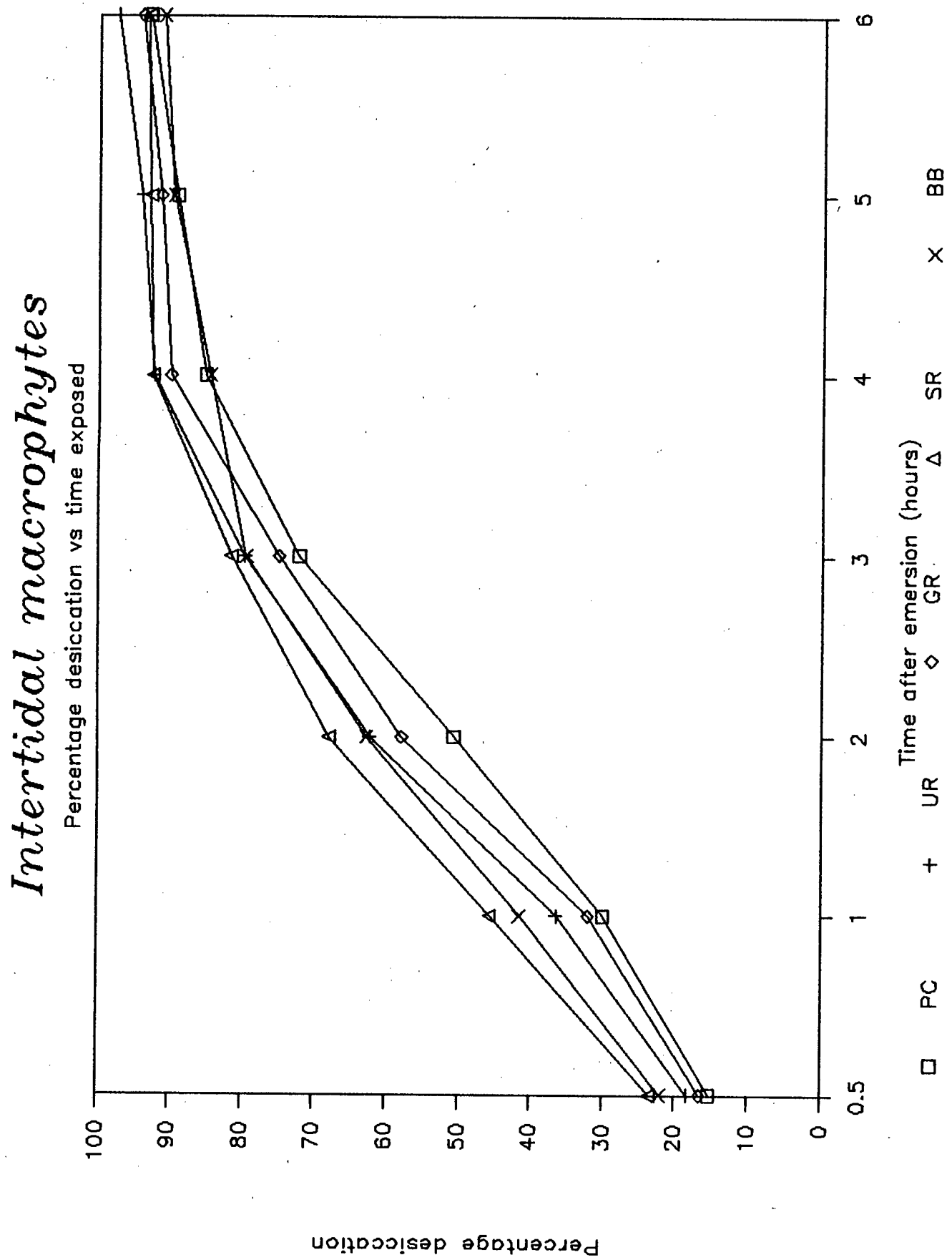


Fig. 6: Percentage desiccation versus time exposed of five intertidal seaweeds at Dalebrook (September-October, 1985).



until a low level of production is reached (at approximately 80% desiccation) after which the decline is slower but continues until a negative net production figure is attained at roughly 91-93% desiccation (six hours after emersion). The slower decline at high levels of desiccation is also shown by *Gigartina radula* and *Bifurcaria brassicaeformis*, but is not shown by *Porphyra capensis* - this species showing the opposite pattern - a slower decline in production as desiccation increases until a level of approximately 80% desiccation is reached, after which production falls rapidly to a minimum at 93% desiccation. *Bifurcaria brassicaeformis* shows a pattern similar to both *Ulva rigida* and *Splachnidium rugosum*, but the decline in production as desiccation increases in the early stages after emersion is much more rapid than in these other two species. From 60% desiccation upwards the decline in production is slower with a negative level of net production being reached at 91% desiccation.

From fig. 6 it can be seen that each species seems to desiccate at a similar rate. The plots of desiccation vs time are hyperbolic, with an initial rapid rate of desiccation after emersion until a desiccation level of 80-90% is reached after four hours emersion, after which the desiccation level only increases slowly to approximately 93% after six hours emersion.

Since each species shows a similar pattern of rate of desiccation, examination of the data from fig. 5 would seem to indicate that the rate of production of an individual species is related to the amount of desiccation experienced by that particular species. However, some species are obviously more adapted to desiccation and can

photosynthesize at a greater rate than other species at similar levels of desiccation. The results from this experiment reveal that *Porphyra capensis* is the most productive plant during the emersed phase. The general pattern displayed by four of the five species investigated is of a rapid decrease in primary production as desiccation increases from approximately 20% half an hour after emersion to approximately 79% three hours after emersion. Thereafter desiccation is slower until approximately 94% is reached six hours after emersion when net production is either negative or very close to zero. The exception to this rule is *Porphyra capensis* which, although desiccating at a rate similar (but slightly slower) to the other species investigated (fig. 6), maintains a rate of production much higher than the other four species (fig. 5). The rate of production of *Porphyra capensis* only begins to fall markedly once a level of desiccation of approximately 89% is reached. *Bifurcaria brassicaeformis* is the plant least resistant to desiccation, the rate of production of this plant falling to a low level only two hours after emersion at a desiccation level of only 63%. *Gigartina radula* is second only to *Porphyra capensis* in maintaining a meaningful net production figure for up to three hours after emersion (fig. 5), and is also the only plant besides *Porphyra capensis* still to have a positive net photosynthetic rate six hours after emersion. The other two species investigated, *Ulva rigida* and *Splachnidium rugosum* show production rates and desiccation tolerances similar to each other and intermediate between *Gigartina radula* and *Bifurcaria brassicaeformis*. Of the two species, *Ulva rigida* is marginally more productive in the

first three hours after emersion, after which the two plants are almost identical in their rates of production, although *Ulva rigida* is the more desiccated plant after six hours (their desiccation values being similar at four and five hours after emersion).

DISCUSSION

The maximum potential rate of photosynthesis of all five species of intertidal seaweed is comparable with those observed in other studies (e.g. Buesa, 1977 - tropical algae at 0.11-7.73mg C fixed.g $dw^{-1}.hr^{-1}$; Wallentinus, 1978 - Baltic macroalgae at 1.5-11.4mg C fixed.g $dw^{-1}.hr^{-1}$; Merrill and Waaland, 1979 on the US east coast species *Gigartina exasperata* (Harvey and Bailey)). The thin sheet-like forms (*Porphyra capensis* and *Ulva rigida* are by far the most productive species investigated. This would seem to indicate that the thin, sheet-like form is more capable of utilizing the available light energy and absorbing nutrients from the environment. This observation is supported by the findings of Littler (1980) in his comparative analysis of photosynthesis and thallus morphology in a large number of intertidal Californian seaweeds. Ramus (1978) demonstrated that *Ulva* has a morphology especially adapted to high light regimes. The thin thallus construction of both *Ulva rigida* and *Porphyra capensis* minimizes self-shading by the thallus. Also, both these species have larger cells than the other seaweeds studied, and this would result in less internal self-shading by non-photosynthetic cell wall and cytoplasmic components due to a smaller cell surface to volume ratio. While these thin, sheet-like forms have a smaller cell surface to volume ratio due to their comparatively large cell size, their thalli have a large surface to volume ratio, due to their thin structure. This large surface to volume ratio allows a more rapid uptake of nutrients and hence a greater rate of photosynthesis. Because the amount

of photosynthesis by a plant is related to its photosynthetic area, it is those thin, sheet-like forms such as *Porphyra capensis* and *Ulva rigida* which have the greater rate of production per gram dry weight since the entire thallus is composed of photosynthetic material. The thick cartilaginous and coarsely branched forms have more of their thallus made up of structural and other non-photosynthetic components, and hence their rate of primary production per unit biomass would be expected to be less than the thin, sheet-like forms.

Although the data is somewhat variable, the late winter-spring seasonal maximum displayed by *Porphyra capensis*, *Ulva rigida* and *Gigartina radula* is similar to observations by various other authors. For example, Brinkhuis (1977a) observed a potential photosynthesis maximum for *Ascophyllum nodusum* (L.) Le Jol. in spring, and a minimum during late summer through to winter. In two other species (*Fucus vesiculosus* L. and *Ulva lactuca* L.), Brinkhuis (1977b) observed spring and summer photosynthetic maxima and winter minima. Littler *et al* (1979) observed summer photosynthetic maxima for nine out of 13 species investigated, and minima in winter through to spring. The season of lowest P_{max} was fairly variable in this study at Dalebrook, ranging from late summer through mid winter. These variable or extended minima have also observed by Brinkhuis (1977a) for *Ascophyllum nodosum* as well as by Littler *et al* (1979), their data showing an extended range of period of mimimum photosynthesis from autumn through winter to spring. It is thus possible to conclude from this study that the magnitude of potential maximum primary production from the dominant

intertidal seaweeds at Dalebrook is at least as great as the average of seaweeds studied elsewhere, and potentially much greater for the thin, sheet-like forms of *Porphyra capensis* and *Ulva rigida*. The study of Buesa (1977) was carried out on tropical algae, whilst this study at Dalebrook concerns temperate algae. This may be of some relevance since the tropical regions are known for their stable environments where the marine seaweeds would tend to persist having reached the climax communities of their particular succession. In the case of this local study where the environment can be regarded as unstable, the slightly higher rates of production encountered could well be because these species are more opportunistic species than the tropical species studied by Buesa (1977) and would therefore be expected to possess higher growth rates.

The absence of a totally uniform pattern of seasonal potential maximum photosynthesis is not too surprising since different intertidal seaweed populations can be (and usually are) regulated by different biotic and abiotic factors. For example, unpredictable wave action (storm turbulence) has been shown to regulate the abundance of large frondose algae on some tropical reefs (Doty, 1971) rather than more regularly seasonal environmental parameters. Smaller (less frondose) plants were less affected by storm turbulence and showed greater seasonal predictability. Factors controlling the seasonal potential rate of primary production on the shore at Dalebrook may thus not be as obvious as simple factors such as total irradiance, day-length or photoperiod.

The results concerning respiration (table IV) show that the species with the higher average P_{max} values, whilst showing

the highest rate of respiration, have lower respiration when expressed as a percentage of P_{max}. This indicates that these species are more photosynthetically efficient. It is noticeable that *Porphyra capensis* is very efficient, having the lowest respiration rate when expressed as a percentage of its P_{max}. The high shore species (e.g. *Porphyra capensis*) tend to show a lower rate of respiration (expressed as a percentage of P_{max}) than the low shore species (e.g. *Bifurcaria brassicaeformis*).

Seasonal biomass data for nine intertidal algae at Dalebrook has been documented by McQuaid (1985). McQuaid (1985) found that significant variation in seasonal biomass occurred at Dalebrook for dominant species. All of the species investigated in this study at Dalebrook can be classified as dominant species, but only seasonal biomass data for *Porphyra capensis*, *Ulva rigida* and *Gigartina radula* is available from McQuaid (1985). Seasonality of biomass of these species was evident in that low biomass was observed during winter and high biomass during summer for these three species. The summer high in biomass could well be due to the high rate of primary production in spring with a lag for the conversion of photosynthetic production to growth. Certainly the broad period of minimum photosynthesis from late summer through to winter is possibly one of the major causes of the generally low biomass observed during the winter months.

According to Chalker (1981), I_K is a parameter indicative of a plant's physiological adaptation to its light environment and can be used to monitor its photosynthetic responses. Seasonal variation in I_K values would be observed because of photoadaptive plant responses to varying levels of

irradiance. A higher I_K value is to be expected during seasons of high incident irradiance (summer), and a lower I_K value during seasons of low irradiance (winter). A seasonal pattern in I_K is not readily apparent in the intertidal species investigated in this study. This fact seems surprising at first, but may be explained by the fact that because there is little light attenuation in the intertidal environment, the plant species are mostly photosynthetically saturated during the daylight period irrespective of the time of year.

This inconclusive evidence seems to indicate that, where light is not limiting (i.e. the intertidal zone as compared to the sublittoral zone - see chapter 3 discussion on subtidal I_K values), variations in I_K could well be a response to short term fluctuations in irradiance as opposed to longer term seasonal changes in total irradiance, the plant always being photosynthetically light saturated. Four of the species investigated have average I_K values greater than $200\mu\epsilon.m^{-2}.sec^{-1}$, and this would seem to indicate that these intertidal seaweeds are all sun-adapted (as opposed to shade-adapted) species - a not too surprising conclusion given the high level of irradiance impinging on the exposed shore. The exception is *Ulva rigida* which has a lower average I_K of $146\mu\epsilon.m^{-2}.sec^{-1}$ and this is evidently the result of the particular form which was collected in this study being a rock pool resident, shading from the sides of the pool and other pool residents possibly being sufficient to alter the light environment in which the plant grows, and hence also the average I_K of this species. This postulation is further borne out by light data from *Bifurcaria*

brassicaeformis, the other species at Dalebrook which tends to grow in less light exposed crevices but is not submersed at low tide so is still exposed to desiccation (this at Dalebrook - at other sites it can occupy a fairly broad band at the bottom of the eulittoral zone). This species displays the next lowest average I_k value of 199$\mu E.m^{-2}.sec^{-1}$. The adaptation of these species to their light environment is obviously not the sole contributory factor to their rate of net photosynthesis, their adaptation to seasonal temperature changes is also of importance - Mathieson and Norall (1976) suggested that optimal temperature and light requirements of seaweeds are adjusted in an adaptive fashion to the varying environmental regimes of their habitats.

The first comparisons of emersed photosynthesis and submersed photosynthesis seemed to indicate (Quadir *et al*, 1979 quoting Stocker and Holdheide, 1938) that the photosynthetic rates of emersed seaweeds was higher than the photosynthetic rates of immersed seaweeds. On the other hand, data from Chapman (1965) shows that the photosynthetic rate of emersed seaweeds is either the same as, or lower, than comparable submersed algae. In between these two extremes, Johnson *et al* (1974) found that intertidal seaweeds growing lower on the shore had a lower photosynthetic rate while emersed compared to when submersed, while plants growing on the upper and middle parts of the shore had maximal photosynthetic rates when they were slightly desiccated. Similarly, Quadir *et al* (1979) reported a higher emersed photosynthetic rate than submersed photosynthetic rate for the high shore *Fucus distichus* L., and the reverse for *Iridaea cordata* Turn.

Bory, a low shore intertidal seaweed which is somewhat similar in form to *Gigartina radula*. The data from this study at Dalebrook shows a lower actual rate of photosynthesis for emersed intertidal seaweeds than potential maximum rate of photosynthesis for submersed intertidal seaweeds. Due to the high incident irradiance and high nutrient availbility, it is likely that the potential maximum rate of photosynthesis is often approached by these intertidal algae while submersed, and since the submersed maximum rates are substantially higher than the emersed rates of photosynthesis, the overall contribution of submerged photosynthesis is likely to be most often greater then the rate of emersed photosynthesis. Inspection of the data reveals that *Porphyra capensis* (fig. 5) is well adapted for its position as the species occurring highest on the shore as the rate of photosynthesis for this species is, throughout the period of desiccation, higher than for the other four species investigated. *Porphyra capensis* maintains a positive net photosynthetic rate even when over 90% desiccated, after six hours emersed. Although the photosynthetic rate of this species (as for all the species investigated) was less when emersed than when submersed, this does not mean that the plant is not desiccation adapted, but rather that the submersed environment is more favourable for achieving the maximum rate of photosynthesis. This is to be expected given the more favourable conditions for nutrient uptake and the high diffusion gradients caused by wave action which are possible in an exposed rocky shore environment. Certainly atmospheric boundary layer effects around an emersed plant, together with the non-continuous

availability of nutrients, must play a contributory role towards reduced photosynthesis in emersed seaweeds. Also, the much higher ambient temperatures experienced by emersed intertidal seaweeds must play a part in reducing the net photosynthetic rate. The maximum monthly average sea temperature in False Bay does not exceed 20·C (Bolton, 1986), while the temperature of exposed seaweeds on the shore could easily reach 30·C or more. The increased rate of respiration due to increased temperature could easily account for the lower rate of net photosynthesis when taken in conjunction with the other inhibitory factors mentioned above. Also, Brinkhuis *et al* (1976) noted that respiration increased as the level of desiccation increased, and this would therefore contribute towards the reduced levels of net photosynthesis observed in this study. Previous studies on exposed seaweed production (e.g. Brinkhuis *et al*, 1976 on *Ascophyllum nodosum*; Quadir *et al* on *Fucus distichus* and *Iridaea cordata*) have indicated that net photosynthesis increases after exposure until approximately 20% desiccation is reached, after which it decreases - very sharply after a level of 50% desiccation is achieved. The apparent initial increase of photosynthesis is normally ascribed to water loss from the fronds in the initial phase of desiccation enhancing the exchange of carbon dioxide from the frond as well as possibly affecting the detection of carbon dioxide within the IRGA itself (CO_2 and H_2O having similar infra-red absorption spectra). The subsequent loss of water due to desiccation of the more internal plant tissues would not tend to interfere with gas exchange as this primarily occurs at the frond surface. In this study it is not possible to

say whether there was any slight increase in photosynthesis in the early stages of desiccation as no measurement of photosynthesis immediately after exposure was performed. It is however likely that no such increase took place as the exposed rate of photosynthesis of the species investigated only 30 minutes after emersion was substantially lower than the submersed P_{max} values obtained.

The broadly similar photosynthesis-desiccation responses shown by *Gigartina radula*, *Ulva rigida* and *Splachnidium rugosum* is in keeping with their habitat. All are mid-shore species, with *Gigartina radula* dominating the biomass (McQuaid, 1985). This species is slightly more productive at similar levels of desiccation than *Ulva rigida* and *Splachnidium rugosum*, both of which show very similar photosynthetic responses to desiccation. *Gigartina radula* desiccates marginally slower than *Ulva rigida* or *Splachnidium rugosum* up to the 70% desiccation level, and this may well contribute towards its better tolerance of desiccation (from the photosynthetic aspect). As a thick cartilaginous species, *Gigartina radula* may be expected to be more tolerant of desiccation stress than the membranous *Ulva rigida*. The fact that *Gigartina radula* maintains (albeit only just) a positive net photosynthetic rate after six hours indicates that this is the case. *Ulva rigida* is a species which grows on the shore at Dalebrook in two distinct morphologies - a large broad form abundant in rock pools and crevices, and a small tuft-like form which grows on exposed rocks at levels nearly as high as *Porphyra capensis*. Different forms of *Ulva* are not unusual, having been reported in other localities (e.g. Mshigeni and

Kajumulo, 1979; Steffensen, 1976). During this study, the broad form was used in the submersed and emersed experiments. The data from the submersed experiments, together with the data from the emersed experiments, would seem to indicate that this broad form may be less tolerant of desiccation stress than the tuft-like form. *Bifurcaria brassicaeformis* is the least tolerant of desiccation of the species investigated. This is not surprising in view of the fact that this species grows in the lower eulittoral region, where it is common in crevices and other areas which do not dry out excessively under the normal tidal regime. Evidence (besides its morphology) for the fact that *Bifurcaria brassicaeformis* is adapted for its position as the species occurring lowest on the shore is that it is almost incapable of positive net photosynthesis at levels of desiccation greater than 40% after less than two hours emersion. Although *Bifurcaria brassicaeformis* does not seem to be well adapted to resist desiccation stress, this should not normally be detrimental to the plant's viability as, being a low shore species, it is emersed for the shortest duration at low tide and is still, even then, occasionally wetted by breakers. The propensity of this species to colonise shaded areas such as crevices at Dalebrook is therefore probably the result of the species' inability to survive the high desiccation stress as would occur under exposed conditions on the flat shore of Dalebrook.

Observation of the rate of desiccation for all the species investigated indicates that most of the desiccation occurs in the first three to four hours after emersion at 25·C, after which the rate of desiccation levels off. Quadir *et al*

(1979) observed almost identical rates of desiccation in three low, mid and high shore species (*Iridaea cordata*, *Ulva fenestrata* P. & R. and *Fucus distichus*). In particular, the high shore species *Fucus distichus* shows very similar adaptations to *Porphyra capensis*. In both species as the thallus loses water the frond folds over on itself trapping moist air between the exposed part of the frond and the inner part of the frond closer to the substratum, which as a result tends to desiccate less rapidly - i.e. the outer exposed frond becomes hard and dry and acts as a protective cover to prevent water loss in the unexposed in part of the thallus.

The habitat of *Bifurcaria brassicaeformis* is an example of one of the two methods which may be utilized by intertidal seaweeds to escape desiccation stress. The survival of prolonged exposure can be by either avoiding tissue dehydration as much as possible (e.g. *Bifurcaria brassicaeformis* habitat) or by tolerating it. It has been suggested (Schonbeck and Norton, 1979b) that since the intertidal environment is characterised by predictable periodic immersion, a plant which loses water slowly (i.e. tolerates desiccation stress) may escape excessive dehydration at low tide. In this regard, hygroscopic polysaccharides present in the plant thallus may play a role in retarding water loss. These polysaccharides may be present in the form of mucus within the plant thallus. Quadir *et al* (1979) quoting Wiltens (1975) suggested that desiccation in *Fucus distichus* may be retarded by a high concentration of unsaturated fatty acids in the epidermal cells which therefore form a false cuticle. Similarly,

Branch and Branch (1981), postulated (without displaying any data) that a high mucus content in *Porphyra capensis* is responsible for the high desiccation tolerance of this species - the mucus losing water as the plant dries while the cells remain unaffected. According to Branch and Branch (1981) *Porphyra capensis* can shrink to one-tenth of its original size as a result of this water loss, this shrinking also reducing the surface area from which further water loss can occur. The high desiccation tolerance of *Porphyra capensis* revealed by this study at Dalebrook seems to indicate that this mucus protection system may be a factor in this species' resistance to desiccation, but other studies (e. g. Dromgoole, 1980) indicate that factors such as mucilage content and cell wall thickness are not significant contributors to desiccation resistance when compared with factors such as the surface area to volume ratio. Dromgoole (1980) found that the most important factor affecting the rate of desiccation of various algae was the surface to volume ratio, those with a higher ratio desiccating more rapidly. In this study at Dalebrook, it can be seen that species of differing morphology all desiccate at a similar rate, thus apparently contradicting the findings of Dromgoole (1980). However this is not neccesarily so, as the object of this study was to desiccate the plants in conditions as close to that found on the shore as possible. In the case of the high surface to volume ratio species (*Porphyra capensis*, *Ulva rigida* and even *Gigartina radula*), this meant positioning the plants in the incubation chamber in the same manner as they lie on the shore while exposed. This means that the frond folding over itself would

contribute to desiccation resistance, thus slowing down desiccation to a rate similar to those species with a lower surface to volume ratio. This method contrasts with that of Dromgoole (1980) which exposed as much of the surface of the plant to desiccation as was possible.

Algal zonation has been explained in terms of tolerance to exposure and desiccation by Biebl (1962), and Quadir *et al* (1979). The results of this study at Dalebrook confirm the observations of Quadir *et al* (1979) that net photosynthetic activity during exposure is an important factor contributing to the observed pattern of algal zonation. Most importantly, the species such as *Porphyra capensis* which are well adapted to photosynthesize at high levels of desiccation, support the conclusions of Johnson *et al* (1974) and Brinkhuis *et al* (1976) that exposure cannot be regarded strictly as a period of extreme physical stress which is tolerated, but that the plant is well adapted to make the most of a hostile environment which constitutes a major proportion of its life span (see table IX)

According to Atkinson and Smith (1983), the Redfield ratio is a unifying concept in biological oceanography. As discussed by Redfield *et al* (1963), this is the ratio of carbon:nitrogen:phosphorus (C:N:P). Redfield *et al* (1963) determined a ratio of 106:16:1 based on extensive analyses of marine plankton. This ratio translates to a C:N ratio of 6.6:1. Deviation of ratios from the Redfield ratio are often used to infer nutrient limitation of growth (Atkinson and Smith, 1983). There has been some discussion about the most appropriate value for the average phytoplankton C:N:P ratio. For example, Parsons *et al* (1961) and Ryther and Dunstan

(1971) suggest the ideal Redfield ratio for phytoplankton should be 70:10:1 (C:N=7:1). On the other hand, seaweed C:N ratios may be different from the Redfield ratio. Atkinson and Smith (1983) reported that C:N:P ratios for benthic macroalgae and seagrasses deviate markedly from the Redfield ratio and suggested that this deviation is ecologically significant. The mean C:N ratio of 17 species of Rhodophyta from seven localities worldwide (from Atkinson and Smith, 1983) was 15.42:1, with a range of 5.96:1 to 28.24:1. The mean is well above the Redfield ratio for phytoplankton, with a few individual analyses as low as the Redfield ratio. The wide range of C:N ratios is probably caused by environmental differences - since the plants were collected from different sites during different seasons, they must have had large differences in their light, temperature, wave action and nutrient regimes. According to Atkinson and Smith (1983), plants collected from high nutrient environments have significantly lower C:N ratios than those collected from low nutrient environments. This is in agreement with various other workers (e.g. Lapointe *et al*, 1976; Jackson, 1977) who observed that the C:N ratio of benthic plants decreases with increased dissolved inorganic nitrogen concentration. Thus varying C:N ratios are presumably a response to nitrogen storage and could possibly be used as an indicator of nitrogen limitation, i.e. high C:N ratios could indicate nitrogen limitation of photosynthesis. Plants seem to approach the Redfield ratio as a limit, rather than showing an average tending towards this ratio. This observation agrees with that of Atkinson and Smith (1983). The data from this study, being significantly seasonally

variable, is therefore of great interest if this is the interpretation that can be applied to it. The significant seasonal variation of C:N ratios of these intertidal algae seem to be the result of significant seasonal variation in total nitrogen levels (except *Bifurcaria brassicaeformis*). The evidence for this is that all but one of these algae (*Bifurcaria brassicaeformis* being the exception) do not show significant seasonal variation in total carbon levels, while all (with the exception of *Bifurcaria brassicaeformis*) show very significant seasonal variations in levels of total nitrogen. The resulting variation in C:N ratios is significant for all the intertidal algae investigated except *Splachnidium rugosum*. The significant seasonal variation in carbon in *Bifurcaria brassicaeformis* would seem to indicate that the rate of incorporation of carbon into this species (both as structural carbon and as carbohydrate) may be varying seasonally, but why this should be the case when light and nutrients are unlikely to be limiting is unclear. On the other hand, the significant seasonal variation in nitrogen levels of the other four species investigated would seem to indicate that levels of nitrogen in the environment are seasonally variable. While Dalebrook is not an upwelling focus (because it is situated in False Bay which does not experience upwelling to the extent of the exposed west coast), due to currents, tidal streams and wind, some upwelled nutrient-rich water will enter the bay during the upwelling season in the summer months. As stated above, a low C:N ratio is commonly found in plants in a high nutrient environment, but the intertidal algae investigated in this study show their highest C:N ratios in summer when upwelling

on the west coast is at a peak. The offshore north-west winter wind causing local winter upwelling cannot be ruled out as contributing to available nutrients during winter, but this is unlikely to be so great as to be especially significant. Rather, winter storms resulting in a larger detritus load with subsequent decomposition and nutrient release is more likely to be the cause of any increase in winter nutrient levels, which are thus unlikely to be limiting. However, this is conjecture as nutrient data for False Bay is unavailable. Carter (1986) also observed a summer minimum in percentage nitrogen levels of the red intertidal seaweed *Gelidium pristoides* (Turner) Kuetzing in the Eastern Cape. As Carter (1986) points out, there is little data available concerning nutrient regimes in the Eastern Cape, so the importance of the role played by these nutrients is unknown.

In this Dalebrook study, the higher C:N ratios in summer would seem to indicate that this is the maximum growth period and is either concurrent with or follows shortly after the maximum photosynthetic period. Evidence for this is usually that the incorporation of carbon as structural carbon as a result of increased photosynthesis in spring would result in higher summer C:N ratios. Also, the reduction in thallus nitrogen due to increased photosynthesis in spring would also result in higher summer C:N ratios. A lag phase behind the maximum period of photosynthesis may also be expected, and hence it is possible that C:N ratios could remain low during the photosynthetic peak and only increase after this peak is passed. This hypothesis of carbon incorporation is not

supported by significant seasonal variation in percentage carbon levels, although inspection of the data would seem to indicate that these levels are slightly higher in the December to February (summer) period. The average C:N ratios for *Porphyra capensis* and *Ulva rigida* are substantially lower than the average obtained from Atkinson and Smith (1983), while that of *Gigartina radula* is significantly less. The average for *Splachnidium rugosum* approximates that of Atkinson and Smith (1983), while that of *Bifurcaria brassicaeformis* is substantially higher. While Atkinson and Smith (1983) attributed deviations from the average to variations in nutrient conditions at the different sites investigated, this explanation cannot apply in this case because this substantial range of C:N ratios is occurring at the same site where the same nutrient conditions apply to each species. It is of interest that the species growing higher on the shore (*Porphyra capensis*, *Ulva rigida* and *Gigartina radula*) exhibit the lower C:N ratios, while the lower shore species (*Splachnidium rugosum* and *Bifurcaria brassicaeformis*) have the higher C:N ratios. This apparent relationship however, is probably coincidental with the fact that, in this instance, the thin, sheet-like forms are the species' growing highest on the shore and are also the most productive - C:N ratio and rate of production normally showing an inverse relationship (Niell, 1976). Thus, this data supports the finding of Niell (1976) that the higher a plants rate of production, the lower the C:N ratio. Niell (1976) also observed that brown algae have higher C:N ratios than members of other groups, and the data from this study supports that observation. The two representatives of the

Phaeophyta (*Splachnidium rugosum* and *Bifurcaria brassicaeformis*) show substantially higher C:N ratios than the other plants investigated. However, these brown algae are structurally more complex than the thin forms, and a higher C:N ratio due to a greater amount of structural carbon is likely.

The significant seasonal variation in water content of *Ulva rigida* is of interest. In this species, the period of maximum water content tends to coincide with the season of maximum potential net photosynthesis and the period of minimum water content with the season of minimum photosynthesis. Similarly, Carter (1986) noted that the intertidal red alga *Gelidium pristoides* displayed a correspondence between increasing and decreasing dry weights and the period of minimum and maximum growth respectively. A similar pattern was also observed in three species of the red alga *Eucheuma* by Dawes *et al* (1974). Since the water content (the reciprocal of dry weight) reflects the cellular condition of the plant cells (Carter, 1986), a higher water content during the summer implies that the cells are, physiologically, in a good condition and may be expected to exhibit high rates of primary production. On the other hand, plants in a dormant or slow growth phase (i.e. low primary productivity) usually exhibit low water content, low ash content and low C:N ratios (Mann, 1972; Niell, 1976). The measurement of water content has sometimes been referred to as a means of determining the seasons of maximum photosynthesis (and hence growth) in intertidal seaweeds, although the data collected in this study does not seem to indicate that this is the case.

Finally, the data concerning percentage inorganic content and energy content of the five species investigated is limited, but can be discussed briefly. Although only one measurement of calorific content was obtained, it may be safe to assume that this does not vary seasonally since carbon content (the source of energy in calorimetry) does not vary significantly in all the species except *Bifurcaria brassicaeformis*. Other studies have also shown there to be no significant seasonal changes in calorific values of seaweeds (e.g Paine and Vadas, 1969; Mann, 1972). The high calorific value displayed by *Porphyra capensis* compared to the other species is the likely result of this species' high productivity - the incorporation of more carbon as a result of increased photosynthesis as high energy carbohydrate (i.e. mucilage) increasing the calorific value obtained. Since *Ulva rigida* does not contain large amounts of mucilage, the high rate of photosynthesis of this species is not translated into increased calorific value, but into a rapid growth rate. This observation is supported by the data of Himmelman and Carefoot (1975) who showed a relationship between calorific value and rate of growth (i.e. production) in temperate seaweeds. Conversely, a high carbon content in this species (on average 30% greater than the other four species studied) would result in a low inorganic content (since carbon is incorporated as organic compounds). The percentage inorganic content of *Porphyra capensis* (8%) supports this hypothesis, it being much lower than the other species (25%).

CHAPTER 3. PRIMARY PRODUCTION IN SUBLITTORAL SEAWEEDS

INTRODUCTION

Local Cape Peninsula benthic seaweed productivity data is so far only available for kelps (Jarman and Carter, 1981). In view of this lack of local benthic productivity data for understorey seaweeds, a complete assessment of the contribution of benthic algae to the carbon flow and nutrient dynamics of the Benguela upwelling region is not yet possible. Furthermore, logistical problems make a complete analysis difficult. The collection of intact algae is difficult due to uneven distribution patterns and depth of growth (Smith, 1981). Collection of algae by means of SCUBA is far less biased than by dredging (Mathieson and Dawes, 1975; Schneider and Searles, 1978). However, sampling using SCUBA is highly weather dependent. A critical problem asociated with long-term studies on primary production is the calculation of daily productivity from short-term measurements. Although daily productivity is the direct source of organic carbon on which the food web is based (Smith, 1981), direct 24-hour measurements of primary production are impossible due to nutrient depletion, build up of auto-inhibitory compounds released by the incubated plant, oxygen saturation and/or depletion and other bottle effects. These difficulties with long incubations remain unresolved despite the attentions of various authors (e.g. Venrick *et al*, 1977 - working with phytoplankton). The higher biomass to incubation bottle volume encountered with seaweeds (as opposed to phytoplankton) compounds these

difficulties. As a result, measurements of primary production of benthic macroalgae are usually conducted under less than ideal conditions.

The aim of this study is to estimate the primary production and photosynthetic responses of three sublittoral understorey red algae, namely, *Botryocarpa prolifera* Greville, *Epymenia obtusa* (Greville) Kuetzing and *Gigartina radula* (Esper) J. Agardh. Both *Botryocarpa prolifera* and *Epymenia obtusa* are abundant along the Cape west coast (Field *et al*, 1980) from a depth of 5m down to about 20m, while *Gigartina radula* is abundant in the intertidal region (McQuaid, 1980) and in the sublittoral down to a depth of about 5m. The objective of this investigation is to determine the seasonal patterns of primary production (if any) of these understorey algae by *in situ* measurements and to evaluate any seasonal photosynthetic responses which may occur by determination of photosynthetic light curves in controlled laboratory conditions.

Some studies on photosynthesis in understorey seaweeds have been completed (e.g. Tschudy, 1934; Brinkhuis and Jones, 1974; Mathieson and Norall, 1975b; Hoffman and Dawes, 1980; Smith, 1981; Heine, 1983). Of the earlier studies, Brinkhuis and Jones (1974) observed a maximum rate of net photosynthesis for *Chondrus crispus* Stackh. of 0.33mg C fixed. g dw^{-1}. hr^{-1} at 10-12·C. More recently, an *in situ* study by Smith (1981) observed P_{max} values of 0.22 and 0.85mg C fixed. g dw^{-1}. hr^{-1} for *Codium carolinianum* Searles and *Lobophora variegata* (Lamour) Womersley in North Carolina, USA, while Hoffman and Dawes (1980) observed a rate of photosynthesis of 4.1-9.6mg C fixed. g dw^{-1}. hr^{-1} for

Gracilaria verrucosa (Hudson) Papenfuss in Florida, USA. Heine (1983) continued the *in situ* study method, but on a seasonal basis. He used an underwater apparatus to conduct light and dark bottle incubations on the sea bed of two Californian understorey red algae, and obtained results showing fairly high rates of primary production. Any mechanism for the *in situ* incubation of marine seaweeds must (Hatcher *et al*, 1977):

i) be free of enclosed air bubbles;

ii) have a stirring mechanism in the incubation chambers to break down diffusion gradients at the plant surface;

iii) have a system whereby the oxygen tension is reduced prior to incubation.

These considerations must be taken into account during the construction of a device for the *in situ* measurement of photosynthesis, as was constructed for this study.

The importance of stirring to counteract the effects of isolation in rigid containers is discussed in Hatcher (1977). It has been put forward that flexible incubation chambers are advantageous in that they provide a relatively accurate duplication of external water movement (Gust, 1977). However, for the *in situ* seabed incubation of understorey seaweeds as carried out in this study a flexible chamber offers little advantage over a rigid chamber. This is because artificial stirring is used to counteract the effects of isolation by supplying enough agitation to preclude the inhibitory effects of the laminar boundary layer around the plant thallus.

Light and dark bottle incubation techniques use two main methods for measuring marine seaweed primary production, namely:

i) the radioactive carbon $NaH^{14}CO_3$ method;

ii) determination of dissolved oxygen methods.

The advantages and disadvantages of the ^{14}C method have been discussed by Peterson (1980). Although the method has been in use for over 30 years, the method often underestimates carbon uptake for reasons not completely understood. While the method is extensively used in estimating phytoplankton primary production, its usefulness as a means of estimating subtidal seaweed primary production is limited by its technical complexity. Besides the problems involved in using a radioactive substance in an at times dangerous and turbulent environment, certain technical difficulties such as natural variations in seawater chemistry (e.g. dissolved inorganic carbon; levels of copper) and incubation pH levels (must be buffered at pH9.5) which affect ^{14}C determinations, make the ^{14}C method impracticable for this study. Dissolved oxygen may be determined in two ways:

i) by oxygen probe;

ii) by the Winkler chemical O_2-fixation technique.

The oxygen probe method lends itself particularly well to *in situ* intertidal studies as well as to laboratory studies, and has been successfully applied (e.g. Littler and Murray, 1974). However, the technically complex (and expensive) field O_2 analyzers available are not suited for the wet and highly corrosive conditions found in the sublittoral marine environment. The Winkler method however, can be used in almost any conceivable situation, and its simplicity and

accuracy (to 0.1% - Carpenter, 1965) make it especially useful for *in situ* studies of primary production. Thus, for this study, dissolved oxygen was determined using the Winkler technique described by Strickland and Parsons (1971).

The data obtained for photosynthesis in this study will be compared with that of other authors, and together with the measurement of other parameters such as percentage carbon, percentage nitrogen, C:N ratios and calorific values, will be used to discuss the importance of Cape Peninsula understorey primary production.

MATERIALS AND METHODS

The primary production of three understorey red algae (*Botryocarpa prolifera*, *Epymenia obtusa* and *Gigartina radula*) was measured monthly from October 1984 to October 1985 at a depth of five metres in a kelp bed offshore of Oudekraal (33·59.4'S, 18·20.6'E) on the Cape Peninsula, Cape Province, Republic of South Africa (fig. 1). The substratum consists of a patchwork of granite outcrops interspersed with sandy areas. The kelp bed is exposed to winter storms driven by north west winds which result from low pressure areas emanating from the sub-antarctic regions. In summer the area is commonly exposed to persistent south east winds which result in the upwelling of colder, nutrient-rich oceanic water (Andrews, 1974).

The three species selected were chosen after laying a 2m x 25m belt transect through the kelp bed at Oudekraal from a depth of 1m close inshore to a depth of 5m approximately 40m offshore (plate 2). Macrophytes were removed from the substratum by divers and were brought back to the laboratory for identification, drying and weighing. Data from the kelp bed survey conducted by Field *et al* (1980) was used to determine whether the three species selected for this study at Oudekraal were representative members of the west coast understorey flora, and also whether they made a significant contribution (by biomass) to this flora. Data extracted from Field *et al* is shown in appendix II. It can be seen from this data that the most abundant understorey seaweeds observed from six sites in the western Cape are *Pachymenia carnosa* (J. Agardh) J. Agardh, *Epymenia obtusa*, *Trematocarpus*

Plate 1: The intertidal rocky shore at Dalebrook.

Plate 2: The sublittoral study site at Oudekraal.

affinis (J. Agardh) De Toni, *Gigartina radula* and *Botryocarpa prolifera*. *Pachymenia carnosa* was not selected for this study because it is a large plant (up to 50cm) and would be impossible to incubate as a whole plant in the apparatus used in this study because of both its physical size and the fact that it would exceed the recommended thallus weight to bottle volume ratio. Incubation of plant fragments is not recommended (Hatcher, 1977 showed increased dark respiration rates for cut tissue strips of *Laminaria longicruris* Pyl.; Littler and Arnold, 1980 showed that physical damage to *Colpomenia sinuosa* (Roth) Derbès et Solier in Castagne reduced its photosynthetic performance by half and nearly doubled its respiration). Thus, cutting of tissue strips of *Pachymenia carnosa* to fit inside the incubation bottles was rejected. *Trematocarpus affinis* was not used because none was present in the transect, although it is present at Oudekraal in small amounts. Another reason for not using this plant was the propensity of the branches to break off the thallus while collecting, causing both physical damage (which results in the problems associated with cut tissue strips) and making it difficult to separate individual plants from broken-off branches. For these reasons, *Botryocarpa prolifera*, *Gigartina radula* and *Epymenia obtusa* were the species selected for this study. In retrospect it may have been worthwhile selecting *Trematocarpus affinis* as it would have provided interesting data on production rates of subtidal species of different morphologies - all the selected species being flat forms, *Trematocarpus affinis* being a proliferously branched form.

All incubations were conducted *in situ* at Oudekraal using SCUBA. Individual thalli were collected, placed in a dark plastic bag to eliminate increased respiration due to light-shock (Hatcher, 1977; Johnston *et al*, 1974) and brought to the surface. Thalli were gently cleaned of visible epiphytes and transferred to light and dark bottles (2000ml bottling jars - capacity large enough to eliminate the bottle-size effect documented by Buesa (1977) and Littler (1979)) containing deoxygenated seawater. Plants were not removed from seawater or exposed to full sunlight throughout this procedure. The seawater was deoxygenated by bubbling nitrogen gas through it for approximately 15 seconds to prevent oxygen supersaturation problems such as the oxygen inhibition of photosynthesis (the Warburg effect). Downton *et al* (1976) demonstrated that photosynthesis in a number of marine seaweeds was inhibited substantially (and sometimes completely) when the oxygen concentration of seawater was between 65 and 90% of oxygen saturation, so removal of excess oxygen from incubation seawater was considered necessary.

The recomendations of Hatcher (1977), Littler (1979) and Littler and Arnold (1980) as regards primary production methodology were adhered to during the course of this investigation. Plants were chosen from the same populations throughout the study, and only healthy, whole non-reproductive thalli were used (Hatcher, 1977). Where epiphytes were present, these were removed prior to incubation. The algal dry weight to bottle volume ratio never exceeded 1.5 grams per litre per incubation hour - a figure well within that used by Littler (1979) in his

determination of the effects of thallus weight on marine algal photosynthetic rates.

Dark bottles were painted black, covered in three layers of masking tape and then painted again to ensure that no light was admitted. Four light and four dark bottles were used per incubation, together with one light and one dark bottle control. The control bottles were incubated simultaneously to correct for oxygen respired or produced by other organisms in the sample seawater. All 10 bottles were placed in two rows of five in a polypropylene rack. Incubations ran for one hour during which the bottles were continuously stirred *in situ* by polypropylene coated magnetic stirrers attached inside the bottles. Three incubations were completed for one particular species per sample day. Stirring was achieved by means of pulleys containing strong magnets situated under each bottle, the pulleys being driven by belts from a 6V DC electric motor attached to a base frame (plate 3) upon which the bottle rack was placed. The base frame was itself clamped (via aluminium prongs) onto a 130kg concrete block which prevented the whole apparatus from moving should strong wave action or currents be present. The block was situated on a convenient rocky shelf under a kelp canopy of *Ecklonia maxima*. The bottle rack was removed for each incubation to change the plant material, the rest of the apparatus being left on the bottom until the end of the sample day, when it was removed. At the beginning of each incubation samples of deoxygenated water were fixed with Winkler reagents for subsequent analysis to determine the initial dissolved oxygen concentration. After each incubation the water samples were carefully siphoned (with

Plate 3: Light and dark bottle incubation apparatus used for *in situ* photosynthesis measurements on site at Oudekraal.

Plate 4: Fixation of water samples with Winkler reagents *in situ* at Oudekraal.

60% overflow - as used by Hatcher, 1977) into 280ml BOD bottles with ground glass stoppers and fixed with Winkler reagents (plate 4). The thalli were placed in labelled plastic bags and returned to the laboratory, where they were dried to constant weight at 60·C.

Oxygen concentration values were converted to milligrams carbon fixed per gram dry weight per hour using a photosynthetic quotient of 1.20 - the average value for carbohydrate-protein-lipid metabolism, used by Heine (1983). Irradiance at the study site was measured underwater by a sensor attached to the base frame (next to the motor), and on the surface by a hand-held sensor. Both sensors were connected via a switch-box to a Licor model LI-188 quantum meter. Both underwater and surface irradiance were measured at 10 minute intervals during each incubation. The bottom water temperature was recorded at each incubation using a diver held thermometer.

Fresh plants were collected every month, freeze dried and analyzed for percentage total carbon, percentage total nitrogen, percentage inorganic matter and calorific value as described in chapter 2.

Twice during the study period i.e. July 1984 (austral winter) and January 1985 (austral summer), samples of each species were collected and taken back to the laboratory for determination of photosynthetic light curves using the methods described in chapter 2.

RESULTS

Biomass Survey

The observed biomass of the various species identified at Oudekraal is shown in table V. It can be seen that the three species selected for this study are amongst the most abundant of the seaweed flora observed, with a combined biomass of 33.60g dry weight.m^{-2}. *Gigartina radula* and *Botryocarpa prolifera* are significant contributors with a biomass of 19.73g dw.m^{-2} and 10.00g dw.m^{-2} respectively. The contribution of *Epymenia obtusa* is rather less at 3.87g dw.m^{-2} but still higher than the majority of the species identified.

It is interesting to note that of the 29 species identified in the transect, eight of them (which include the three species investigated in this study) account for 90% of the understorey seaweed biomass measured. Another interesting finding from the Oudekraal biomass survey is the dominance of members of the Rhodophyta, with only one representative each of the Phaeophyta and Chlorophyta being observed, namely the fucoid *Axillariella constricta* (J.Agardh) Silva and the filamentous green alga *Cladophora mirabilis* (C.Agardh) Rabenhorst in Hohenacker. The data of Field *et al* (1980) shown in appendix II also shows dominance by members of the Rhodophyta, although the Chlorophyta are better represented than at Oudekraal (three species). The Phaeophyta are poorly represented in both studies (one species at Oudekraal (*Axillariella constricta*), three species in appendix II - two of which are kelps - *Ecklonia*

TABLE V: Biomass and C & N survey at Oudekraal (Feb 1985)

SPECIES	G DRY WT PER M^2	%C	%N	C:N RATIO
Pachymenia carnosa	46.76	34.95	3.05	11.46:1
Aeodes orbitosa	21.20	31.50	3.25	9.69:1
Gigartina radula	19.73	29.95	2.70	11.09:1
Botryocarpa prolifera	10.00	33.10	4.10	8.07:1
Gigartina stiriata	9.59	31.45	2.70	11.65:1
Axillariella constricta	6.38	37.80	1.60	23.63:1
Gelidium versicolor	5.52	41.85	4.25	9.85:1
Epymenia obtusa	3.87	27.90	3.75	7.44:1
Heringia mirabilis	3.50	34.80	3.80	9.16:1
Polyopes constrictus	2.51	39.80	5.30	7.51:1
Epymenia capensis	1.89	29.45	4.05	7.27:1
Iridaea capensis	1.78	31.90	3.70	8.62:1
Champia lumbricalis	1.63	26.45	3.45	7.67:1
Gigartina bracteata	1.36	25.20	2.00	12.60:1
Neuroglossum binderianum	0.70	32.80	4.10	8.00:1
Hymenena venosa	0.21	30.85	3.80	8.12:1
Rhodymenia sp	0.17	30.85	4.05	7.62:1
Kallymeniaceae	0.16	27.75	3.30	8.41:1
Schizymenia obovata	0.12	25.50	2.85	8.95:1
Botryoglossum platycarpum	0.06	29.60	5.20	5.69:1
Plocamium rigidum	0.06	30.55	4.70	6.50:1
Gigartina scutellata	0.05	30.45	2.15	14.16:1
Pterosiphonia cloiophylla	0.05	29.65	3.45	8.59:1
Cladophora mirabilis	0.02	34.95	4.10	8.52:1
Aristothamnion collabens	0.01	17.40	2.90	6.00:1
Porphyra capensis	<0.01	37.35	4.80	7.78:1
Champia compressa	<0.01	25.45	3.45	7.38:1
Hypnea spicifera	<0.01	29.35	3.50	8.39:1
Acrosorium unicinatum	<0.01	25.05	4.10	6.11:1

Authorities for the above species may be found in:
Seagrief, S. C.: *A catalogue of South African green, brown and red marine algae.* Memoirs of the Botanical Survey of South Africa, No. 47 (1984)

maxima, *Laminaria pallida* and *Desmarestia firma* Skottsberg in Nordenskjöld).

Sublittoral light measurements

The irradiance of incident light at the surface (in air) and at 5m depth observed during the incubation of each species each month is displayed in fig 7a-c. Irradiance was highest in late spring (November) and early to mid-summer (December, January) with levels of 2488-3847$\mu\epsilon.m^{-2}.sec^{-1}$ (at surface) and 295-544$\mu\epsilon.m^{-2}.sec^{-1}$ (at 5m). Lowest light levels were recorded in autumn (April - May) and mid-winter (June) with observed levels of 405-623$\mu\epsilon.m^{-2}.sec^{-1}$ (at surface) and 35-103$\mu\epsilon.m^{-2}.sec^{-1}$ (at 5m). The seasonal pattern of surface irradiance shown in fig. 7 was emulated by underwater (5m) light levels - surface and bottom light levels being positively correlated (r^2=0.72).

Sublittoral temperature measurements

Bottom water temperature (fig. 8) was at a minimum during late spring to mid-summer (13·C) and at a maximum during autumn and early winter (16·C). This is a typical Western Cape seasonal pattern (Fricke and Thum ,1975; Dieckmann, 1980; Anderson and Bolton, 1985).

Photosynthesis

Net production of all three species was greatest in spring (October), with observed values of 2.39mg C.g $dw^{-1}.hr^{-1}$ for *Botryocarpa prolifera*, 1.14mg C.g $dw^{-1}.hr^{-1}$ for *Epymenia obtusa* and 1.82mg C.g $dw^{-1}.hr^{-1}$ for *Gigartina radula* (figs 9-11). Similarly, net production of all three species was lowest in winter (June), with observed values of 0.15mg C.g $dw^{-1}.hr^{-1}$ for *Botryocarpa prolifera*, 0.03mg C.g $dw^{-1}.hr^{-1}$

Fig. 7a: Seasonal irradiance at the surface and at 5m depth observed at Oudekraal during *Botryocarpa prolifera* incubations.

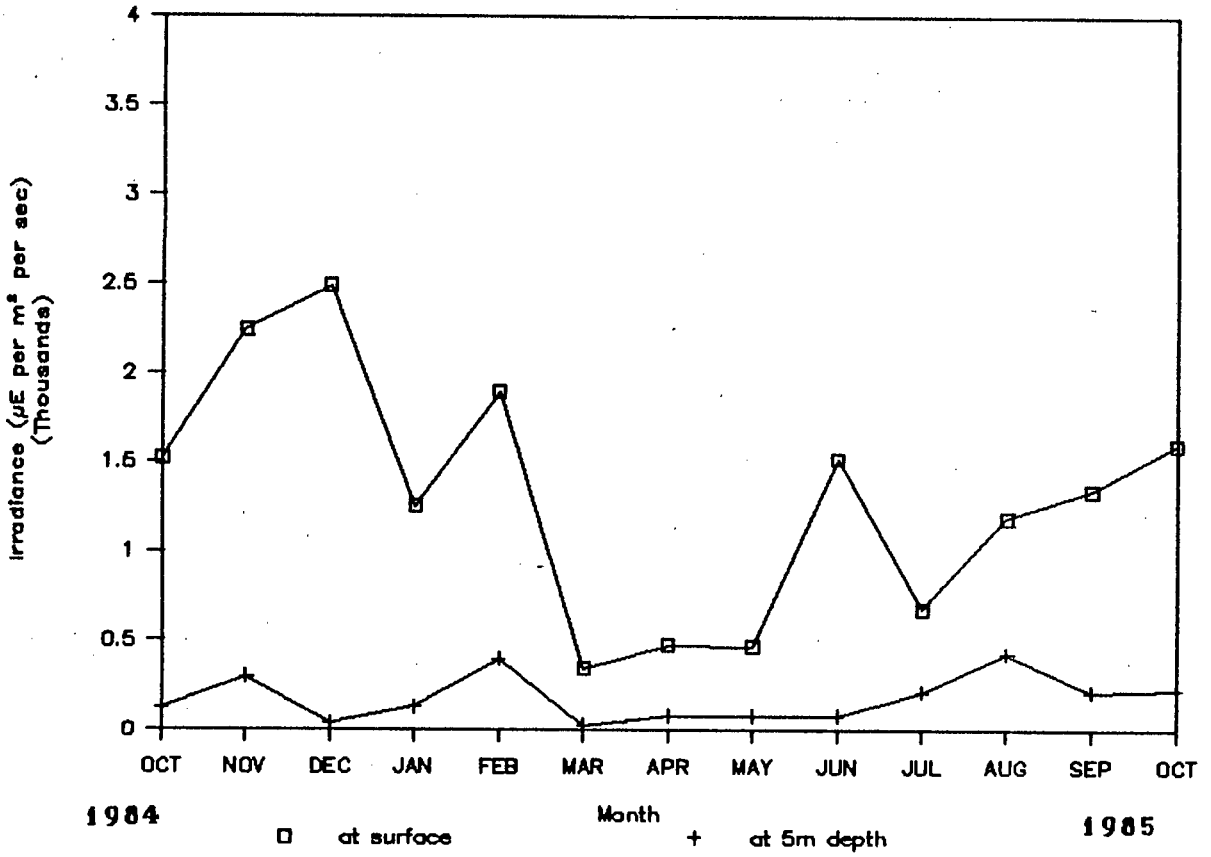


Fig. 7b: Seasonal irradiance at the surface and at 5m depth observed at Oudekraal during *Epymenia obtusa* incubations.

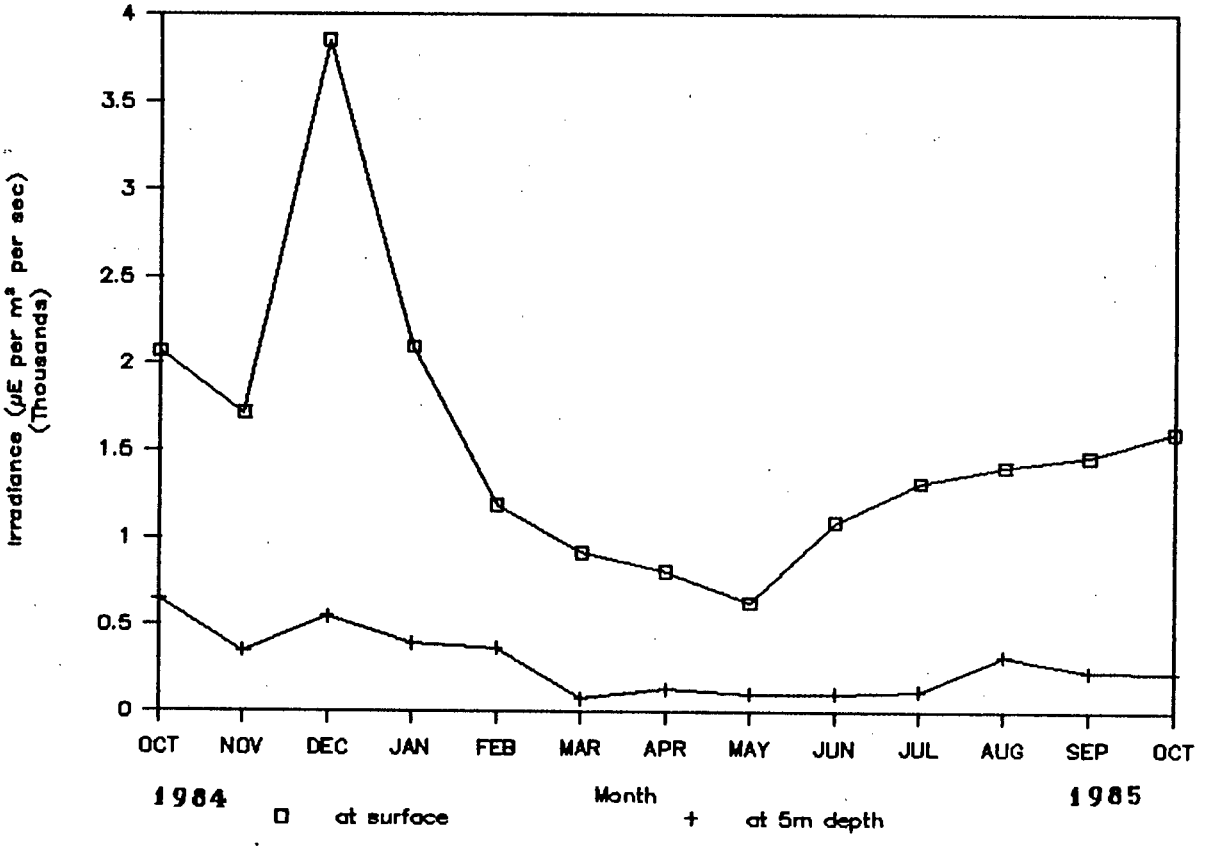


Fig. 7c: Seasonal irradiance at the surface and at 5m depth observed at Oudekraal during *Gigartina radula* incubations.

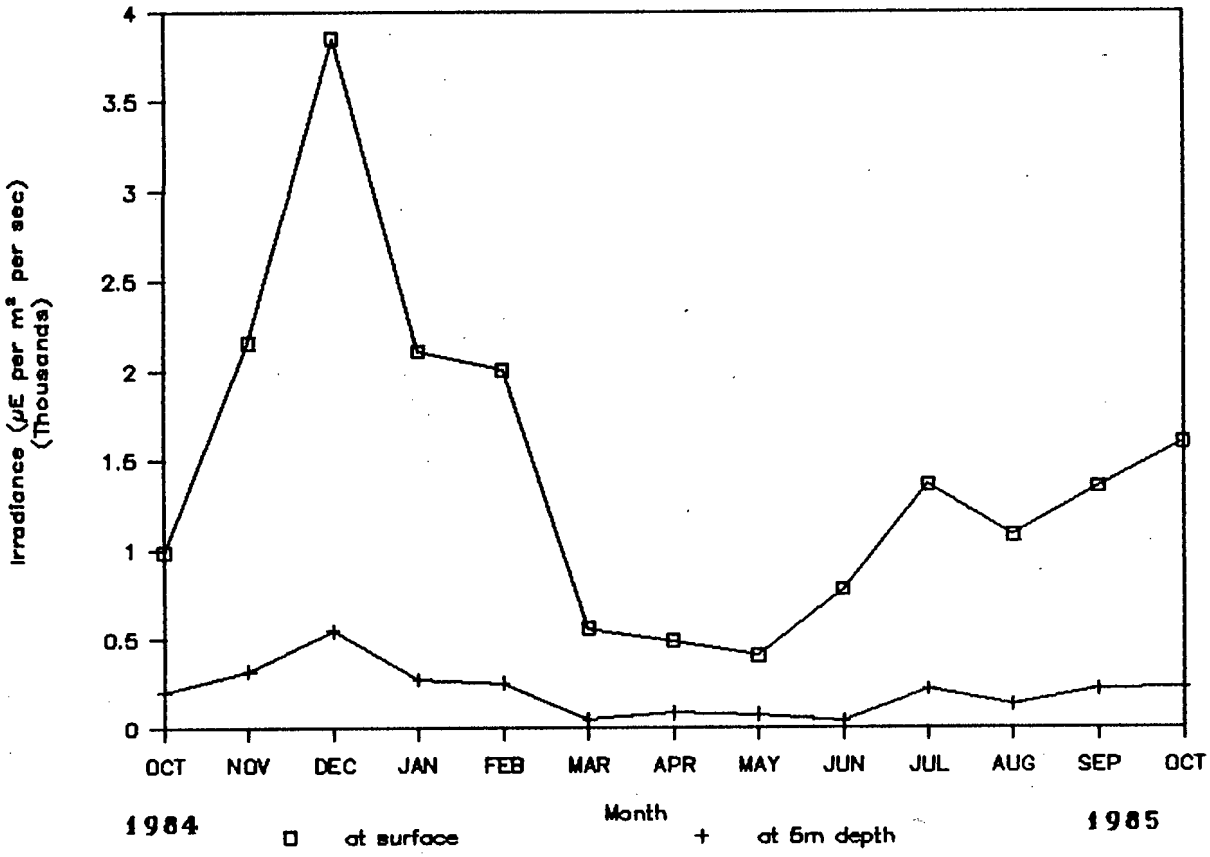
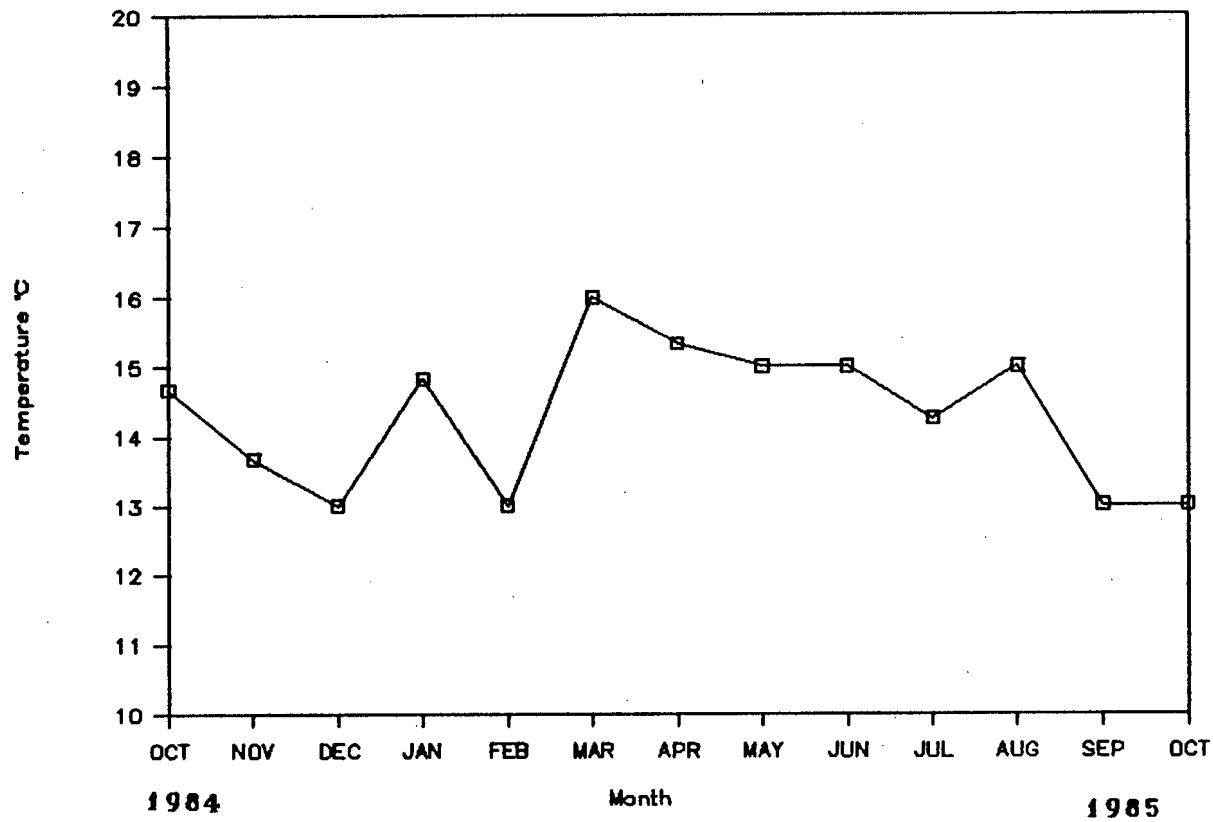


Fig. 8: Average bottom water temperature measured at Oudekraal during *in situ* photosynthesis incubations.

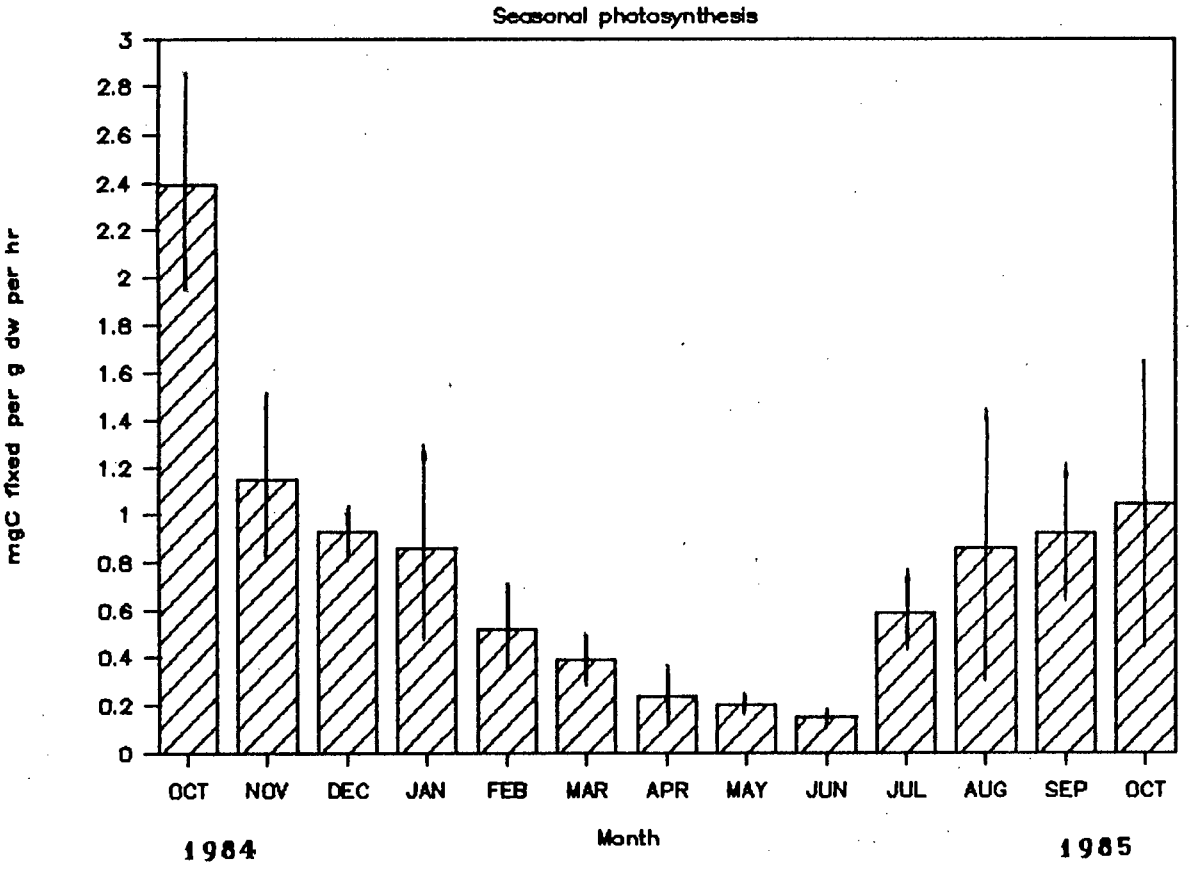


for *Epymenia obtusa* and 0.24mg C.g $dw^{-1}.hr^{-1}$ for *Gigartina radula*.

Respiration also followed a seasonal pattern with greatest values in spring or early summer (October or November). Observed maximum respiration rates were 0.86mg C.g $dw^{-1}.hr^{-1}$ for *Botryocarpa prolifera* (October), 0.50mg C.g $dw^{-1}.hr^{-1}$ for *Epymenia obtusa* (November) and 0.34mg C.g $dw^{-1}.hr^{-1}$ for *Gigartina radula* (November) (figs 9-11). Lowest respiration rates were observed in late autumn (May) and mid-winter (June and July). Observed minimum respiration rates were 0.01mg C.g $dw^{-1}.hr^{-1}$ for *Botryocarpa prolifera* (June), 0.01mg C.g $dw^{-1}.hr^{-1}$ for *Epymenia obtusa* (July) and 0.06mg C.g $dw^{-1}.hr^{-1}$ for *Gigartina radula* (May).

Summer and winter light curves (appendix IV) show that *Botryocarpa prolifera* and *Epymenia obtusa* have greater P_{max} values in summer than in winter (table VI), *Gigartina radula* having a slightly higher P_{max} value in winter. In actual figures, P_{max} values for *Gigartina radula* are substantially higher in both winter and summer than either *Botryocarpa prolifera* or *Epymenia obtusa* (3.26 and 2.58mg C.g $dw^{-1}.hr^{-1}$ as opposed to 0.49 and 1.61 (*Botryocarpa prolifera*) and 0.83 and 0.97mg C.g $dw^{-1}.hr^{-1}$ (*Epymenia obtusa*). All three species have greater I_K values in summer than in winter. The I_K values of *Gigartina radula* in both winter and summer are significantly higher than the I_K values of the other two species, *Gigartina radula* having summer and winter I_K values of 307 and 216$\mu E.m^{-2}.sec^{-1}$ respectively, compared with values of 63 and 28$\mu E.m^{-2}.sec^{-1}$ for *Botryocarpa prolifera* and 49 and 42$\mu E.m^{-2}.sec^{-1}$ for *Epymenia obtusa*.

Fig. 9: Seasonal patterns of sublittoral photosynthesis and respiration in *Botryocarpa prolifera*. 95% confidence limits indicated.



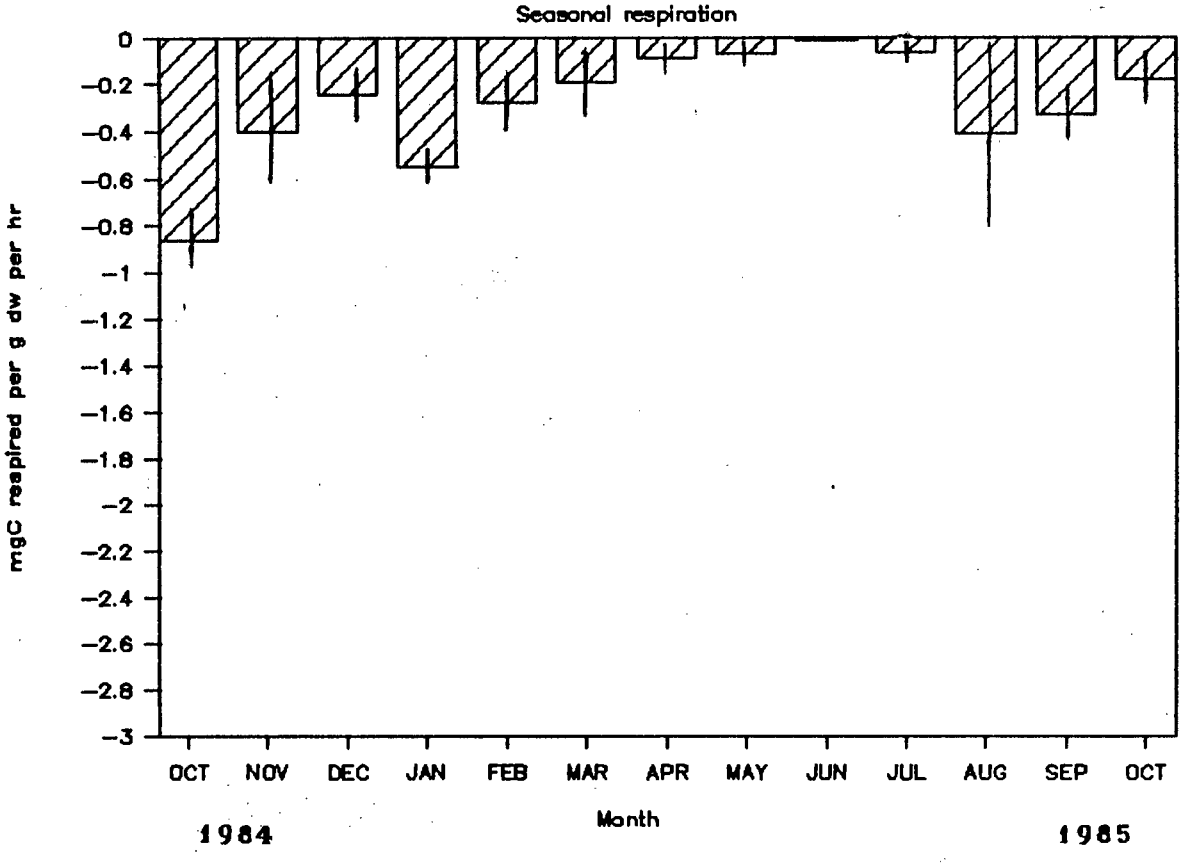
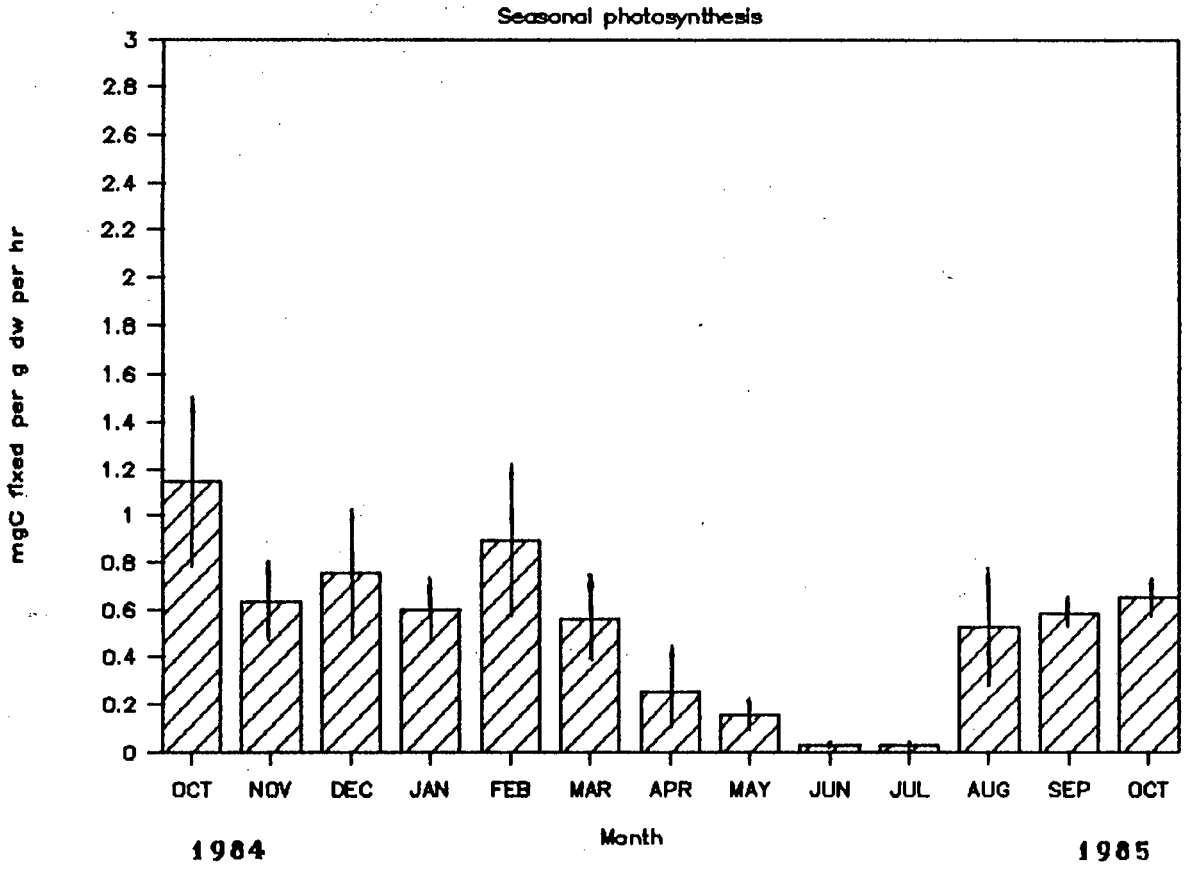


Fig. 10: Seasonal patterns of sublittoral photosynthesis and respiration in *Epymenia obtusa*. 95% confidence limits indicated.



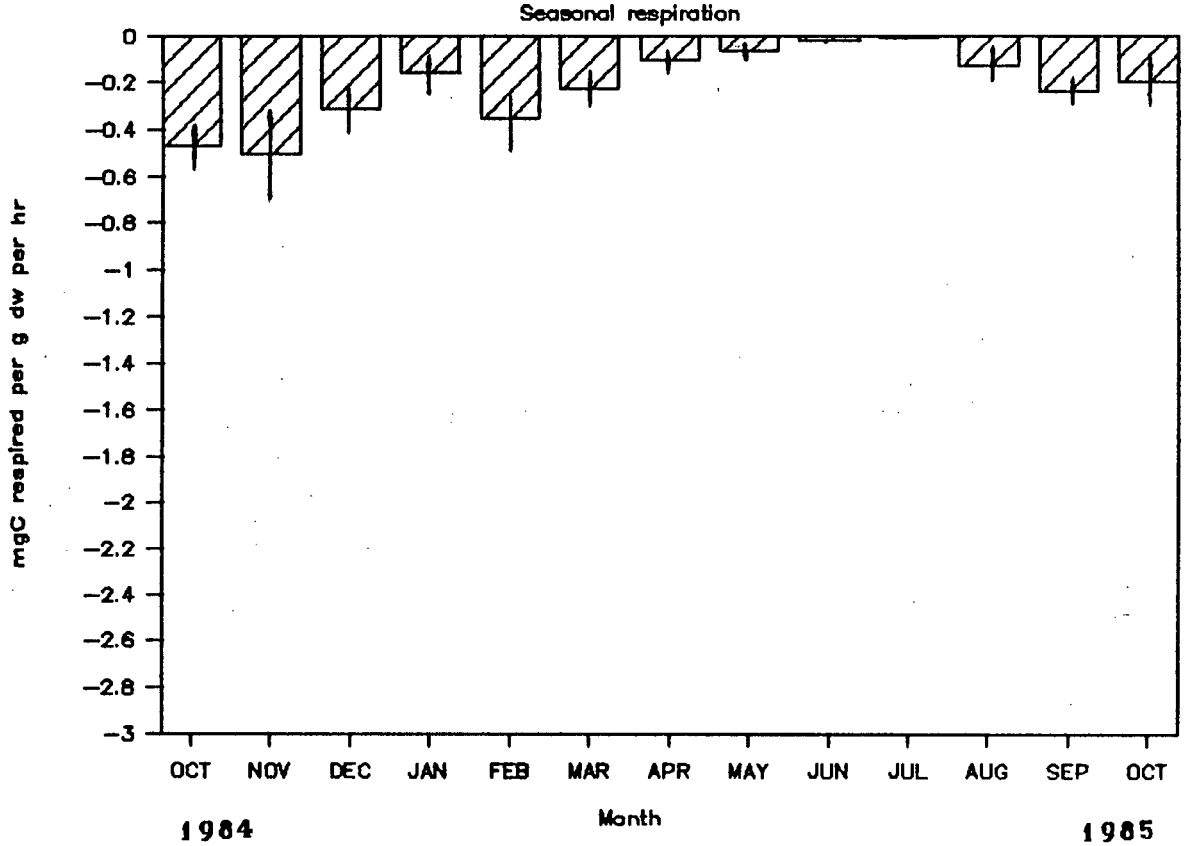
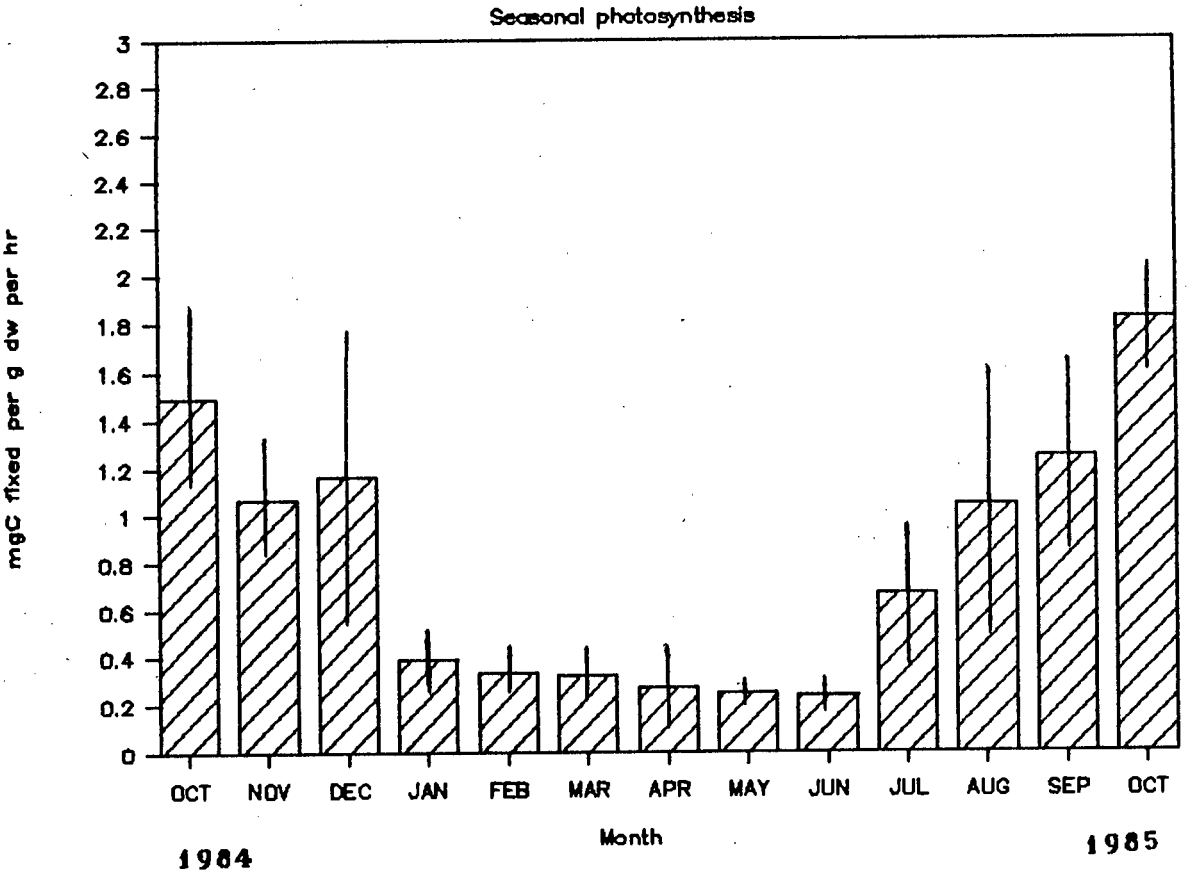
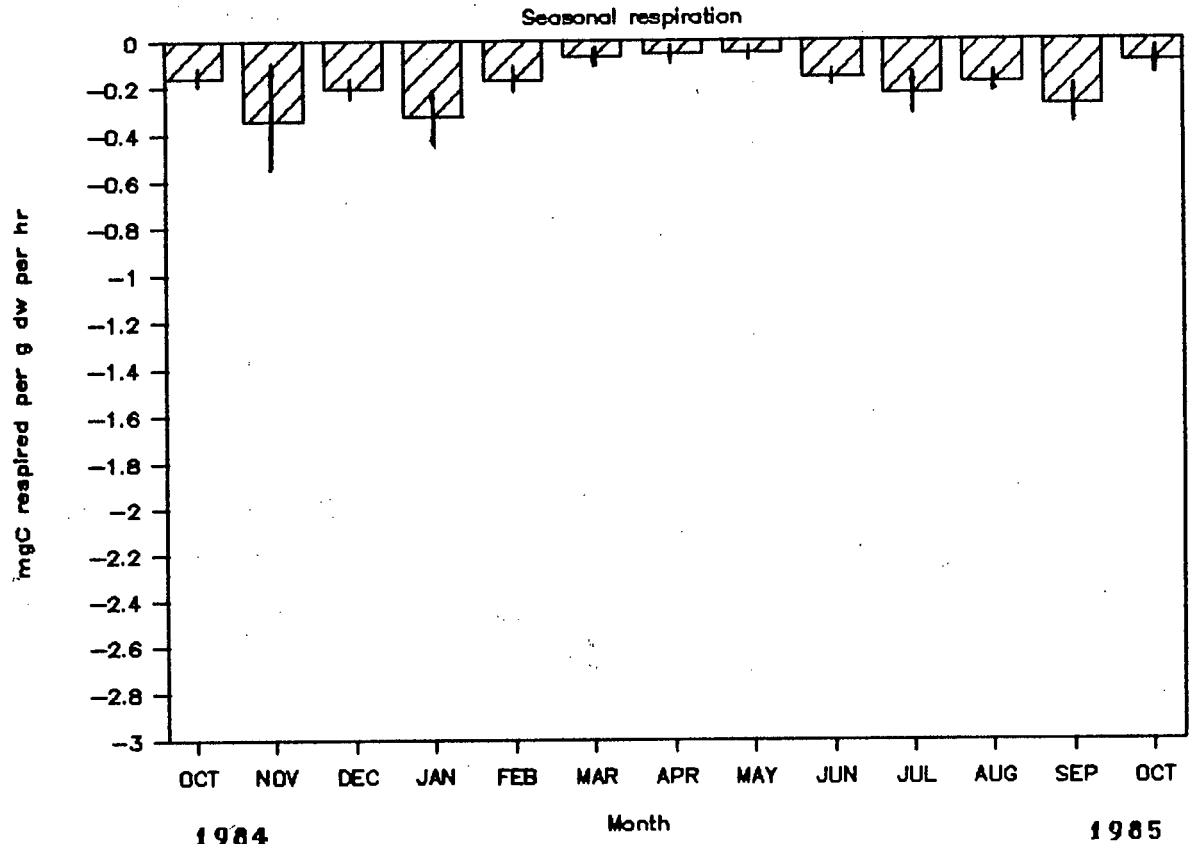


Fig. 11: Seasonal patterns of sublittoral photosynthesis and respiration in *Gigartina radula*. 95% confidence limits indicated.





Percentage Carbon, Percentage Nitrogen and C:N Ratios

Fig. 12a-c shows the percentage carbon, percentage nitrogen and C:N ratios of all three species of understorey seaweed during the study period. One way analysis of variance analyses using the monthly data to compare means between seasons showed that at the 5% level only the C:N ratio of *Botryocarpa prolifera* showed any significant seasonal variation ($F = 5.34 > F_{.05, 3, 9} = 3.86$). The percentage carbon values ranged from 26-32% for *Epymenia obtusa*, from 24-35% for *Botryocarpa prolifera* and from 26-30% for *Gigartina radula*. Values for percentage nitrogen range from 3.15-4.15% for *Epymenia obtusa*, from 3.15-4.10% for *Botryocarpa prolifera* and from 2.30-3.15% for *Gigartina radula*. C:N ratios were generally low, with a minimum of 7.00:1 for *Epymenia obtusa* and a maximum of 12.04:1 for *Gigartina radula* being observed. The higher C:N ratios in *Gigartina radula* were due to percentage nitrogen values being lower than in the other two species, while percentage carbon values amongst all three species remained comparable with each other. The seasonal C:N ratio of *Botryocarpa prolifera* varies signficantly, with the highest ratios being observed in autumn and early winter, and the lowest ratios being observed in spring and summer. Those species collected during the transect survey at Oudekraal had percentage carbon levels of 17-42% and percentage nitrogen levels of 2-5% (table V). The resulting C:N ratios ranged from 6.11:1 to 23.63:1. However, the high end of this range is due to one species, the fucoid *Axillariella constricta* with percentage carbon and nitrogen levels of 37.80% and 1.60% respectively. The moderately high carbon percentage and the very low

Fig. 12a: Seasonal variation in percentage carbon of three sublittoral seaweeds at Oudekraal.

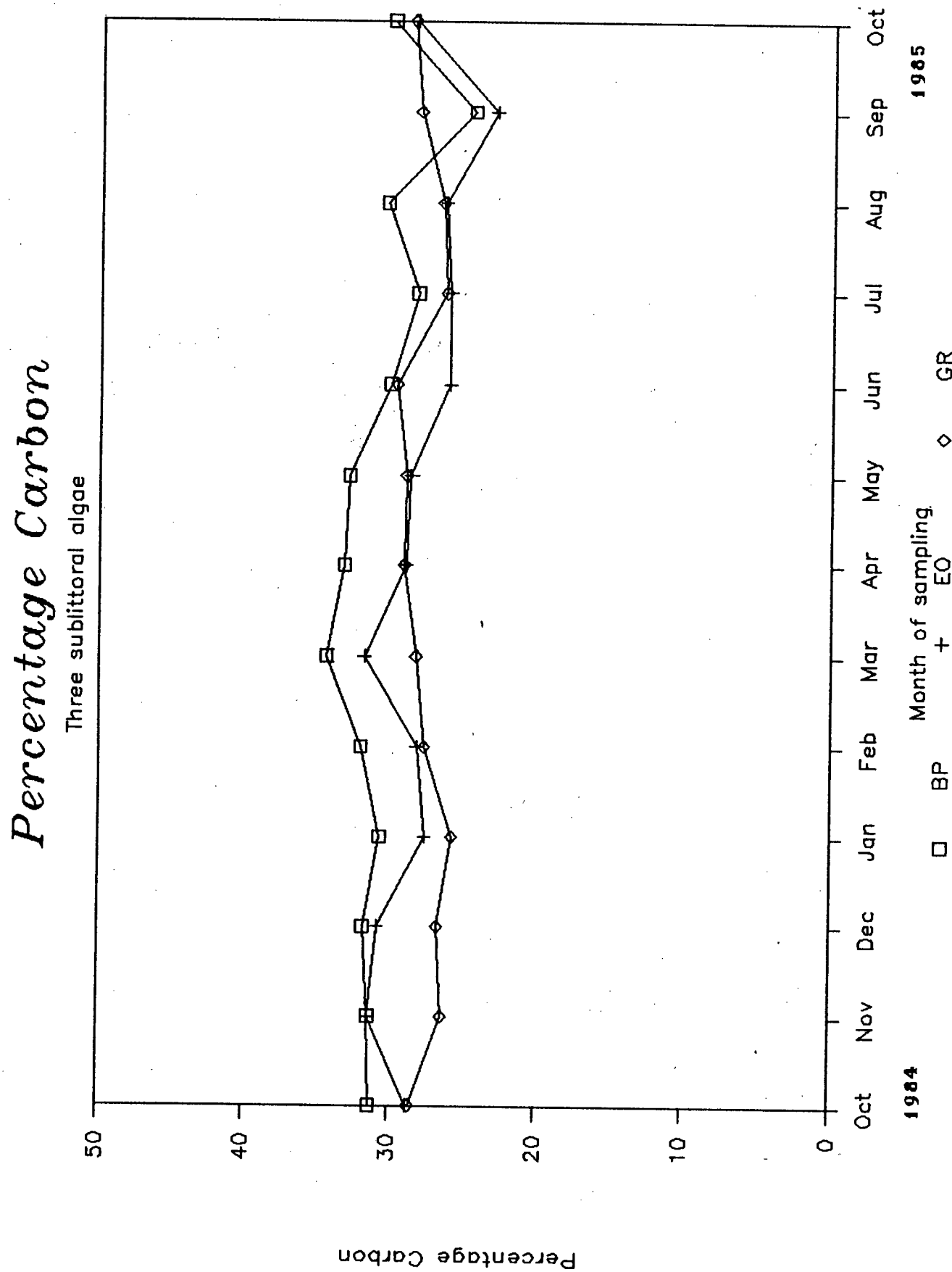


Fig. 12b: Seasonal variation in percentage nitrogen of three sublittoral seaweeds at Oudekraal.

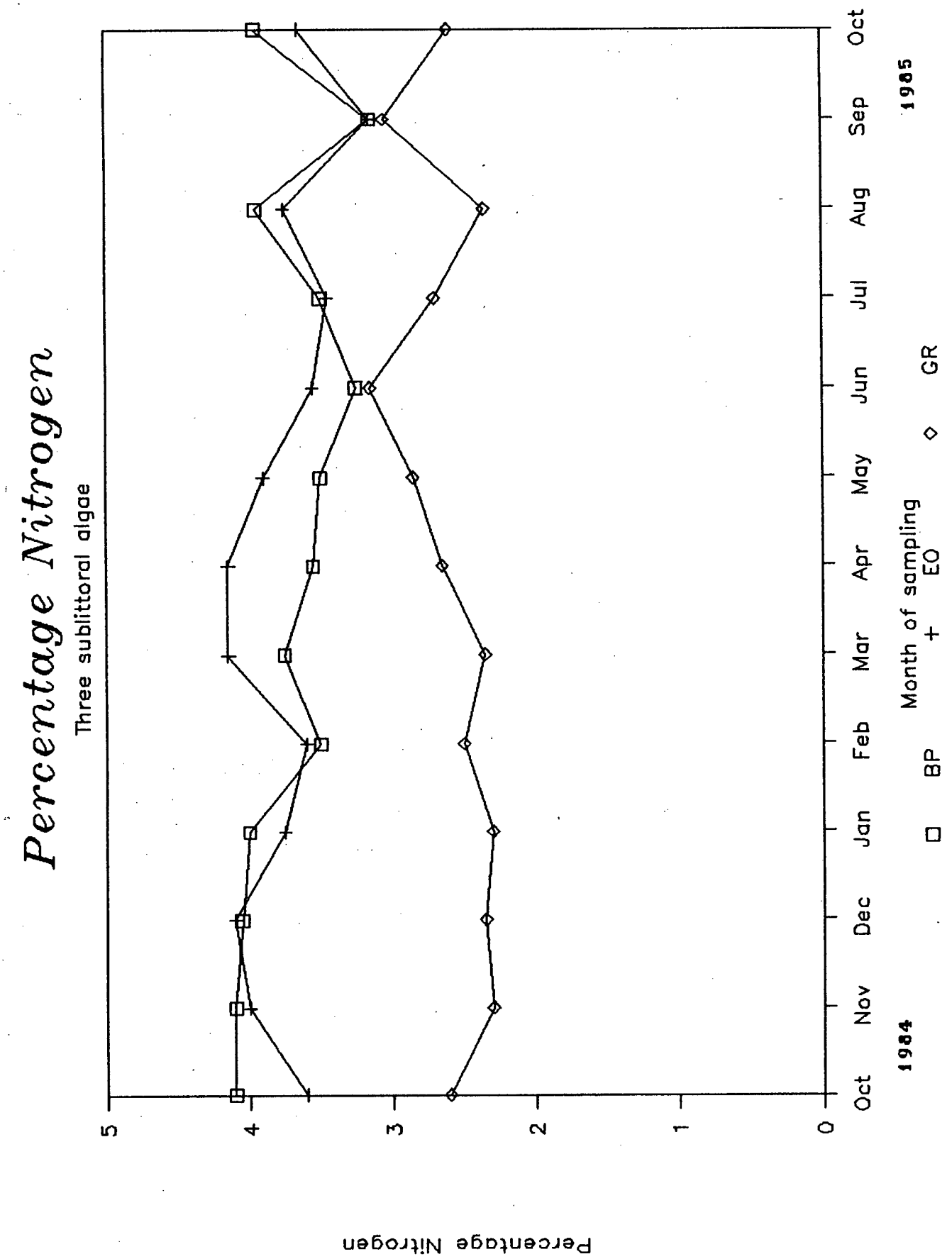
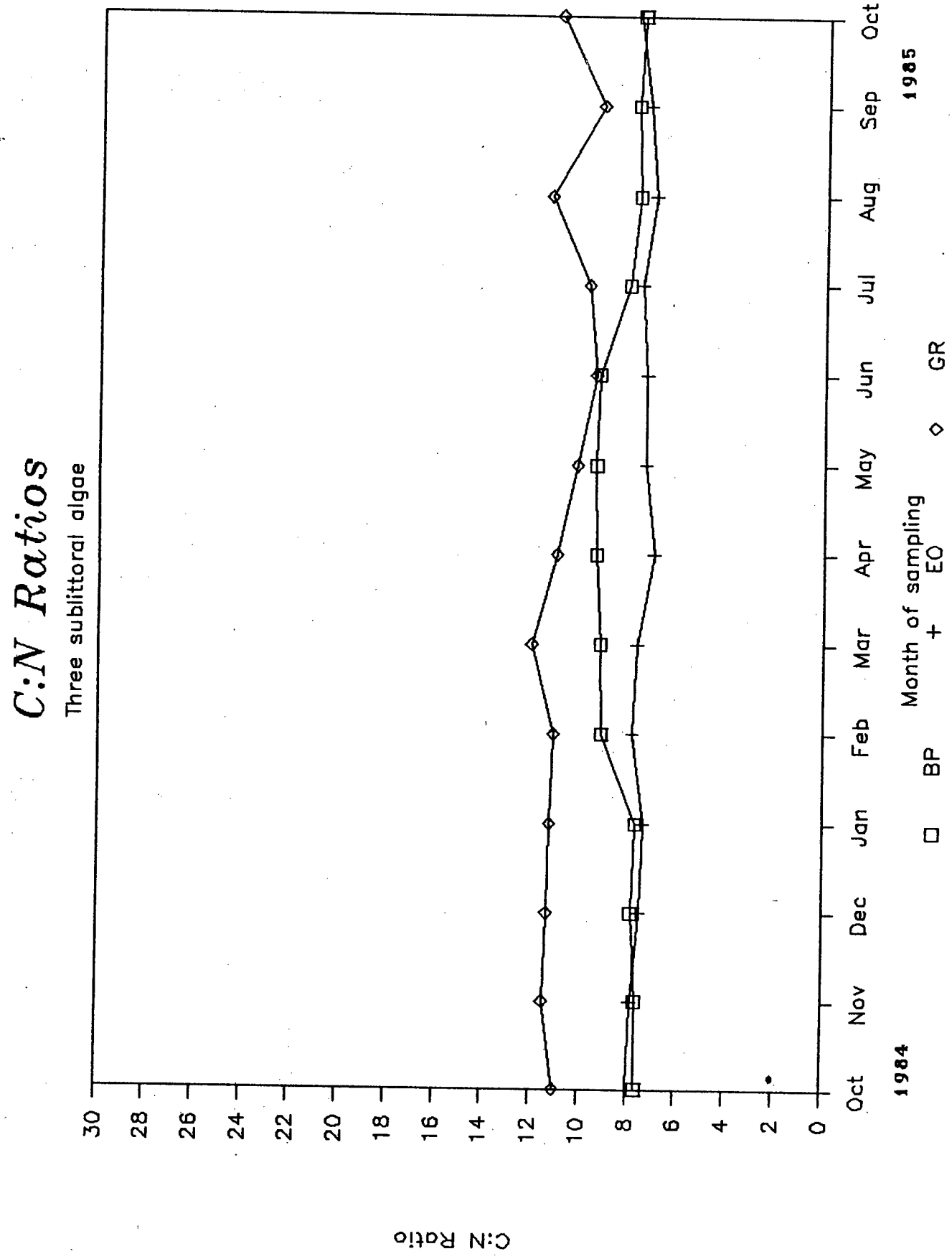


Fig. 12c: Seasonal variation in C:N ratios of three sublittoral seaweeds at Oudekraal.



nitrogen percentage result in the high C:N ratio of 23.63 for this species.

Energy Content and Inorganic Matter

The data in table VII shows the total inorganic matter expressed as a percentage of total matter, as well as the calorific value (in kiloJoules per gram dry weight) of the three sublittoral species investigated. This data represents the average of these values throughout the study because the analyses were performed on the combined equal samples of each separate species remaining freeze-dried material following bomb calorimetry. The percentage inorganic matter content of all three species are comparable (ranging from 24.51% to 27.71%) as are the calorific values (ranging from 11.08 to 12.53 $kJ.g^{-1}$ dw).

TABLE VI: Seasonal Pmax & Ik values for three understorey algae.

	Jul 84		Jan 85	
	Pmax	Ik	Pmax	Ik
Botryocarpa	0.49	28	1.61	63
Epymenia	0.83	42	0.97	49
Gigartina	3.26	216	2.58	307

TABLE VII: Percentage Inorganic Matter and Energy content of three understorey red algae.

	Inorganic matter (%)	kJ. g^{-1} dry weight
Gigartina radula	27.55	11.08
Epymenia obtusa	24.51	11.64
Botryocarpa prolifera	27.71	12.53

DISCUSSION

The biomass data of Field *et al* (1980), in their examination of five separate sites around the Cape Peninsula and vicinity (appendix II), showed an average biomass of 8.24g dw.m^{-2} for *Botryocarpa prolifera*, 15.38g dw.m^{-2} for *Epymenia obtusa* and 10.32g dw.m^{-2} for *Gigartina radula*. These figures are comparable with the results of the transect undertaken as part of this study at Oudekraal .

Inspection of the light data obtained in this study, together with the seasonal light data of Dieckmann (1980), shows that total irradiance varies seasonally (summer being higher than winter - appendix VI), but also that single daily irradiance measurements on the seabed fluctuate markedly on a daily basis (although still showing an overall seasonal trend of higher summer irradiances, fig.7). The rate of photosynthetic production is seasonal and appears related to the total irradiance - the highest production rates of the three species being in October and matching exactly the highest rates of frond elongation observed by Dieckmann (1980) in the subtidal kelp *Laminaria pallida*. The period of minimum photosynthesis by the understorey seaweeds also coincides with period of minimum frond elongation in *Laminaria pallida* (June). The fact that maximum rates of photosynthesis follow a seasonal pattern identical to the frond elongation rates observed by Dieckmann (1980) in *Laminaria pallida* at Oudekraal, together with the fact that seasonal variation in mean monthly global radiation (appendix VI) lags behind the photosynthesis peak and also that direct daily irradiance (e.g. December 1984 and February

1985 light (fig. 7a) and photosynthesis (fig. 9-11) data) does not directly affect production rates, strongly suggests that an innate mechanism controlling seasonal patterns of photosynthetic rate exists. This innate mechanism was suspected by Dieckmann (1980) and this data supports his view. This innate mechanism seems to be principally regulated by light - the onset of highest rates of photosynthesis of understorey algae (this study) coinciding with, and kelp frond elongation (Dieckmann, 1980) lagging slightly behind, increasing day-length and irradiance. The influence of either total irradiance received and/or photoperiod as factors controlling this innate mechanism of seasonal primary production may therefore be significant and may possibly be the factors most affecting seasonality. Photoperiod especially may be important since its effects are not greatly influenced by ambient atmospheric and oceanographic factors which are responsible for significant attenuation of subtidal irradiance (e. g. cloudy weather and turbulent waters). The fact that photosynthetic rates of understorey algae (this study) and kelp frond elongation rates (Dieckmann, 1980) begin to decline while mean monthly global radiation is on the increase detracts from the light regulation (but not the innate mechanism) hypothesis. Light availability and factors affecting light attenuation in the water column have been shown to be important in determining the net daily carbon fixation of macroalgae on the North Carolina continental shelf (Smith, 1981), and their importance cannot be discounted in this study. Seasonal variation in nutrient availability may be at least partially responsible for the observed seasonality in production,

Smith (1983) demonstrated that P_{max} is related to the availability of cellular phosphorus (in a freshwater phytoplankton, this is not neccesarily so in a sublittoral seaweed, where phosphorus is unlikely to be limiting). It is well-known that the nutrient status of the sea along the west coast of South Africa changes on a seasonal basis as a result of the seasonal patterns of upwelling caused by summer south east winds. The upwelled water is characterized by high nutrient levels (Andrews, 1974) of the order of 20µg-at. l^{-1} $N\text{-}NO_3$ and 1-1.5µg-at. l^{-1} $P\text{-}PO_4$. These high nutrient levels, combined with continuous water movement and high surface irradiance, provide very favourable conditions for the growth of those plants that can withstand the wave action (Field *et al*, 1980). Occasional warmer water temperatures during the upwelling season are the result of occasional downwelling which is accompanied by a drop in nutrient levels. While Dieckmann (1980) suggested that the sporadic occurence of low nitrate concentrations (due to summer downwelling) and simultaneous competition for nutrients with phytoplankton may be responsible for the observed decline in growth rates of fronds of *Laminaria pallida* while seasonal irradiance appears optimal, this is unlikely to be a factor affecting the photosynthetic rates of the understorey species in this study since photosynthetic rates are still generally declining during obvious days of upwelling (e.g. *Epymenia obtusa* - figs. 7b and 10), and also because nutrients are unlikely to be limiting in the kelp beds during periods of upwelling as the phytoplankton blooms are blown offshore by the south east winds leaving the kelps in newly upwelled nutrient-rich

water. In other words, nutrients are unlikely to be limiting for photosynthesis during the summer (upwelling) months, while the extremely heavy wave action and consequent rapid turnover rate of seawater in the kelp beds during the more nutrient poor winter months are also probably keeping sufficient nutrients available for winter photosynthesis. Seasonal nutrient availability is probably only partially responsible for the seasonal changes in primary production observed in this study because upwelling and its resultant nutrient enhancement of the west coast region continue throughout the summer - well after the rates of production observed in this study have begun to decline.

In view of the high summer nutrient levels and the possible innate photosynthesis mechanism, it is not possible to say whether nutrients are ever a limiting factor affecting photosynthesis in sublittoral Cape Peninsula algae, but the available evidence seems to indicate that this is unlikely. The data of Dieckmann (1980) while generally showing high nutrient values in summer (18µg-at. l^{-1} $N\text{-}NO_3$, 1µg-at. l^{-1} $P\text{-}PO_4$), was erratically sampled and therefore inconclusive. Although winter nutrient levels are much lower than summer nutrient levels, they are not so low as to be limiting in respect of photosynthetic rates (e.g. winter 4.2µg-at. l^{-1} $N\text{-}NO_3$, 0.9µg-at. l^{-1} $P\text{-}PO_4$ - from Dieckmann, 1980). Also, although upwelling is a common phenomenon along the Cape west coast, it is by no means a regular phenomenon and therefore probably plays a less significant role in seasonal sublittoral seaweed production patterns than was previously thought.

Heine (1983) in his study of two Californian understorey red algae (*Botryocladia pseudodichotoma* (Farlow) Kylin and *Rhodymenia californica* Kylin) observed that primary production was higher in spring and lower in summer. King and Schramm (1976) in a study of 22 benthic seaweeds in the Baltic observed that most had spring or summer net photosynthesis peaks. The net photosynthesis of *Laminaria longicruris* observed by Hatcher *et al* (1977) was highest in mid-summer and lowest in winter and paralleled seasonal changes in light. Heine (1983) points out the problems involved in statistically correlating the light and productivity measurements of *in situ* experiments. The results from this study are similar to those of Heine (1983) in that primary production shows a spring maximum, but are closer to those of Hatcher *et al* (1977) in the period of minimum production being in winter. King and Schramm (1976) found that the highest rates of light saturated photosynthesis (in spring and summer) corresponded with the seasonal growth patterns, and this may well be the case in respect of *Botryocarpa prolifera* and *Epymenia obtusa* in this study, as they appear to grow rapidly in size from the end of winter through to the end of summer. This observation is supported by the data of McQuaid (1985), in a study of Cape Peninsula intertidal species (including *Gigartina radula*), who observed a cyclical pattern of low biomass in winter, and peaks in late summer-autumn for abundant species such as *Gigartina radula*, *Porphyra capensis* and *Gelidium pristoides*. These results (and those of Heine (1983), Hatcher *et al* (1977) and King and Schramm (1976)) contrast with those of Hata and Yokohama (1976) who (working with seaweeds from the

colder regions of Japan) recorded highest rates of photosynthesis in four out of seven species during winter, irrespective of experimental temperatures. Furthermore, Littler and Arnold (1980) demonstrated opposite seasonal patterns of photosynthesis for two species (*Corallina officinalis* L. and *Egregia menziesii* (Turn.) Aresch.) from the same site and at the same time. The actual rates of photosynthesis observed in this study are on a par with those observed by Heine (1983), who observed maximum seasonal values of 1.25mg C fixed.g $dw^{-1}.hr^{-1}$ for *Botryocladia pseudodichotoma* and 4.6mg C fixed.g $dw^{-1}.hr^{-1}$ for *Rhodymenia californica*. Maximum values observed in this present study range from 1.14mg C fixed.g $dw^{-1}.hr^{-1}$ for *Epymenia obtusa* to 2.39mg C fixed.g $dw^{-1}.hr^{-1}$ for *Botryocarpa prolifera*. These figures also compare well with those observed by Wassman and Ramus (1973), who observed maximum rates of primary production of 2.6-3.9mg C fixed.g $dw^{-1}.hr^{-1}$ for *Codium fragile* (Suhr) Harvey in Long Island Sound, USA.

The seasonality in respiration of a spring maximum and an autumn/winter minimum displayed by these three species is of interest, and may well be related to the seasonal temperature changes noted by Dieckmann (1980) and Anderson and Bolton (1985), where summer months are characterized by lower mean daily and monthly sea temperatures than winter months - although the latter did note that rapid short-term temperature fluctuations are common. The effects of temperature on respiration rates are documented in Dring (1982), while Lüning (1971) showed that a marked increase in respiration rates of blades of *Laminaria hyperborea* (Gunn.)

Fosl. adapted to winter temperatures occurred as a result of a rise in temperature of only 4·C. The difference between the maximum and minimum temperatures observed during this study at Oudekraal was 3·C, and may consequently be responsible for the apparently seasonal variation in respiration although this is unlikely since seasonal temperature changes normally result in seasonal adaptation to such changes by the plants so affected. However, seasonal temperature changes in Helgoland where the study of Lüning (1971) was carried out are regular, while in the west coast upwelling regime they are not (Anderson and Bolton, 1985). Respiration is directly related to both ambient temperature and photosynthetic rate - the more a plant photosynthesizes, the more it respires due to an increase in the metabolic processes related to the photosynthetic process. Simultaneous changes in temperature will also affect the respiration rate, this primarily chemical enzyme catalysed process normally having a Q_{10} of approximately 2.0 when substrates are not limiting (Dring, 1982). However, it is possible that the Q_{10} value can vary seasonally, the plant showing a measure of adaptation to seasonal temperature changes, and being more susceptible to temperature changes during periods when the ambient water temperature is low (i.e. summer in the western Cape). Thus, if the plant is seasonally adapted to low temperatures in the summer, variability in respiration rates are to be expected when sudden temperature increases occur - such as during the sudden periods of downwelling which commonly occur along the Cape west coast during the summer and are responsible for the rapid short-term temperature fluctuations noted by

Anderson and Bolton (1985). Because the rapid rise of respiration in the spring is related to the increase in photosynthetic rate, it is also probably reflected in growth rate of the three species studied - Dieckmann (1980) recorded a spring/summer maximum and winter minimum growth rate in *Laminaria pallida*, as did Lüning (1971) in *Laminaria hyperborea*.

The fact that all three species observed show the same pattern of seasonal primary production is interesting since individual seaweed species and populations are potentially regulated by different biotic and abiotic factors. This seems to indicate that the populations of these species are regulated by the same or similar biotic and abiotic factors - especially so in the case of *Botryocarpa prolifera* and *Epymenia obtusa* which are found at similar depths in similar light and temperature regimes. On the other hand, while *Gigartina radula* shows similar seasonal patterns of primary production to those of *Botryocarpa prolifera* and *Epymenia obtusa*, the majority of the population at Oudekraal is found at depths of less than 5m and abiotic factors such as irradiance may be more important than for the other two species. This is borne out by the fact that the seasonal I_K values of *Gigartina radula* are five times greater than the I_K values of both *Botryocarpa prolifera* and *Epymenia obtusa*. The use of I_K as a parameter indicative of a plant's adaptation to the environment is an accepted form of investigation of plant photosynthetic light responses and has been used by Wethey and Porter (1976) and discussed by Chalker (1981). It is anticipated that photo-adaptive differences should be observed between plants growing in

high irradiances (shallow water) and those growing in low irradiances (deep water) i.e. a decrease in I_K values in shade-adapted (deep water) plants would be expected compared to sun-adapted (shallow water/intertidal) plants. Bearing this in mind, the large I_K values determined for *Gigartina radula* would seem to indicate that this is a sun-adapted species, while *Botryocarpa prolifera* and *Epymenia obtusa* would seem to be shade-adapted. Comparable I_K values have been observed by Smith (1981) for *Lobophora variegata* and *Codium carolinianum* (60$\mu\epsilon . m^{-2} . sec^{-1}$ and 83$\mu\epsilon . m^{-2} . sec^{-1}$ - subtidal algae). This further supports the idea that *Gigartina radula* is a sun-adapted plant, an idea which is lent further credence by the fact that I_K values observed in an intertidal population of *Gigartina radula* over a period of 16 months were similar to those of the subtidal I_K values of the same species (see chapter 2). Furthermore, the I_K values observed in four other species of intertidal seaweed were also similar to those observed in *Gigartina radula* (chapter 2). This evidence suggests that *Gigartina radula* is predominantly an intertidal and shallow water plant adapted to high incident irradiances.

The seasonal pattern and sun/shade-adaptation strategy shown by the P_{max} and I_K values of the three species investigated in this study is further supported by the evidence of Mathieson and Norall (1975) who found seasonal differences in the photosynthesis-light responses of four subtidal red algae (*Euthora cristata* C. Ag., *Phycodrys rubens* (L.) Batt., *Phyllophora truncata* (Pallas) A. Zin. and *Ptilota serrata* Kütz.). Deep water (shade adapted) populations of *Ptilota serrata* showed lower irradiance optima (I_K values) and

smaller P_{max} values than shallow subtidal plants of the same species. Furthermore, Mathieson and Norall (1976) demonstrated adaptation to seasonal temperature changes in *Euthora cristata*, *Phycodrys rubens* and *Phyllophora truncata*, and suggested that optimal temperature and light requirements of seaweeds are adjusted in an adaptive fashion to the environmental regimes of their habitats. This further supports the ideas concerning temperature adaptation expressed previously. Heine (1983) regarded variability in net production to respiration (Pn:R) ratios as indicative of whether a plant species is adapted to utilize available light regardless of the time of year (season). The Pn:R ratios of the three sublittoral seaweeds investigated in this study are shown in table VIII.

With the exception of the June & July 1985 data for *Botryocarpa prolifera*, both *Botryocarpa prolifera* and *Epymenia obtusa* display a fairly constant Pn:R ratio, thus implying that their photosynthetic processes are governed more by seasonal variations in irradiance than instantaneous light availability. In the case of *Gigartina radula*, the Pn:R ratios are much more variable, and this implies that this species is more responsive to sudden changes in light, and may as a result (according to Foster, 1982) be adapted for rapid growth during periods of high irradiance.

While abiotic parameters such as wave height and velocity (ZoBell, 1971) and tidal height (McQuaid, 1985) have been found to be strongly correlated with seaweed abundance, their effect is purely physical as opposed to physiological, and longer term seasonal variations in abiotic factors such as photoperiod, mean seasonal irradiance and water

temperature are more likely to be the cause of the seasonal patterns of production and respiration observed in this study. Nevertheless, other factors such as environmentally-induced alterations in life history patterns (Wynne and Loiseaux, 1976) and preferential grazing (Vadas, 1977) could be important in affecting patterns of primary production although they are largely independent of those parameters that regulate photosynthesis. Similarly, a uniform correlation between seasons of maximum and minimum photosynthesis and growth rate, such as noted by King and Schramm (1976), would probably not occur universally under natural conditions - although in the case of this study the observed season of growth of understorey species investigated seems to begin at roughly the same time (or shortly thereafter - a lag phase being possible). However, this is conjecture as growth rates were not measured in this study.

The calculations of productivity, which show the average amount of carbon fixed per hour for three one hour incubations at various times during the sample day, are accurate in as much as both time and period of incubation were standardized as much as possible during the study. However, the extrapolation of short-term rates of production to daily rates could be problematical because of the possible existence of endogenous metabolic rhythms. Daily photosynthetic rhythms have been observed in some macroalgae (Oohusa *et al*, 1977) but not in others (Blinks and Givan, 1961). In this study, the effect of any daily periodicity was standardized by conducting incubations at approximately the same time of day.

The calorific values obtained in this study compare well with those obtained by Field *et al* (1980). Values of 11.08kJ. g^{-1} for *Gigartina radula*, 11.64kJ. g^{-1} for *Epymenia obtusa* and 12.53kJ. g^{-1} for *Botryocarpa prolifera* are close to the values of 11.39kJ. g^{-1}, 11.20kJ. g^{-1} and 15.11kJ. g^{-1} determined by Field *et al* (1980) for the same three species. The C:N ratios of *Gigartina radula* and *Epymenia obtusa* average 10.79:1 and 7.51:1 respectively (no significant seasonal variation), and range from 7.61:1 to 9.41:1 for *Botryocarpa prolifera* (with significant seasonal variation at the 5% level). This is in agreement with the results found by Atkinson and Smith (1983), since the west coast is a high nutrient environment and low C:N ratios would be expected. The seasonality in C:N ratio observed in *Botryocarpa prolifera* supports the observation that the C:N ratio increases in that time of the year (winter) when upwelling of nutrient-rich water does not occur. The higher C:N ratios observed in *Gigartina radula* (with no significant seasonal variation) are of interest, and are due to the lower nitrogen content observed in this species. Why *Gigartina radula* should have a lower amount of nitrogen than the other two species is perplexing considering it is growing in the same locality and is thus exposed to the same nutrient regime. It may possibly be due to the fact that *Gigartina radula*, being a plant which thrives in high irradiances, is utilizing nitrogen in metabolism and growth at a faster rate than it can be incorporated from the environment. However, if this is the case, this high rate of metabolism and growth is not reflected in an increased rate of photosynthesis when compared to the other two sublittoral

species. Since plants with low C:N ratios are generally attributed to high nutrient levels (see previous page), the high C:N ratio observed in *Axillariella constricta* growing in the same supposedly nutrient-rich environment at Oudekraal is of interest. This is normally attributable to the belief that benthic seaweeds have large amounts of structural carbon (Atkinson and Smith, 1983). However, while the percentage carbon level of *Axillariella constricta* is moderately high, it is no higher than many of those species observed at Oudekraal with much lower C:N ratios. The high C:N ratio of this species is due in part to the moderately high level of carbon, but is mostly attributable to the low level of nitrogen observed in this species. Taxonomically, the higher C:N ratio observed for *Axillariella constricta* agrees with data of Niell (1976) who observed that members of the Phaeophyta have higher C:N ratios than other divisions (excluding calcified algae).

CHAPTER 4: GENERAL DISCUSSION

From the data obtained in chapters 2 and 3 it is possible to estimate the annual primary production of the five littoral and three sublittoral species investigated in this study. From these figures, comparisons will be made with other local seaweed production estimates, as well as with estimates from other world regions.

Although the extrapolation of observed rates of primary production in conjunction with seasonal patterns of primary production to annual figures is likely to be, at best, only an estimate of actual production due to the various assumptions involved, it is nevertheless worthwhile performing the necessary calculations in order that an approximate figure may be arrived at. This approximate figure is useful for comparative purposes with figures obtained for primary production in other macroalgal populations and communities.

The assumptions which must be made to complete the calculations to estimate the annual primary production of the species investigated are as follows. Firstly, a standard rate of respiration for the species being investigated must be decided upon. Various studies (e.g. Kanwisher, 1966; Doty, 1971; Buesa, 1977; Arnold and Murray, 1980) have reported respiratory rates ranging from 3-10% of P_{max}. Choice of an average respiration rate is complicated by the use of different methods of measurement by various authors, but the data from this study seems to favour the higher end of this scale. Fortunately, the choice of a higher or lower rate would produce only relatively small changes in the final

productivity values. In the case of the sublittoral seaweeds investigated, the rate of respiration observed in a particular species during any one month was assumed to be constant for that species for that month. In the case of the intertidal seaweeds investigated, the measured respiration rate expressed as a percentage of P_{max} was used for calculations. Furthermore, because respiration was not measured during the emersed incubations, the respiration expressed as a percentage of P_{max} of the submersed algae was assumed to be constant throughout this period. In addition to this, the average day-length on a monthly basis from 1976-1982 (Department of Transport light data) was used to determine the total amount of gross production for each species investigated. Photorespiration in the sublittoral seaweeds is not accounted for although Black *et al* (1976), Tolbert and Garey (1976) and Hough (1976) have shown that photorespiration does occur in some marine macroalgae. Photorespiration in sublittoral seaweeds is regarded as minimal in this study because of the low temperatures and low irradiances experienced in the Cape west coast environment, (Hough (1976) stated that high temperatures and irradiances are optimal for photorespiration), and also because Black *et al* (1976) showed that the inhibition of P_{max} due to photorespiration of various marine algae was nil (in all but one of a number of species examined) if plants were incubated in seawater directly after bubbling the seawater with nitrogen gas to remove oxygen as was done during this study for the sublittoral seaweeds. Photorespiration was assumed to be of some importance in the intertidal seaweeds studied because they are exposed to an

environmental regime of common high irradiance and temperature, the problem being in assigning a value to any such photorespiration. Hough (1976) in his study of photorespiration in some tropical marine algae observed a ratio of photorespiration to dark respiration ranging from 1.83:1 to 0.48:1, with an average of 0.92:1. Therefore, for the purposes of this intertidal study, the rate of photorespiration was taken as 0.92 x the applicable respiration rate.

A third assumption concerns the amount of available light for photosynthesis. Means of the average hourly global irradiance at D.F. Malan airport (33·54'S;18·32'E), 30km from Dalebrook, between 1976-1982 are shown on a monthly basis in appendix VI. These means are used to determine whether a particular plant species is photosynthetically light-saturated at a particular time of day for a particular month. If the plant is light-saturated, P_{max} is taken as the net level of photosynthesis, whereas if the plant is not light saturated at the particular level of photosynthesis for that plant in that month (or the closest month thereto) then the mean level of irradiance for the particular hour being calculated is read off from the P-I curves shown in appendices III and IV. The actual calculations for gross primary production are shown in appendix V.

Calculations of emersed primary production are further complicated by the sparsity of the emersed photosynthesis data. While the limitations imposed on the acceptability of meaningful figures based on non-replicated observations, especially when observations may be seasonal, is fully recognised, the author feels that for the purpose of this

study the use of the once-off emersed primary productivity data contributes significantly to our understanding of the exposed primary production of local intertidal seaweeds. Furthermore, data concerning the time spent exposed by each intertidal species are the result of a single day's observation mid-way between a spring and neap tide. In this particular instance, the average time of exposure of each intertidal species was calculated from the amount of time spent exposed during one tidal cycle by plants from the mid-region of the zone occupied by each species. These figures are shown in table IX. These figures are thus related to the position of each species on the shore, those lower down (e. g. *Bifurcaria brassicaeformis*) being exposed for a much shorter period than those higher up (e. g. *Porphyra capensis*). Thus any adaptation to survive long periods of emersion may be expected to have some relation to the photosynthetic ability of the species in question while exposed. From the data accumulated in this study, this does seem to be the case, the most striking example being *Porphyra capensis* which is able to maintain a considerable overall positive net rate of primary production throughout its extended exposure period.

Appendix VII and table X show the overall seasonal rate of carbon fixation of the five intertidal seaweeds investigated. The emersed contribution in appendix VII remains static since it is based on a one-off unreplicated sampling of each species. It can be seen that in the case of *Porphyra capensis*, the overall rate of carbon fixation is extremely dependent upon the period of exposure of this plant at low tide. The adaptation of this species to

TABLE IX: Relative and actual times of exposure of 5 intertidal seaweeds mid-way between spring & neap tides at Dalebrook.

Date: 6 August 1987

Species	Proportion of day exposed (%)	Time exposed (mins. day^{-1})	Time exposed per tidal cycle (mins)
Porphyra	78.85	1136	568
Ulva	51.37	740	370
Gigartina	21.15	305	153
Splachnidium	36.26	522	261
Bifurcaria	8.79	126	63

TABLE X: Gross seasonal production of five intertidal seaweeds (mg C fixed. g dw^{-1}. month^{-1}).

	Jan	Feb	Mar	Apr	May	Jun
Porphyra	527.01	446.88	408.82	358.58	526.91	500.09
Ulva	772.25	673.24	912.60	734.06	816.72	763.82
Gigartina	545.01	450.77	441.62	375.80	820.25	777.23
Splachnidium	421.51	359.40	838.63	716.35	626.02	573.32
Bifurcaria	402.35	383.68	1070.51	861.40	319.52	309.22

	Jul	Aug	Sep	Oct	Nov	Dec	Total
P	516.55	540.02	763.71	450.39	614.09	629.06	6282.90
U	1052.34	1052.34	2145.98	509.48	1288.73	1325.06	12059.33
G	535.29	557.78	1597.58	818.54	405.85	638.14	7963.86
S	718.30	757.03	776.01	556.27	663.58	692.41	7698.84
B	658.26	699.54	705.71	834.41	968.84	819.68	8110.54

photosynthesize while under desiccation stress is evident in the overall contribution of emersed photosynthesis to the gross photosynthesis. Conversely, the importance of the fact that *Porphyra capensis* is extremely productive (as shown in the P-I curves) while submersed is reduced by the relatively little time the plant spends underwater. However, the submersed productivity is still of such an order as to contribute to over half this species' gross production (appendix VII). In contrast to *Porphyra capensis*, the data indicates that *Ulva rigida* performs most of its gross production while submersed. It must however be remembered that the form of *Ulva rigida* collected during this study is a rock pool resident and therefore cannot be expected to photosynthesize as well as *Porphyra capensis* while emersed. The strong seasonal production pattern of *Ulva rigida* (peaking in spring) is very evident. The other three intertidal seaweeds investigated (*Gigartina radula*, *Splachnidium rugosum* and *Bifurcaria brassicaeformis*) also show a greater proportion of submersed production than emersed production. This is because these species are more often submersed than emersed. They also show less adaptation to desiccation stress than the two sheet-like forms. *Splachnidium rugosum* and *Bifurcaria brassicaeformis* exhibit bimodal annual productivity patterns, with peaks in spring and autumn. Bimodal productivity patterns in production have also been observed in other studies of primary production - Littler *et al* (1979) observed spring and autumn production peaks for a number of Californian intertidal seaweeds. Also of extreme importance in ecological studies such as this, is the determination of the actual rate of turnover of the

species investigated. For this to be calculated, the total net production is required and this is shown in table XI. The total annual net photosynthesis (mg C fixed.g $dw^{-1}.yr^{-1}$) is known (table XI), so use of the average of the monthly observations of percentage carbon allows the turnover rate to be calculated. The turnover rates per annum are as follows:

Porphyra capensis: Total production= 5.23200g C fixed.g $dw^{-1}.yr^{-1}$. Thallus is on average 41.26% carbon, therefore annual turnover rate (ATR) = 5.23200/0.4126 = 12.68 times per annum.

Ulva rigida: ATR = 10.23043/0.3092 = 33.09

Gigartina radula: ATR = 6.44243/0.2793 = 23.07

Splachnidium rugosum: ATR = 6.30994/0.2635 = 23.95

Bifurcaria brassicaeformis: ATR = 6.59833/0.2826 = 23.35

Of much interest is the fact that *Porphyra capensis* has the lowest turnover rate - the fact that the species is emersed for such a long time and photosynthesizing at a slower rate than when submersed obviously plays a key role here. The other four species which have a gross annual production contributed to mainly by submersed carbon fixation have much higher turnover rates. The highest rate shown by *Ulva rigida* is expected considering the high photosynthetic rate and considerable time spent submersed by this species, thus allowing considerable photosynthesis. The turnover rates of the other three species are almost identical to each other, which is interesting considering the different periods of emersion and rates of carbon fixation displayed by them.

TABLE XI: Net seasonal production of five intertidal seaweeds (mg C fixed. g dw^{-1}. $month^{-1}$).

	Jan	Feb	Mar	Apr	May	Jun
Porphyra	430.48	370.18	332.92	293.63	445.89	422.50
Ulva	652.12	556.61	771.17	629.75	708.91	650.33
Gigartina	416.32	351.76	336.63	292.18	693.02	654.10
Splachnidium	310.46	296.02	689.65	613.24	526.77	473.65
Bifurcaria	364.57	303.89	875.78	738.62	257.69	249.37

	Jul	Aug	Sep	Oct	Nov	Dec	Total
P	435.53	459.00	648.82	369.57	506.06	517.42	5232.00
U	928.86	917.47	1842.83	413.64	1060.28	1098.46	10230.43
G	429.51	452.00	1352.63	669.06	301.17	494.05	6442.43
S	610.61	645.53	631.02	448.33	520.30	544.36	6309.94
B	554.29	595.57	571.16	682.66	760.24	644.49	6598.33

TABLE XII: Gross seasonal production of five intertidal seaweeds on an average Cape Peninsula shore (g C fixed. m^{-2}. $month^{-1}$).

	Jan	Feb	Mar	Apr	May	Jun
Porphyra	45.68	38.74	35.44	31.08	45.68	43.35
Ulva	27.02	23.56	31.93	25.68	28.58	26.73
Gigartina	28.35	23.45	22.97	19.55	42.66	40.43
Splachnidium	4.90	4.18	9.75	8.33	7.28	6.67
Bifurcaria	28.46	27.14	75.71	60.92	22.60	21.87

	Jul	Aug	Sep	Oct	Nov	Dec	Total
P	44.78	46.81	66.20	39.04	53.23	54.53	544.64
U	36.82	36.82	75.09	17.83	45.09	46.36	421.96
G	27.84	29.01	83.10	42.58	21.11	33.19	414.24
S	8.35	8.80	9.02	6.47	7.72	8.05	89.52
B	46.56	49.48	49.91	59.01	68.52	57.97	573.63

Further additional data (the biomass data of McQuaid, 1980), is used to determine the overall production of the intertidal seaweeds on an area of shore basis. To calculate the average actual production in the intertidal zone of various Cape Peninsula sites the biomass of the various species is required. The average of a biomass survey of intertidal seaweeds at 12 Cape Peninsula sites has been extracted from McQuaid (1980) in order to facilitate the calculation of seasonal and annual production per unit area of shore. This biomass survey indicated the biomass (g dw. m^{-2}) of each species in the particular zone occupied by that species. The total gross production by each intertidal seaweed in the zone occupied by each species on an average Cape Peninsula shore is shown in table XII.

McQuaid (1980, 1985) showed seasonal trends in biomass for various algae at Dalebrook, including *Porphyra capensis*, *Ulva rigida* and *Gigartina radula*. This biomass data was expressed in kg dw over the whole shore at Dalebrook for each species. Using McQuaid's biomass data together with the seasonal productivity data from this study, the gross production of each of these three species on the Dalebrook shore as a whole can be determined. The data is shown in table XIII.

The advantage of this data is that the apparent seasonality of biomass at Dalebrook can be taken into account to give an actual figure for annual primary production of these three species at Dalebrook, whereas the figures for production obtained from the McQuaid (1980) biomass survey at various sites probably give a representative figure for production on a unit area basis for the zone occupied by each species

TABLE XIII: Gross seasonal production of three intertidal seaweeds at Dalebrook (Kg C fixed on entire shore).

	Jan	Feb	Mar	Apr	May	Jun
Porphyra	5.516	6.572	5.892	2.426	1.550	0.735
Ulva	6.435	4.455	4.563	2.243	2.609	4.986
Gigartina	16.350	23.910	23.425	23.855	24.608	13.716

	Jul	Aug	Sep	Oct	Nov	Dec	Total
P	0.380	1.271	2.134	0.795	1.445	6.106	34.822
U	8.769	7.308	20.864	3.963	12.619	17.023	95.837
G	9.446	7.136	18.325	8.306	6.267	22.667	198.011

TABLE XIV: Gross seasonal production of three intertidal seaweeds at Dalebrook (g C fixed per running metre of shore).

	Jan	Feb	Mar	Apr	May	Jun
Porphyra	301.6	359.3	322.1	132.6	84.7	40.2
Ulva	351.8	243.6	249.5	122.6	142.6	272.6
Gigartina	893.9	1307.3	1280.8	1304.3	1345.4	749.9

	Jul	Aug	Sep	Oct	Nov	Dec	Total
P	20.8	69.5	116.7	43.5	79.0	333.8	1903.9
U	479.4	399.6	1140.7	216.7	689.9	930.7	5239.9
G	516.5	390.2	1001.9	454.1	342.6	1239.3	10826.2

in the Cape Peninsula (table XII). Furthermore, the seasonal biomass data shown by McQuaid (1985) is only for three of the species investigated in this study, and limits comparisons both with the other two intertidal species investigated and with the sublittoral species investigated. In fact, comparisons of entire ecosystems based on the data from only three species in each ecosystem cannot really be justified except as a possible indication of the differences between the two ecosystems. The most striking aspect of table XIII is that although *Ulva rigida* is the most productive species on a rate per unit thallus weight basis as well as on a rate per area of species zone basis, based on the seasonal Dalebrook shore biomass data *Gigartina radula* is by far the most important primary producer (the two species not measured are not nearly as abundant on the shore at Dalebrook as *Gigartina radula* (McQuaid, 1980)).

Comparisons with other studies of intertidal seaweed productivity may now be drawn. Turnover rates of various Californian intertidal seaweeds are given in Blinks (1955). He found an annual turnover rate of 15-38 times for *Ulva* sp, 13-26 times for *Porphyra* sp and 26 times for *Gigartina* sp. These figures compare very closely with those observed in this study for these three genera. However, comparison with the data of Littler *et al* (1979) shows the annual production on an area basis to be apparently much greater in this local study. Littler *et al* (1979) observed an annual production of 25.66g C fixed.m^{-2}.yr^{-1} for *Gigartina canaliculata* Harvey and 2.19g C fixed.m^{-2}.yr^{-1} for *Ulva californica* Wille. Their data is expressed as production of a particular species over the whole shore, and is considerably less than the whole

shore figures from Dalebrook. This may be the result of a much lower biomass of these species than observed in the Dalebrook species, the similarity in turnover rates between the Californian species and those at Dalebrook is indicative of this. Further calculations to convert the figures obtained to production per running metre of shoreline allow further comparisons with other studies to be made. The values obtained are shown in table XIV.

The calculations of monthly production on a unit area and weight basis provide the most meaningful data from this study because as many environmental factors as possible were taken into consideration to give an as accurate estimate as possible of seasonal total production, and also because this data allows comparison with figures obtained by other authors. Factors which may further affect production patterns (such as grazing, seasonal growth strategies and changes in life-history patterns) may also be important (as suggested by Littler *et al*, 1979), but are beyond the scope of this investigation. The average combined production of *Porphyra capensis*, *Ulva rigida* and *Gigartina radula* is 5.990kg C fixed per running metre of shoreline per annum. In the case of the Dalebrook intertidal rocky shore studied by McQuaid (1980, 1985) (62.09m x 18.29m), the combined gross production of these three species would be a total of 17.970kg C fixed per annum. When it is understood that a considerable portion of the Cape Peninsula coastline consists of rocky shore, the total amount of carbon fixation by these three species alone must be of considerable importance.

The gross seasonal rates of production of the three sublittoral species investigated are shown in appendix VII and table XV.

The strong seasonal patterns of photosynthesis discussed previously can be clearly seen. The seasonal variation in net photosynthesis of these three species is shown in table XVI.

Using the average levels of carbon from the seasonal data shown in chapter 3, and the annual total net carbon fixation shown in table XVI, turnover rates of the sublittoral seaweeds can be calculated. These are as follows:

Botryocarpa prolifera: Total g C fixed. g dw^{-1}. yr^{-1}/(average percentage carbon/100) = 3.4349/0.3088 = 11.12.

Epymenia obtusa: Annual turnover rate = 2.3852/0.2820 = 8.46.

Gigartina radula: Annual turnover rate = 3.4398/0.2780 = 12.73.

While growth investigations were not performed, a general description of the growth habit observed by the author of the species investigated may be of interest. *Botryocarpa prolifera* and *Gigartina radula* are particularly abundant at Oudekraal, the plants being fairly large and always healthy in appearance. The similar turnover rates for these two species are therefore not surprising. *Epymenia obtusa* on the other hand, is generally a much smaller plant found in areas of lesser irradiance in the kelp beds i.e. vertical rock faces and crevices. The lower rates of carbon fixation and turnover are therefore not unexpected given the conditions under which it lives.

TABLE XV: Annual gross submersed photosynthesis for three subtidal seaweeds (mg C fixed. g dw^{-1}. $month^{-1}$)

	Jan	Feb	Mar	Apr	May	Jun
Botryocarpa	502.2	206.7	168.9	73.8	63.8	48.9
Epymenia	308.8	346.6	239.9	76.5	50.8	8.7
Gigartina	240.9	130.8	133.3	85.5	81.5	69.6

	Jul	Aug	Sep	Oct	Nov	Dec	Total
B	197.4	267.8	378.6	723.3	585.0	477.0	3693.8
E	9.6	169.3	240.6	381.5	373.5	389.7	2595.4
G	214.2	343.5	500.4	674.7	538.2	544.0	3595.7

TABLE XVI: Annual net submersed photosynthesis for three subtidal seaweeds (mg C fixed. g dw^{-1}. $month^{-1}$).

	Jan	Feb	Mar	Apr	May	Jun
Botryocarpa	399.90	190.97	157.17	79.20	68.20	49.50
Epymenia	279.00	326.85	225.68	82.50	54.56	9.90
Gigartina	181.35	121.19	128.96	89.10	85.25	79.20

	Jul	Aug	Sep	Oct	Nov	Dec	Total
B	201.19	293.26	358.88	691.15	513.00	432.45	3434.87
E	10.23	177.32	226.20	360.69	283.50	348.75	2385.18
G	228.47	354.64	483.60	666.97	477.00	544.05	3439.78

A comparison that is of interest is of the I_K values exhibited by sublittoral and littoral individuals of the same species, namely *Gigartina radula*. While (as discussed in chapter 3) both *Botryocarpa prolifera* and *Epymenia obtusa* exhibit I_K values which would seem to indicate that they are shade-adapted species, sublittoral *Gigartina radula* exhibits very similar I_K values to those of littoral *Gigartina radula*. This is interesting in that it thus seems that *Gigartina radula* is genetically adapted to being exposed to high irradiances. If it is exposed to lower irradiances (such as in the sublittoral environment), it will still photosynthesize substantially, but not at the maximum rate (P_{max}) for the particular time of year. Furthermore, these similar I_K values would indicate that low-light adapted ecotypes of *Gigartina radula* do not exist in the sublittoral environment. This possibility is made more likely by the fact that at 5m depth *Gigartina radula* is nearing the limit of its sublittoral depth range (most likely due to light limitation of photosynthesis), while the two shade-adapted species (*Botryocarpa prolifera* and *Epymenia obtusa*) are still present substantially deeper.

Once the biomass of each understorey species has been taken into account (from the data of Field *et al*, 1980 - see appendix II), the relative contribution of each species to the kelp bed ecosytem as a whole can be estimated. Data from the transect survey at Oudekraal can also be incorporated into this data to give a more accurate reflection of the Oudekraal kelp bed ecosytem. Unfortunately, there is no seasonal data on biomass variation of understorey seaweeds available. Personal observation by this author suggests that

the understorey biomass of all three of these species is seasonally variable, with a biomass peak in mid to late summer. This seems logical since this would be at the end of the period in which the highest rate of carbon fixation for these species occurs. The average biomass of the three sublittoral species investigated is shown in table XVII (data from this study at Oudekraal and from Field *et al*, 1980 - see appendix II). The total gross production by the sublittoral seaweeds calculated using this biomass data is shown in table XVIII.

Wassman and Ramus (1979) calculated an annual production figure for sublittoral *Codium fragile* of 4.7kg C fixed.$m^{-1}.yr^{-1}$, a figure much greater than those calculated above. However, rates of carbon fixation for these species are similar (see chapter 3), so the fact that *Codium fragile* has a high standing crop at the site investigated by Wassman and Ramus (1979) (an intertidal site) is responsible for the very large annual rate of carbon fixation by this species. Furthermore, *Codium fragile* is a member of the Chlorophyta, and intertidal members of the Chlorophyta tend to be more productive than sublittoral members of the Rhodophyta. Further examination of the Field *et al* (1980) sublittoral biomass data allows the biomass of the three species investigated in this study to be extracted on a per metre of running shoreline basis (table XIX), and calculations of seasonal productivity per metre of running shoreline can therefore be performed (table XX).

On a running metre of shoreline basis, *Gigartina radula* is the most productive of the three understorey seaweeds on average at six Cape Peninsula kelp beds (Kreeftebaai

TABLE XVII: Average biomass (g dw. m-2) of three sublittoral seaweeds from various Cape Pensinsula sites (g dw. m^{-2})

Botryocarpa prolifera	8.53
Epymenia obtusa	13.46
Gigartina radula	11.89

TABLE XVIII: Annual gross submersed photosynthesis for three subtidal seaweeds (g C fixed. m^{-2}. $month^{-1}$)

	Jan	Feb	Mar	Apr	May	Jun
Botryocarpa	4.2838	1.7632	1.4407	0.6295	0.5442	0.4171
Epymenia	4.1551	4.6652	3.2291	1.0297	0.6838	0.1171
Gigartina	2.8631	1.5540	1.5849	1.0166	0.9690	0.8275

	Jul	Aug	Sep	Oct	Nov	Dec	Total
B	1.6838	2.2843	3.2295	6.1697	4.9901	4.0688	31.5081
E	0.1292	2.2774	3.2385	5.1336	5.0273	5.2440	34.9341
G	2.5468	4.0830	5.9498	8.0222	6.3992	6.9331	42.7529

TABLE XIX: Understorey biomass (g dw) per running metre of shoreline (partly extracted from Field et al, 1980)

Species	Kreeftebaai	Melkbosstrand	Sea Point
Botryocarpa prolifera	469.40	25.12	0.00
Epymenia obtusa	122.80	476.00	26.00
Gigartina radula	348.40	184.00	1.56

	Kommetje	Oliphantsbosch	Oudekraal	Average
Botryocarpa prolifera	244.80	55.80	250.00	174.20
Epymenia obtusa	68.58	773.96	96.75	260.68
Gigartina radula	104.04	368.94	493.25	250.03

TABLE XX: Annual gross submersed photosynthesis for three sublittoral seaweeds (g C fixed per running metre of shoreline)

	Jan	Feb	Mar	Apr	May	Jun
Botryocarpa	87.48	36.01	29.42	12.86	11.11	8.52
Epymenia	80.47	90.35	62.54	19.94	13.24	2.27
Gigartina	60.21	32.68	33.33	21.38	20.38	17.40

	Jul	Aug	Sep	Oct	Nov	Dec	Total
B	34.39	46.65	65.95	126.00	101.91	83.09	643.46
E	2.50	44.11	62.72	99.42	97.36	101.56	676.57
G	53.56	85.86	125.12	168.70	134.57	145.79	899.03

(33·44.7'S, 18·26.6'E), Melkbosstrand (33·42.9'S, 18·26.0'E), Sea Point (33·55.4'S, 18·22.5'E), Kommetje (34·08.1'S, 18·18.6'E), Oliphantsbosch (34·15.4'S, 18·22.7'E) and Oudekraal). However, its primary production is only slightly in excess of the production rates of the other understorey seaweeds. This can be compared with the intertidal situation at Dalebrook where *Gigartina radula* is very much more productive than the other intertidal species on a metre of running shoreline basis (table XIV). This further bears out previous discussion concerning the apparent preference shown by *Gigartina radula* for a high irradiance environment.

To compare the above data with the data for Cape Peninsula kelp beds a number of calculations (and assumptions) are required. Field *et al* (1980) provide combined biomass data for *Ecklonia maxima* and *Laminaria pallida* per running metre of shoreline. From Yzerfontein (33·19.5'S, 18·08.9'E - near Kreeftebaai), to Cape Point the average kelp standing stock is 4.48kg dw.m^{-2}. The total kelp standing stock between these two points is 552 568 tonnes, which averages 6.02 tonnes per running metre of shoreline. This works out to five times the figure for *Laminaria longicruris* found by Mann (1972a) in St. Margarets Bay, Canada. According to Field *et al* (1980), half the kelp standing stock exists as fronds which turn over their biomass four times per annum. Since the fronds (primary blades and secondary blades) are the major source of primary production in that they consist of "moving belts of meristematic tissue" (Mann *et al*, 1979), a reasonable approximation of kelp bed productivity may be calculated for comparison purposes with this study if the

rate of primary production of these blades is known. Mann *et al* (1979) determined that a biomass increase in *Ecklonia maxima* of 1% per day was a reasonable estimate of blade productivity. Similarly, *Laminaria pallida* is highly productive, frond elongation rates as high as 13mm. day^{-1} being recorded (Dieckmann, 1980). Since the two species are closely associated within the Cape Peninsula ecosystem, it can be expected that the Cape Peninsula kelp beds are highly productive. From the figures of Field *et al* (1980), there are 3.01 tonnes (fresh mass) of productive frond per running metre of shoreline, which equates to 10.99 tonnes of biomass produced per annum per running metre of shoreline at an increase rate of 1% per day. This equates to 0.35 tonnes C fixed per running metre of shoreline per annum, using the percentage carbon data of Dieckmann (1978). In comparison, the average gross production of the three understorey seaweeds investigated in this study is a mere 740g C fixed per running metre of shoreline per annum. Thus, the kelps are the most important primary producers of the Cape Peninsula benthic seaweeds, but this does not mean the understorey primary producers are irrelevant. The calculated yearly production for the three understorey seaweeds investigated in this study is 67.903 tonnes C fixed per annum in the South Western Cape region from Yzerfontein to Cape Point (91.8km). Although miniscule when compared to the kelp production of 36220 tonnes C per annum from Cape Point to South Head (98.5km) - Jarman and Carter (1981), the amount of carbon fixation attributable to the understorey flora as a whole (not just three species) must exert some influence on nutrient utilization and trophic dynamics of

the west coast ecosystem, most likely in the effects of the carbon fixation being translated into biomass for utilization by grazers and the creation of habitats within the understorey ecosystem. When compared with the figures for phytoplankton, it can be seen that the primary production of the understorey seaweeds is less than for the phytoplankton. Carter (1982) estimated phytoplankton production to be 1.13kg C fixed.$m^{-2}.yr^{-1}$ at Oudekraal. Comparison with the figures calculated previously of the total amount of production for the three intertidal species (*Porphyra capensis*, *Ulva rigida* and *Gigartina radula*) shows that their production is much greater than the production of the three species of understorey seaweed investigated, average values of 5990g C fixed per running metre of shore (intertidals) as opposed to 740g C fixed per running metre of shore (subtidals) being calculated. The reason for this is the much greater standing stock of intertidal seaweeds observed at Dalebrook by McQuaid (1980, 1985) than of understorey seaweeds at the sites investigated by Field *et al* (1980). However since biomass itself is the result of the amount of carbon fixation taking place, the difference in total carbon fixation taking place must be the result of some other factor. The main factor is obviously light, the irradiance levels being much greater on the intertidal shoreline than in the sublittoral (due to downwelling and kelp shading as well as light attenuation by the water column in the sublittoral environment). Also, irradiance levels on the shore are prone to less variation in that they are much less likely to fall to levels lower than the saturation point for photosynthesis (except at night). On

the other hand, the sublittoral environment as a whole is often at levels of irradiance low enough to be even below compensation point. Other factors such as grazing, wave action and substratum will also play a role in the amount of biomass present. In this respect, the aspect of the Dalebrook shore may be important, it being a flat fairly uniform rocky surface as opposed to the patchy distribution of rocky outcrops surrounded by sand found at Oudekraal.

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APPENDIX 1: RUNSTREAM FOR BMDP AR P-I CURVE ANALYSIS

```
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/variable names are Light, Photosyn.
/save file is 'c:filename.ext'.
      format is free.
/regress dependent is Photosyn.
         parameters are 2.
         iteration=500.
         halving=50.
         tolerance=1.0e-32.
/parameter initial are 5.00, 400.
/fun f=(p1*(2.718281828**(Light/p2)-(1/2.718281828)**
(Light/p2))/(2.718281828**(Light/p2)+(1/2.718281828)**
(Light/p2))).
/plot variable=Light.
      normal.
/end.
data
/end.
```

NOTE: Because computers do not have the hyperbolic tangent function (tanh) built in, the tanh part of the photosynthesis equation has been resolved into powers of e (e = 2.718281828).

APPENDIX II: Kelp bed macrophyte biomass at various west coast sites (Extracted from Field et al,1980)

Species	Kreeftebaai	Melkbosstrand	Sea Point	Kommetje	Oliphantsbosch	Average
Botryocarpa prolifera	23.47	1.57	0.00	13.60	2.54	8.24
Carradoria virgata	0.00	3.07	0.00	0.00	0.00	0.61
Champia lumbricalis	0.04	0.00	0.00	0.00	0.00	<0.01
Cladophora mirabilis	0.71	0.00	0.00	0.00	4.86	1.11
Codium papenfussii	1.45	0.00	0.00	12.09	0.00	2.71
Codium stephensiae	1.20	0.00	0.00	0.00	0.00	0.24
Desmarestia firma	0.00	0.00	9.01	0.00	0.00	1.80
Ecklonia maxima	77.72	282.34	165.25	710.39	449.62	337.06
Epymenia obtusa	6.14	29.75	2.00	3.81	35.18	15.38
Gelidium sp	0.00	4.17	0.00	0.00	0.00	0.83
Gigartina radula	17.42	11.50	0.12	5.78	16.77	10.32
Heringia mirabilis	0.00	0.00	0.00	0.00	0.65	0.13
Hymenena venosa	0.14	0.54	0.00	0.05	25.01	5.15
Kallymenia sp	27.51	0.00	1.64	2.77	0.00	6.38
Laminaria pallida	112.77	102.74	179.30	689.72	226.91	262.29
Neuroglossum binderianum	4.04	5.06	0.00	0.15	0.32	1.91
Pachymenia carnosa	8.72	0.00	0.00	0.28	76.88	17.18
Pachymenia cornea	7.13	0.00	0.00	0.43	9.80	3.47
Polyopes constrictus	1.03	0.00	0.00	5.43	3.83	2.06
Pterosiphonia cloiophylla	0.00	0.07	0.00	2.88	0.14	0.62
Rhodymenia sp	2.62	0.00	0.24	0.02	0.25	0.63
Thamnophyllis sp	1.14	0.00	0.00	0.03	0.00	0.23
Trematocarpus affinis	0.00	4.13	0.00	29.94	36.39	14.09
Trematocarpus fragilis	8.89	0.00	0.00	0.00	2.54	2.29
Trematocarpus scutellatus	4.36	0.00	0.00	10.11	17.21	6.34

g dw. m^{-2}

APPENDIX III: SEASONAL PHOTOSYNTHETIC LIGHT CURVES FOR INTERTIDAL SEAWEEDS

This appendix contains the photosynthetic light curves (P-I curves) observed in the five intertidal seaweeds investigated.

The figures are as follows:

Fig. AP 1a-g: Seasonal photosynthetic light curves for *Porphyra capensis*, mg C fixed per g dry wt per hr versus irradiance ($\mu\epsilon . m^{-2} . sec^{-2}$). Fig. AP 1a = June, 1984; fig AP 1b = September, 1984; fig AP 1c = February, 1985; fig AP 1d = April, 1985; fig AP 1e = June, 1985; fig AP 1f = August, 1985; fig AP 1g = November, 1985.

Fig. AP 2a-g: Seasonal photosynthetic light curves for *Ulva rigida*, mg C fixed per g dry wt per hr versus irradiance ($\mu\epsilon . m^{-2} . sec^{-2}$). Fig. AP 2a = June, 1984; fig AP 2b = September, 1984; fig AP 2c = February, 1985; fig AP 2d = April, 1985; fig AP 2e = June, 1985; fig AP 2f = August, 1985; fig AP 2f = November, 1985.

Fig. AP 3a-h: Seasonal photosynthetic light curves for *Gigartina radula*, mg C fixed per g dry wt per hr versus irradiance ($\mu\epsilon . m^{-2} . sec^{-2}$). Fig. AP 3a = June, 1984; fig AP 3b = September, 1984; fig AP 3c = November, 1984; fig AP 3d = February, 1985; fig AP 3e = April, 1985; fig AP 3f = June, 1985; fig AP 3g = August, 1985; fig AP 3h = November, 1985.

Fig. AP 4a-g: Seasonal photosynthetic light curves for *Splachnidium rugosum*, mg C fixed per g dry wt per hr versus irradiance ($\mu\epsilon . m^{-2} . sec^{-2}$). Fig. AP 4a = June,

1984; fig AP 4b = September, 1984; fig AP 4c = February, 1985; fig AP 4d = April, 1985; fig AP 4e = June, 1985; fig AP 4f = August, 1985; fig AP 4g = November, 1985.

Fig. AP 5a-g: Seasonal photosynthetic light curves for *Bifurcaria brassicaeformis*, mg C fixed per g dry wt per hr versus irradiance ($\mu\epsilon . m^{-2} . sec^{-2}$). Fig. AP 5a = June, 1984; fig AP 5b = September, 1984; fig AP 5c = November, 1984; fig AP 5d = February, 1985; fig AP 5e = April, 1985; fig AP 5f = August, 1985; fig AP 5g = November, 1985.

Fig. AP 1a *Porphyra capensis*

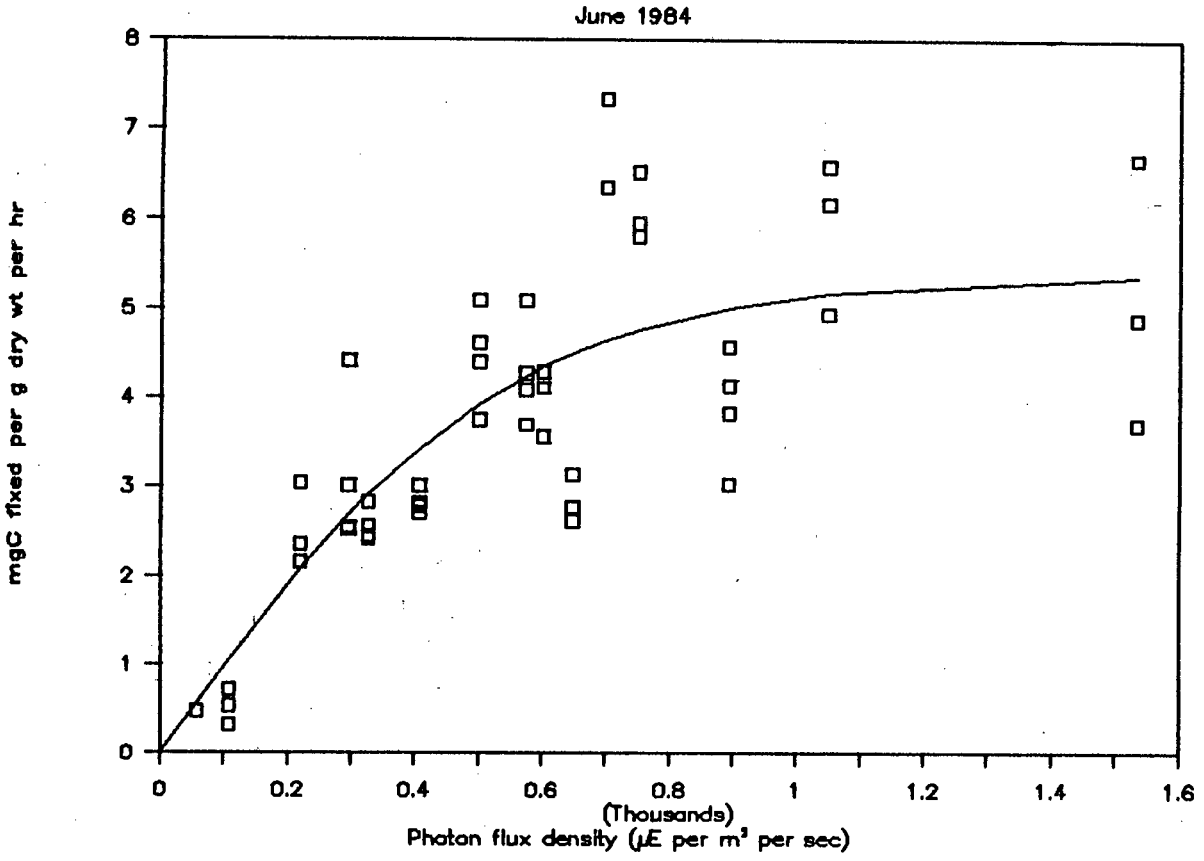


Fig. AP 1b *Porphyra capensis*

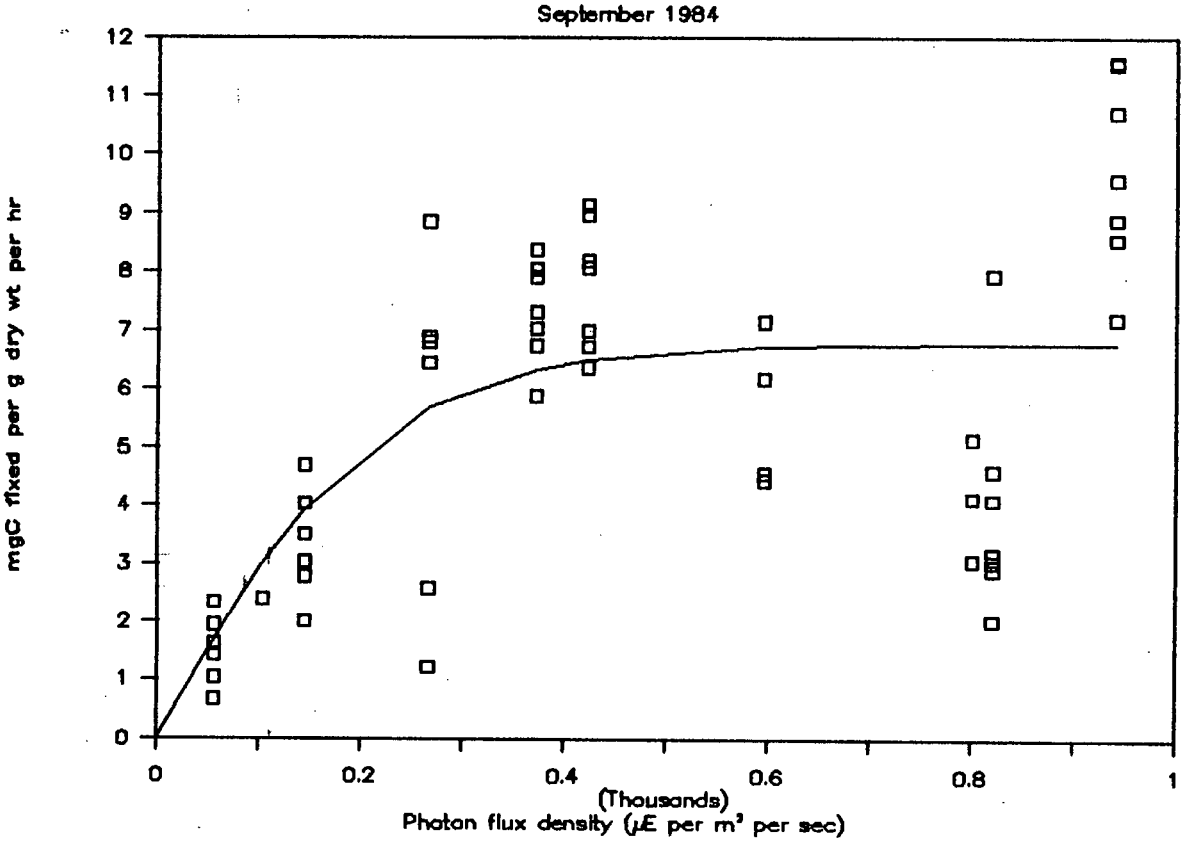


Fig. AP 1c

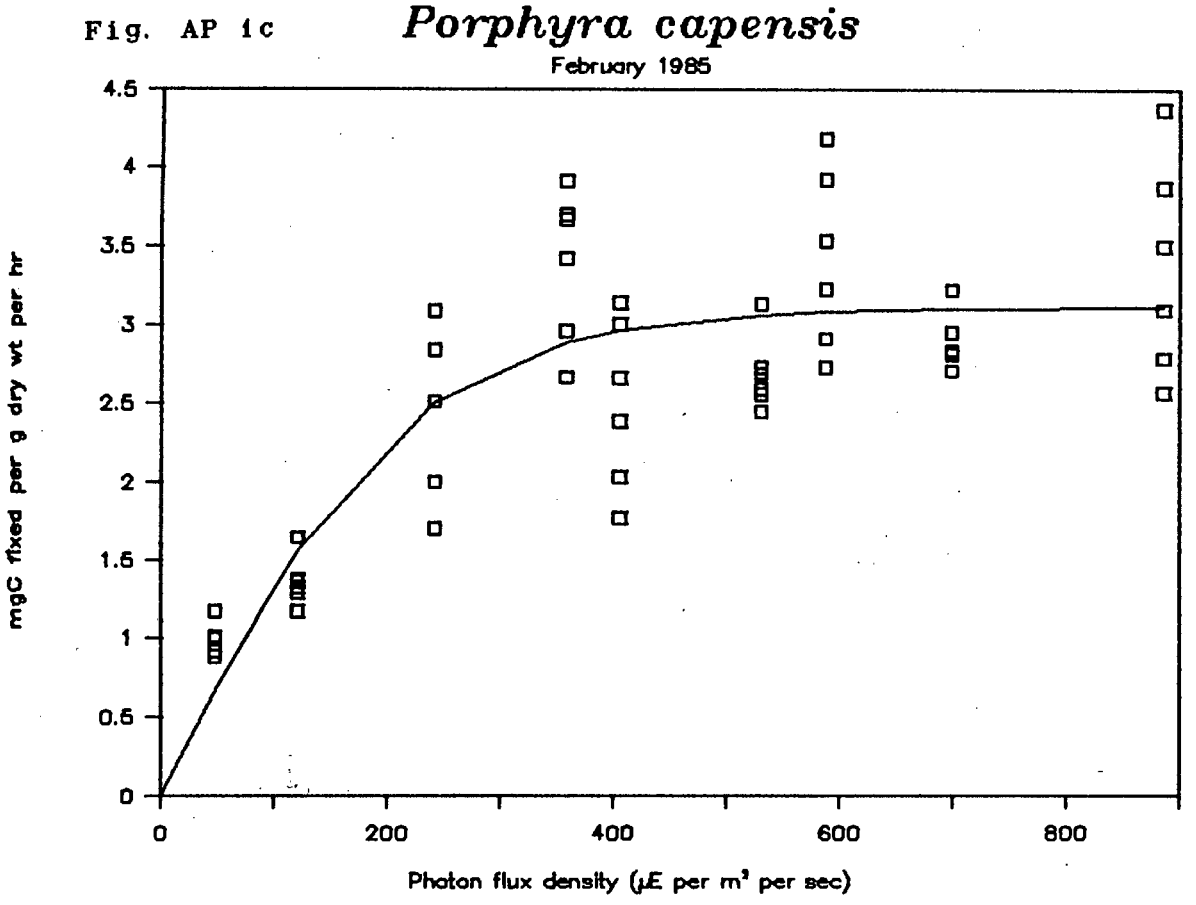


Fig. AP 1d

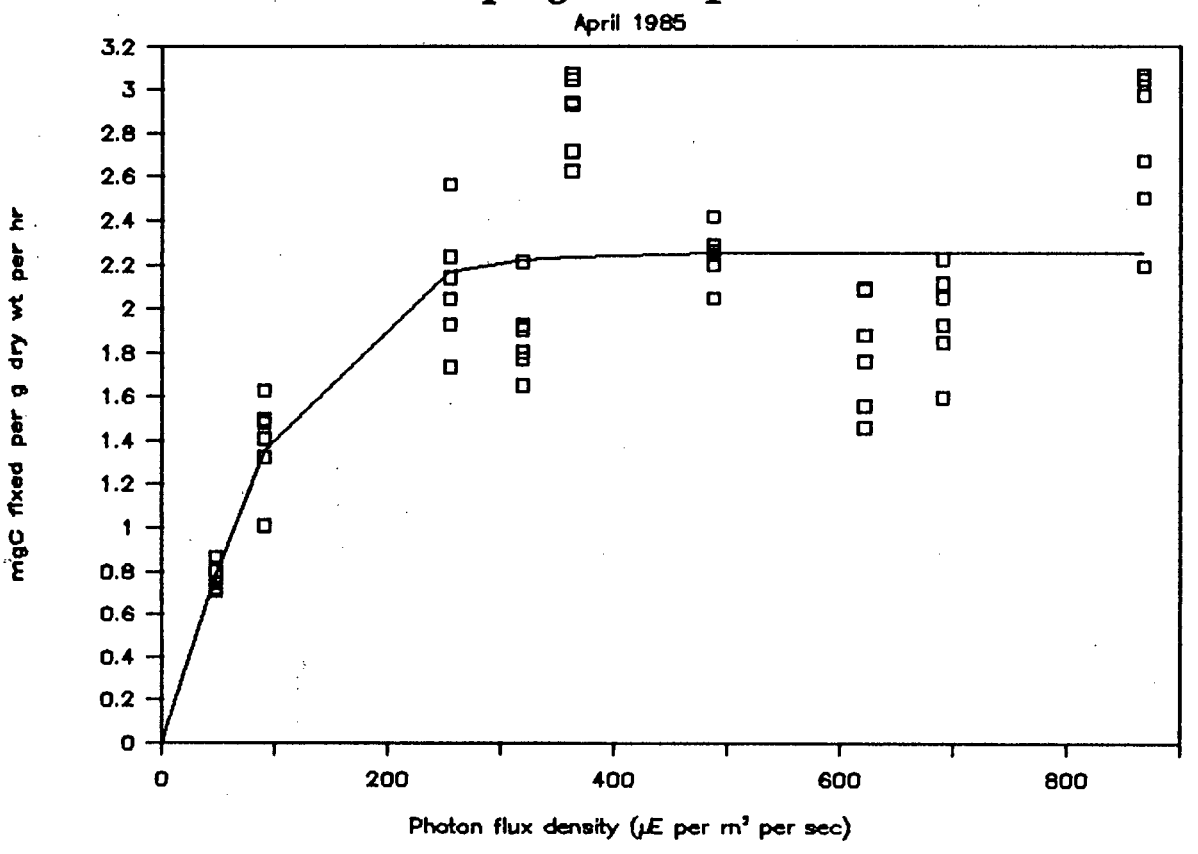


Fig. AP 1e *Porphyra capensis*

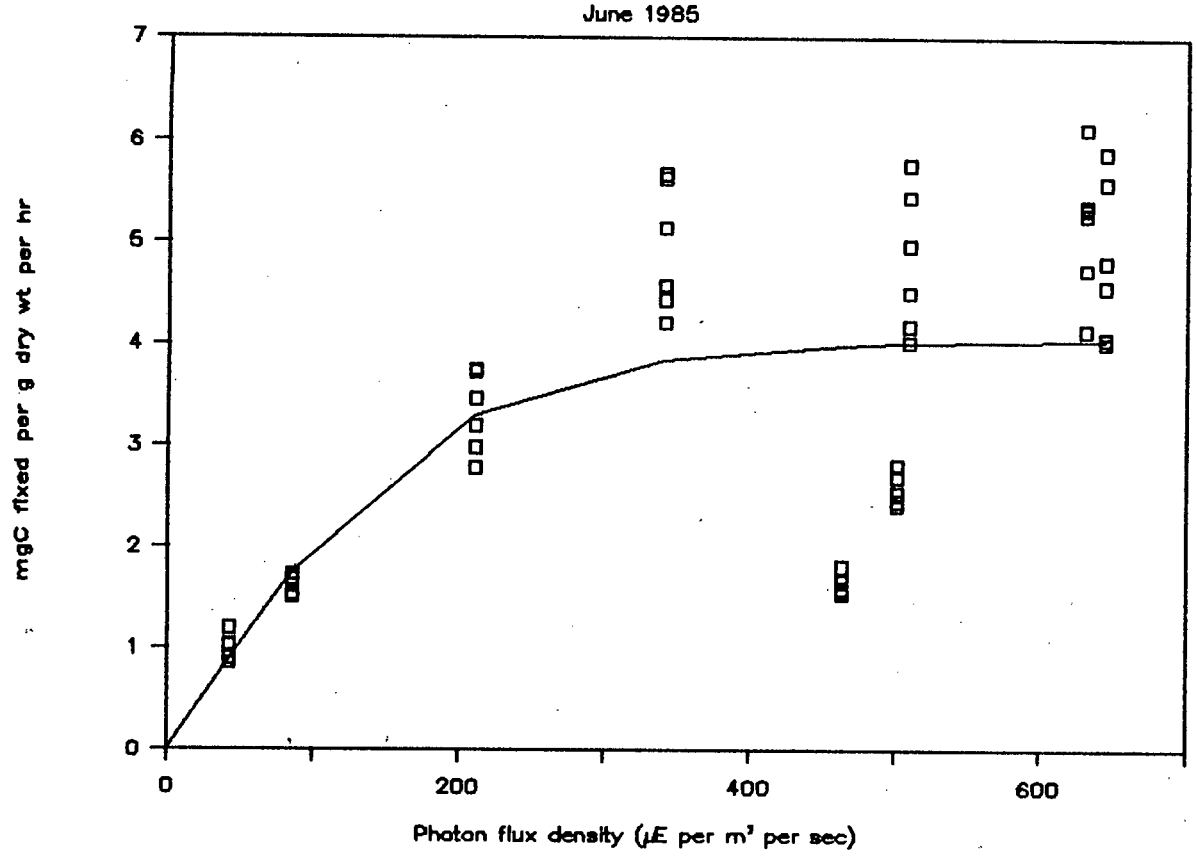


Fig. AP 1f *Porphyra capensis*

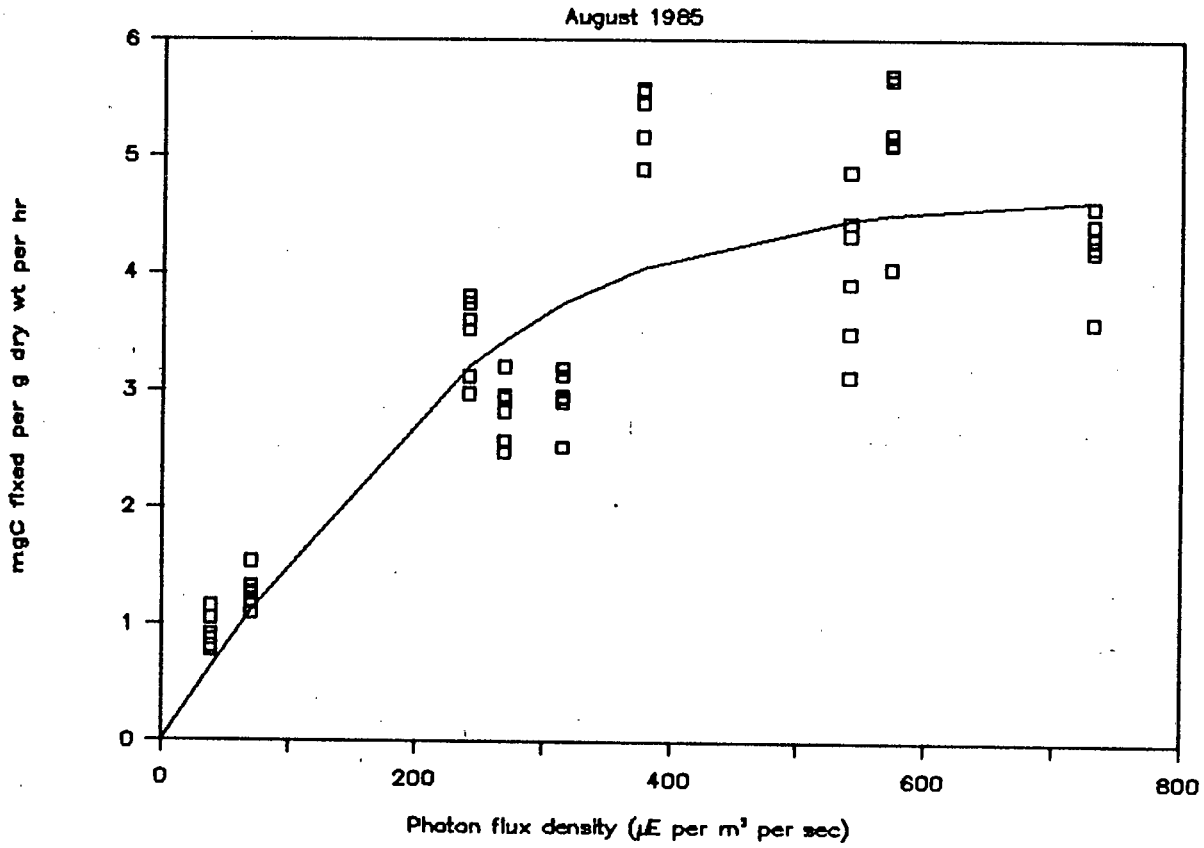


Fig. AP 1g *Porphyra capensis*

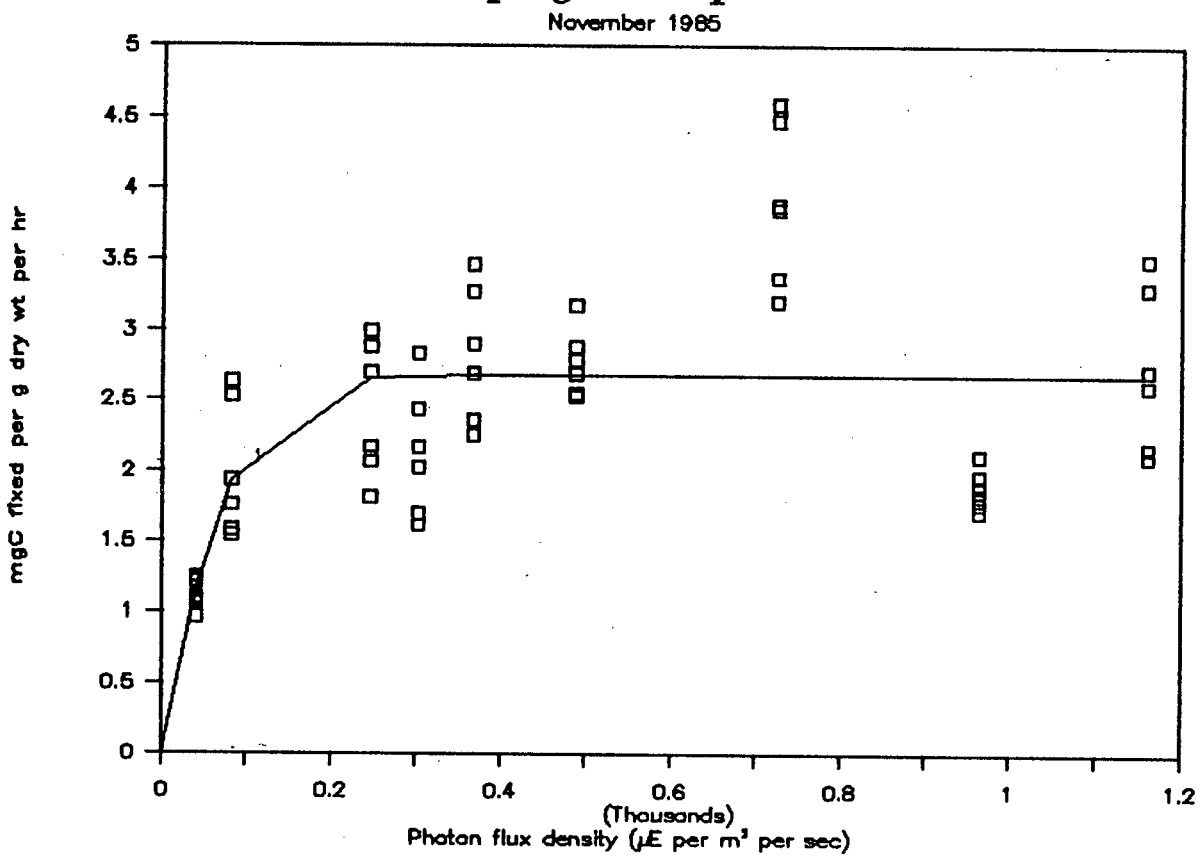
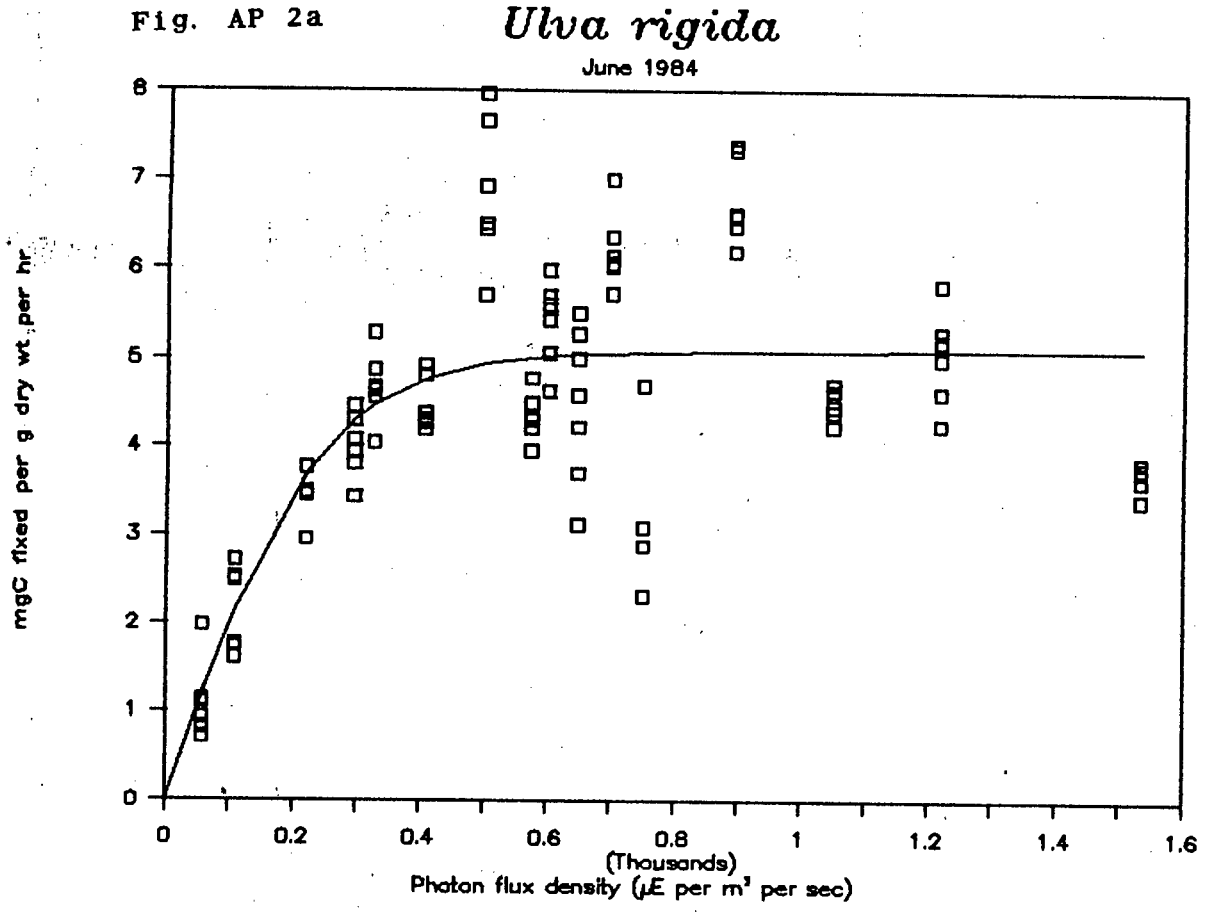


Fig. AP 2a



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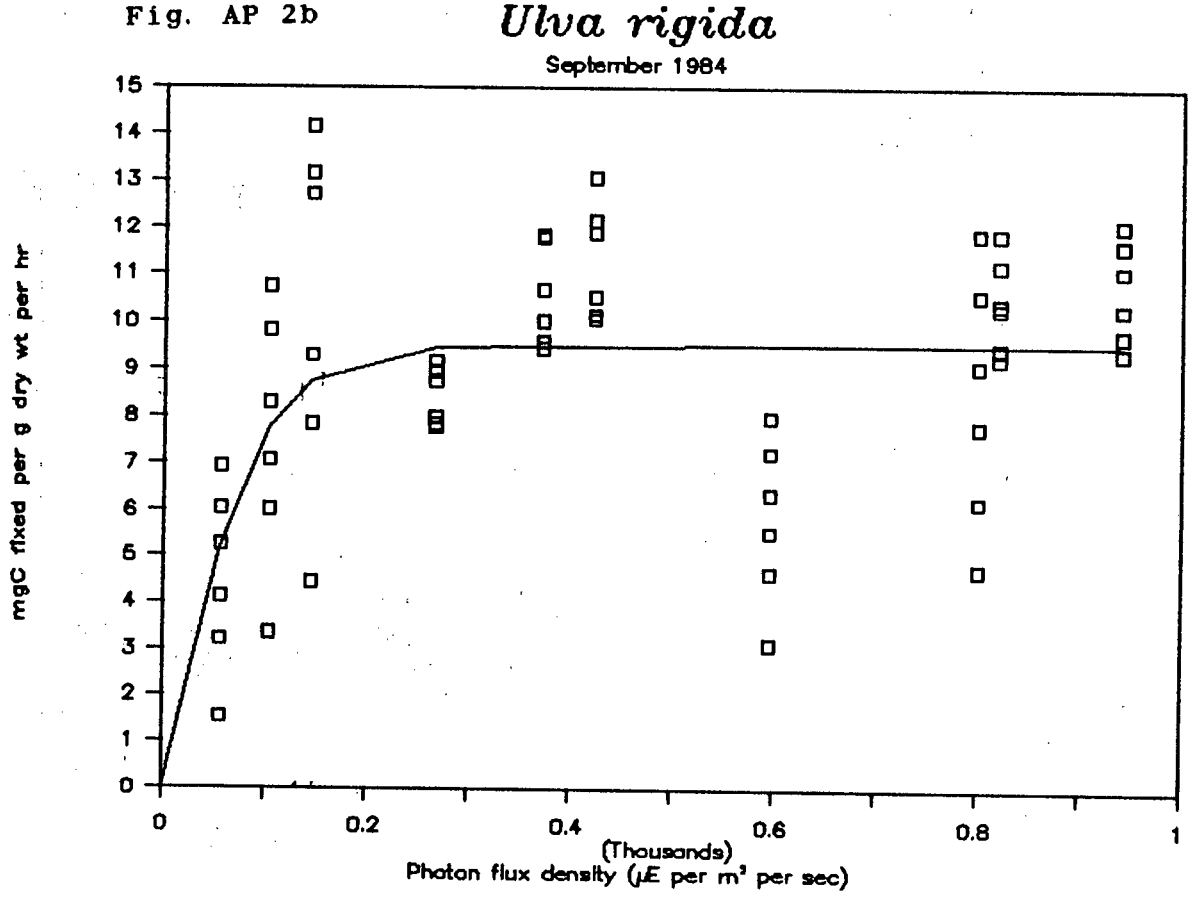
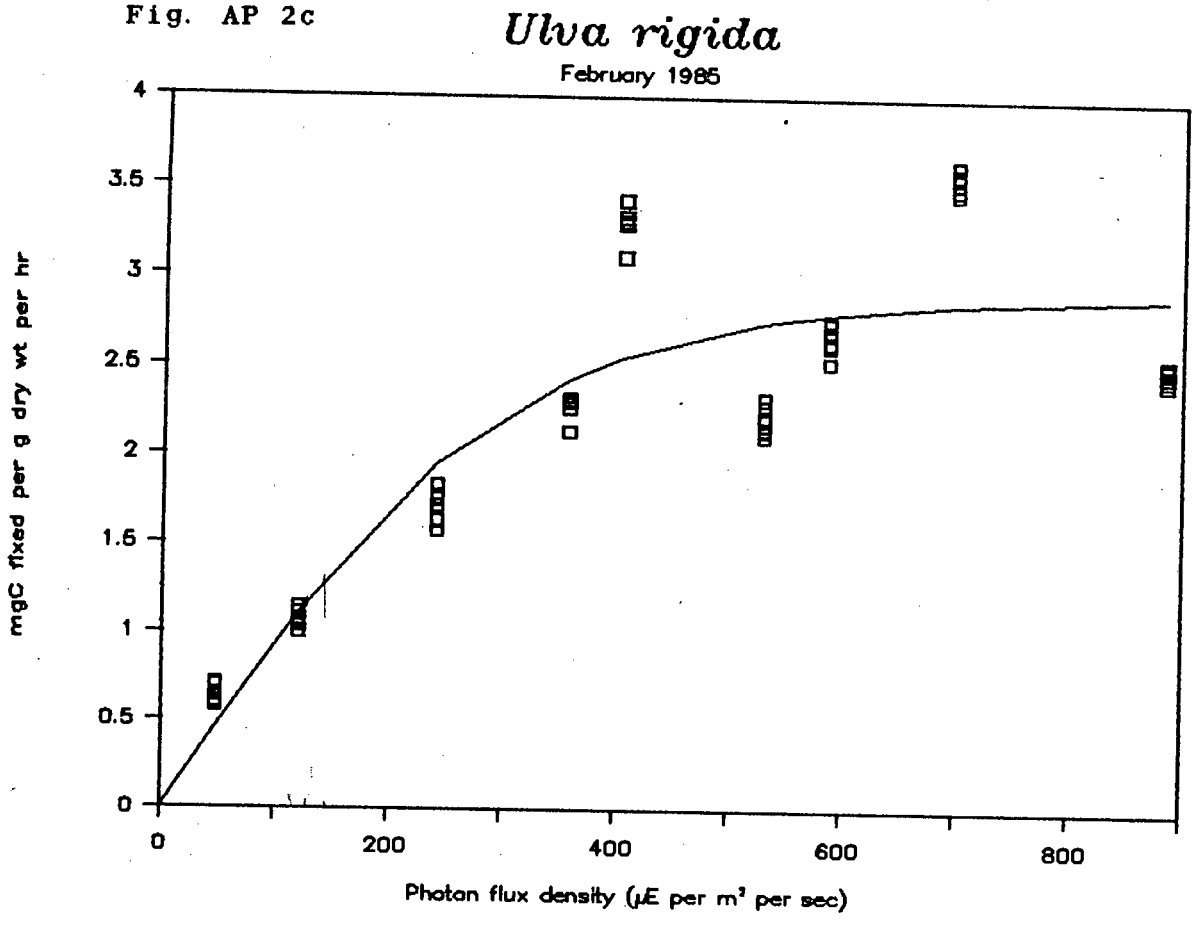


Fig. AP 2c



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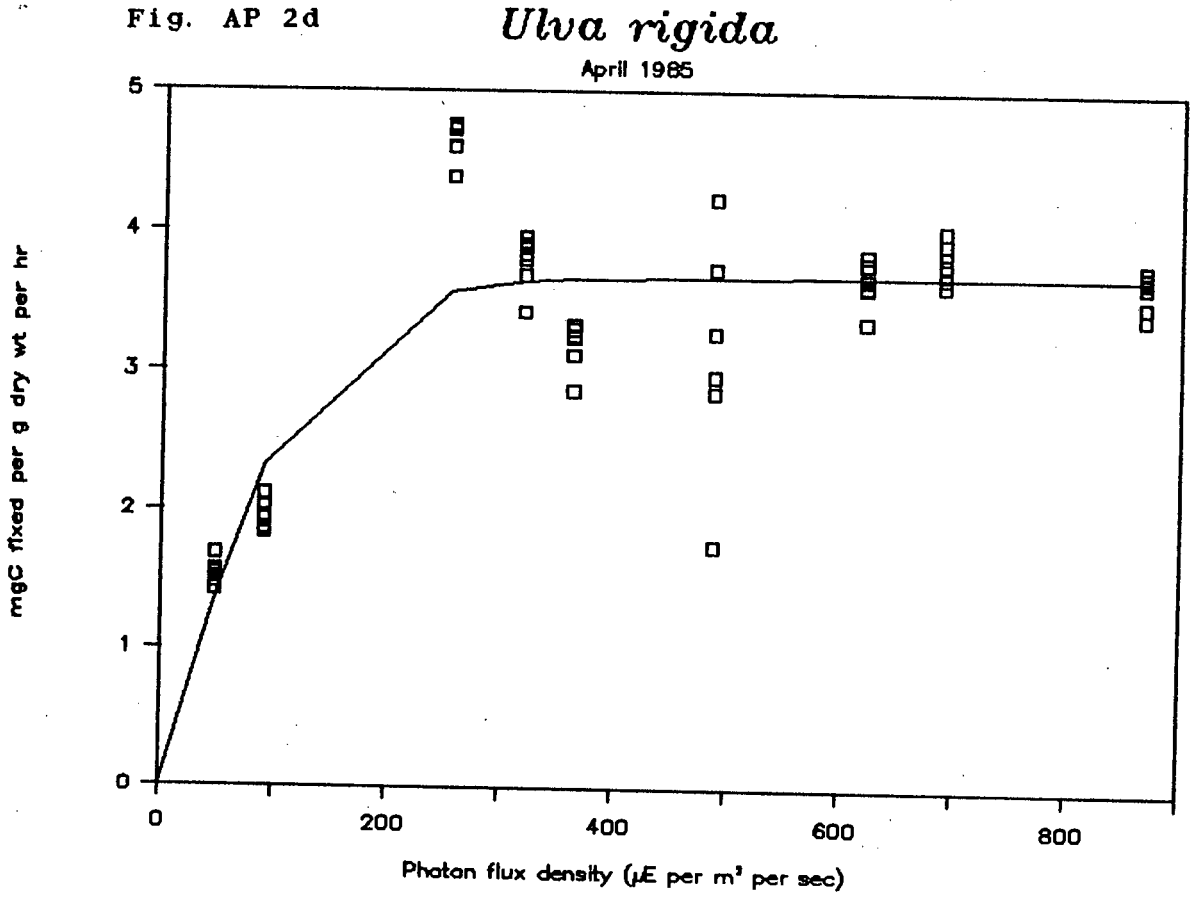
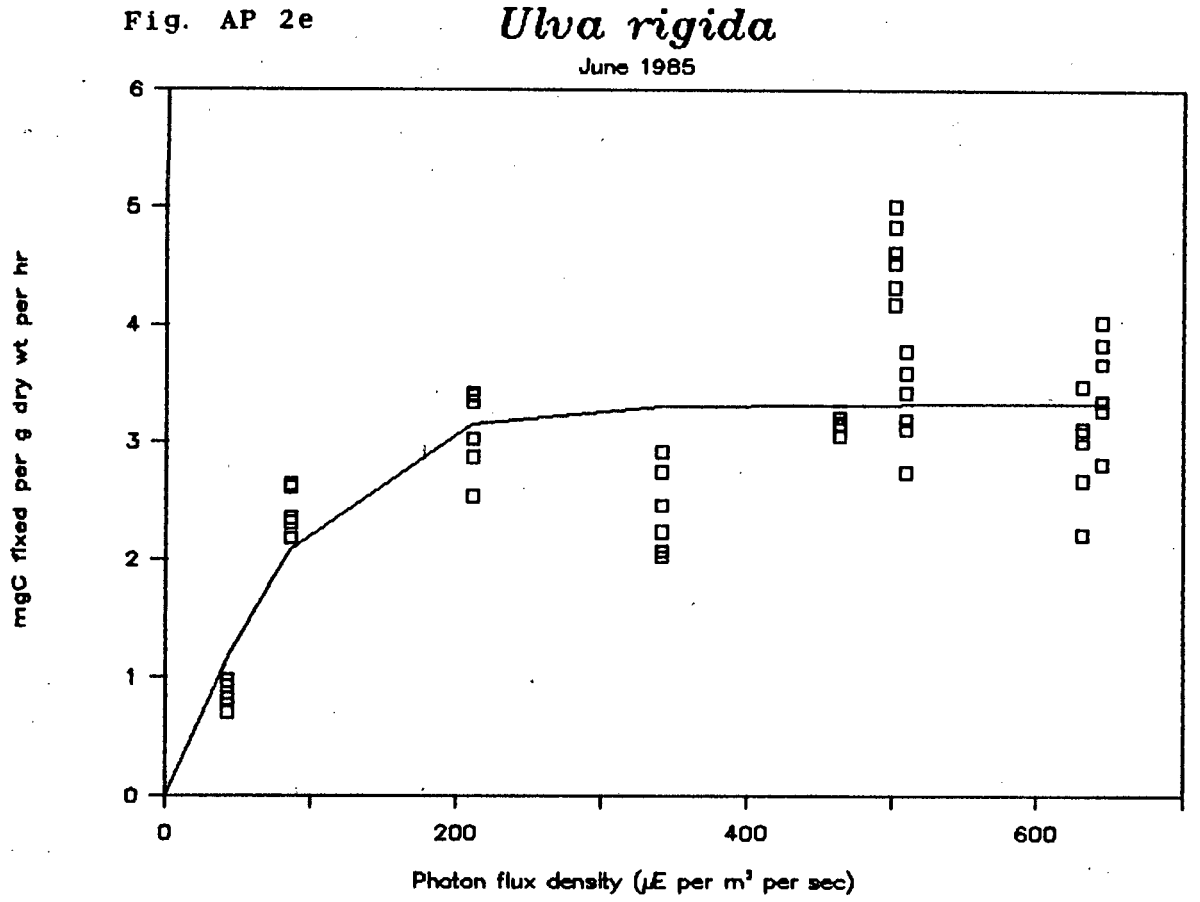


Fig. AP 2e



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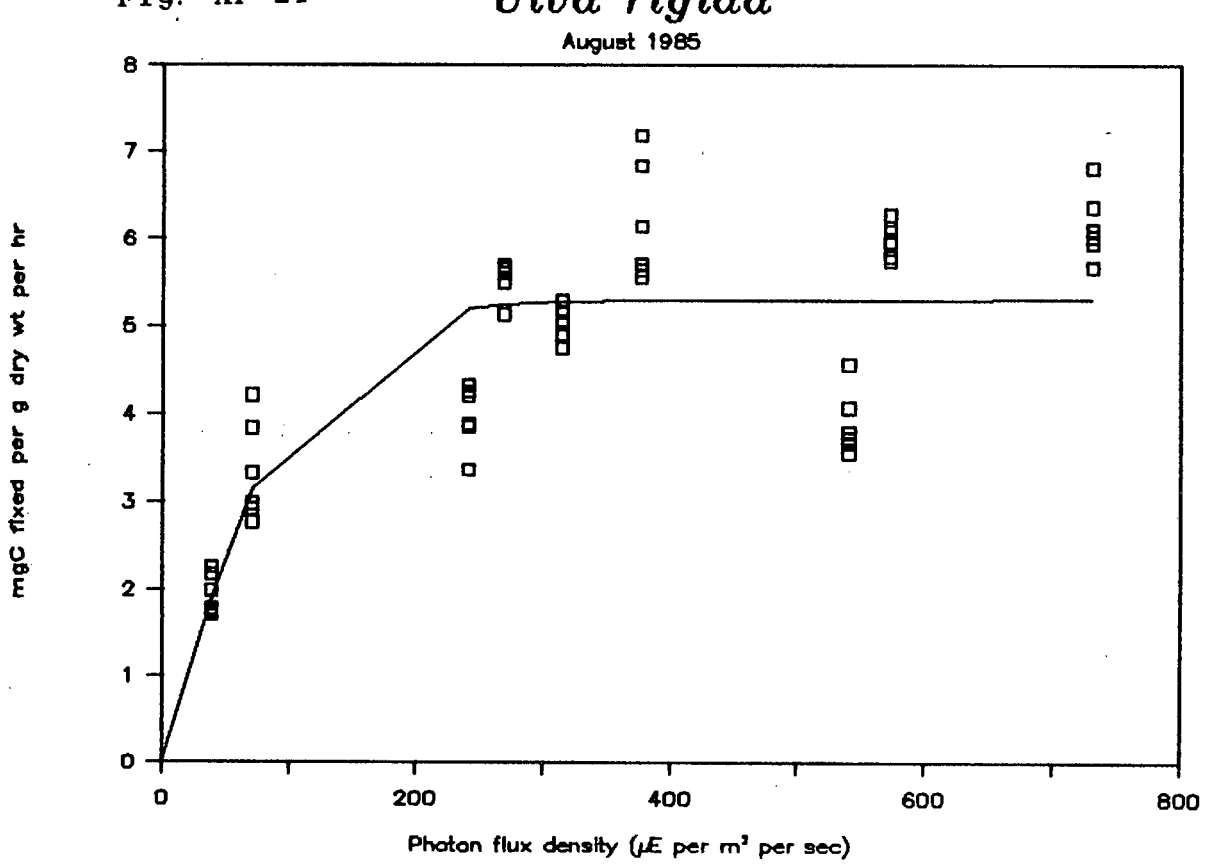


Fig. AP 2g

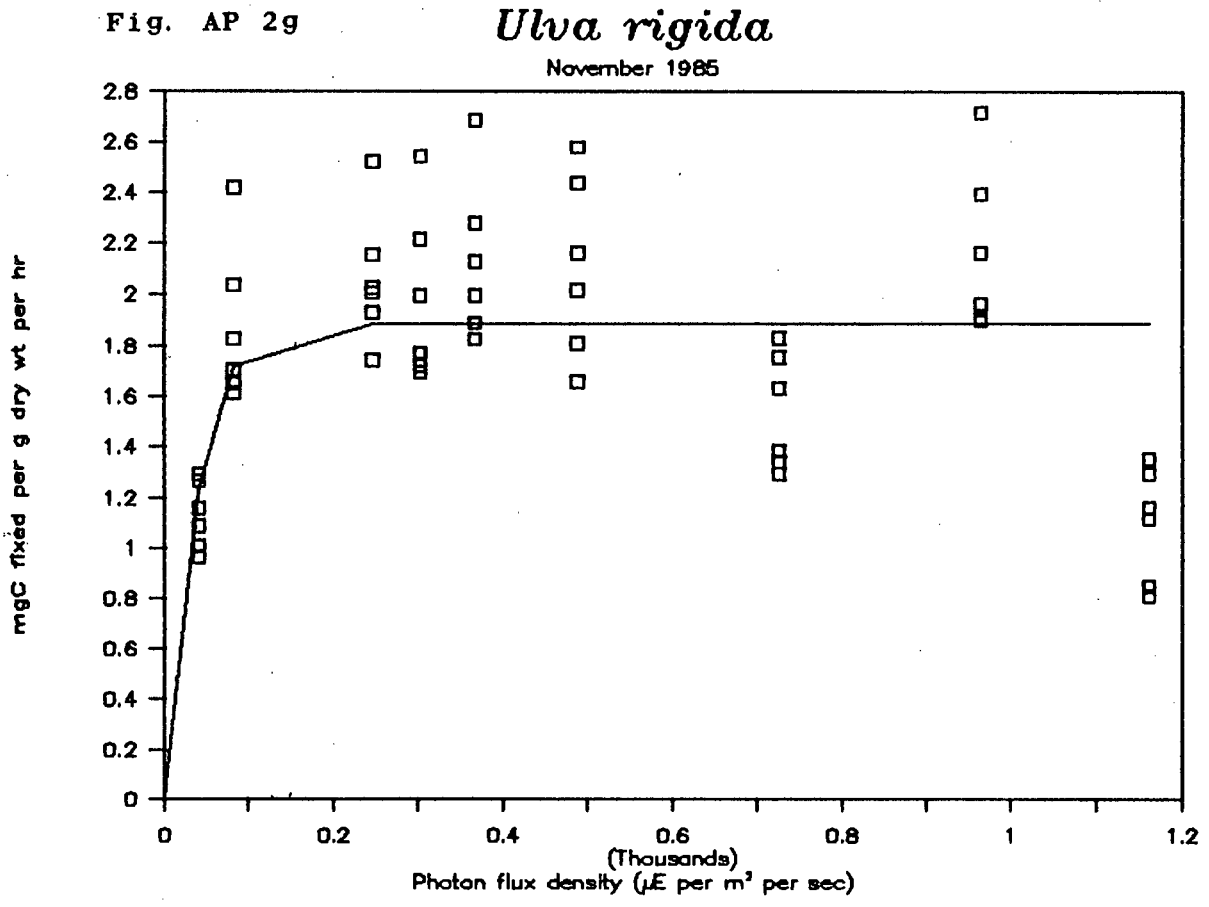

Ulva rigida
November 1985
mgC fixed per g dry wt per hr
2.8
2.6
2.4
2.2
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0
0.2
0.4
0.6
0.8
1
1.2
(Thousands)
Photon flux density (μE per m² per sec)

Fig. AP 3a *Gigartina radula*

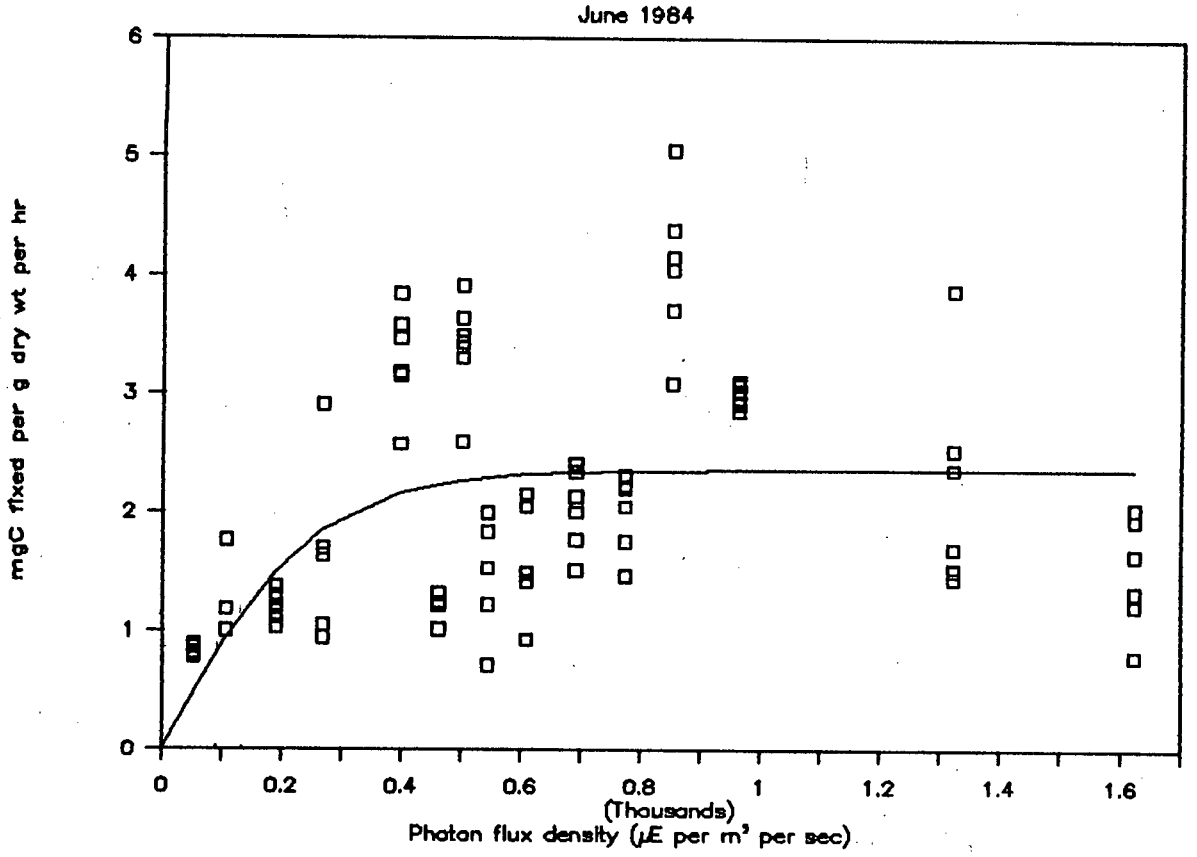


Fig. AP 3b *Gigartina radula*

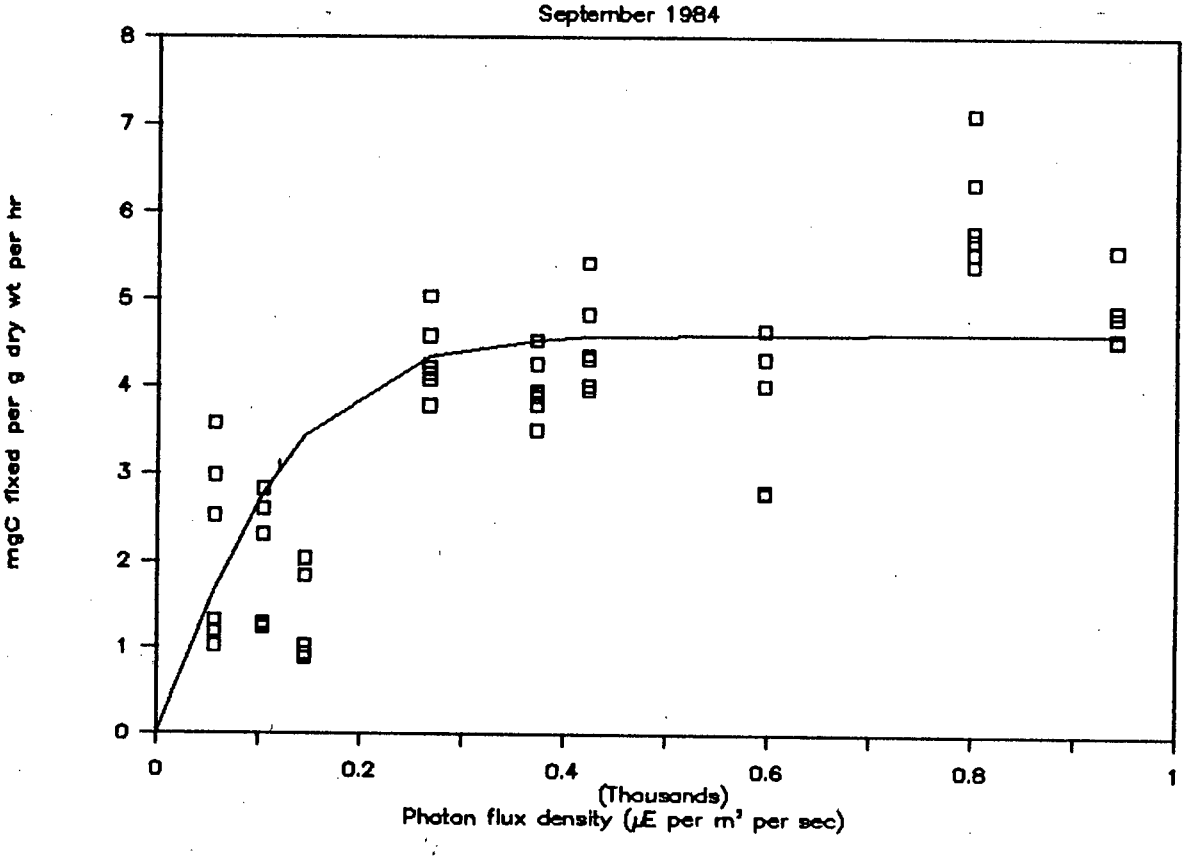


Fig. AP 3c

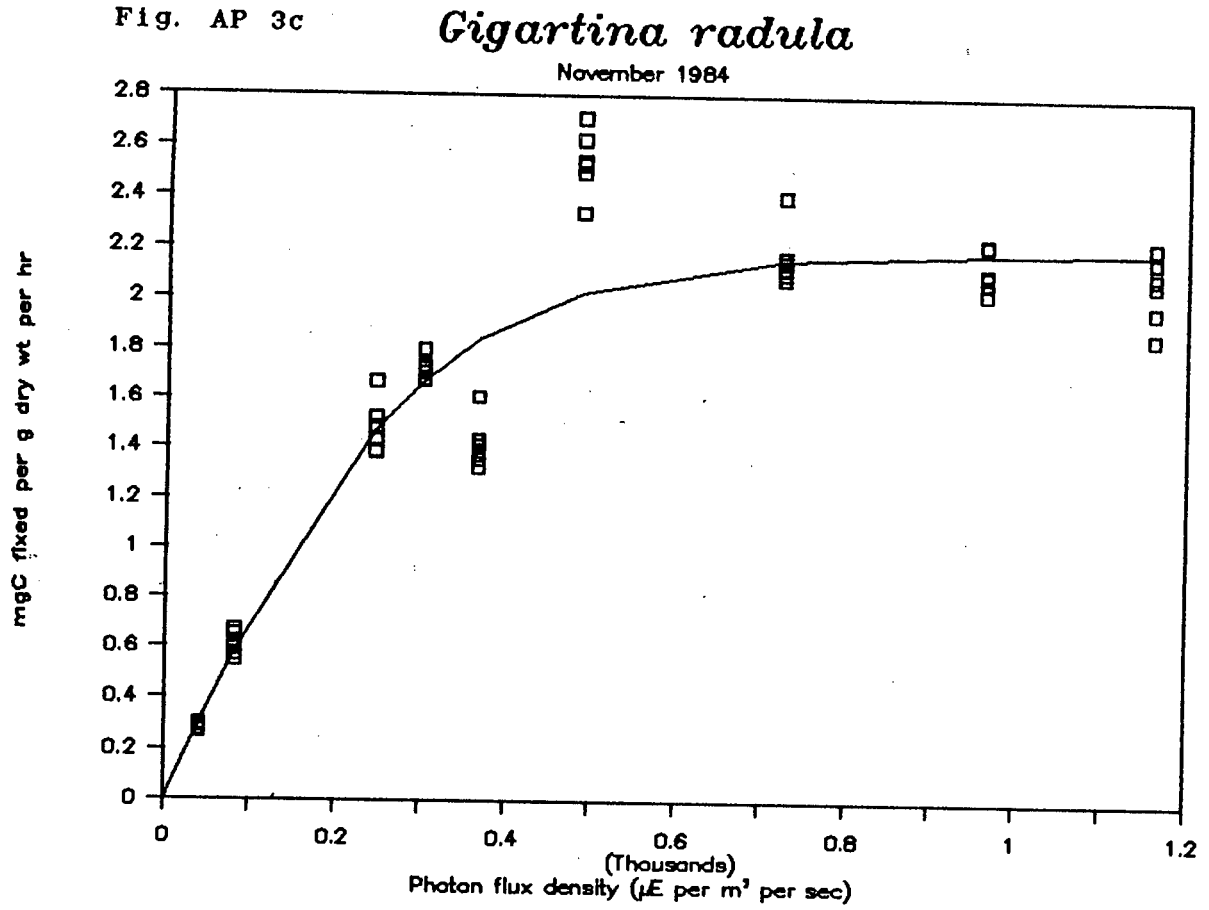


Fig. AP 3d

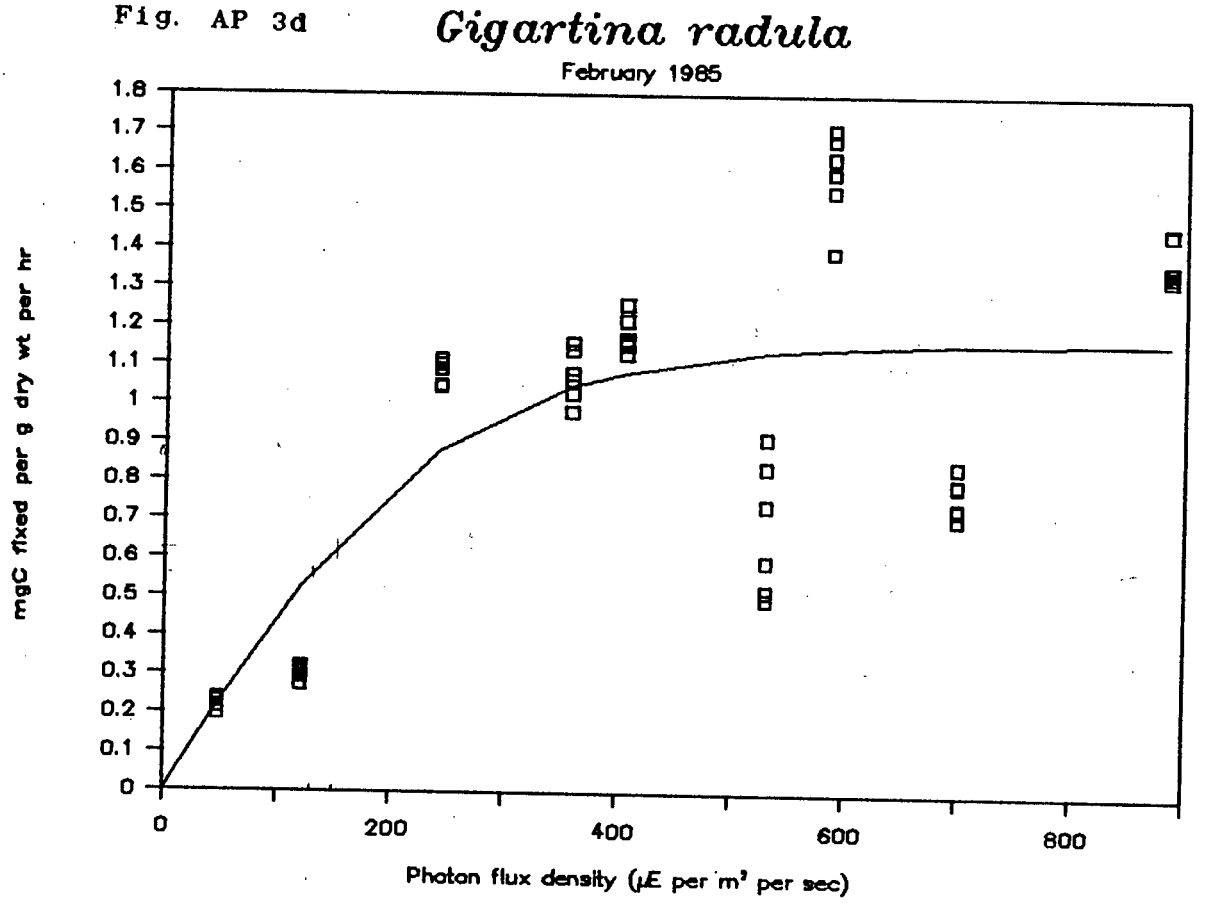


Fig. AP 3e *Gigartina radula*

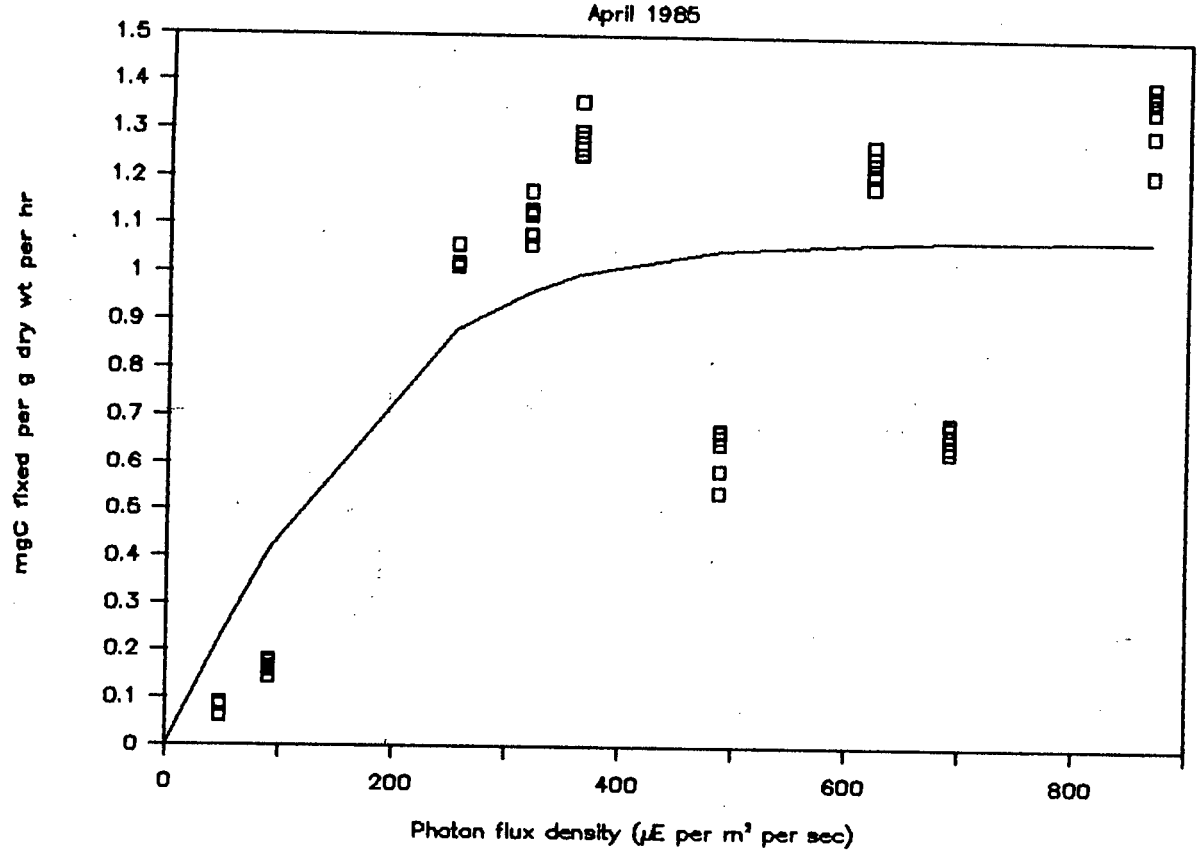


Fig. AP 3f *Gigartina radula*

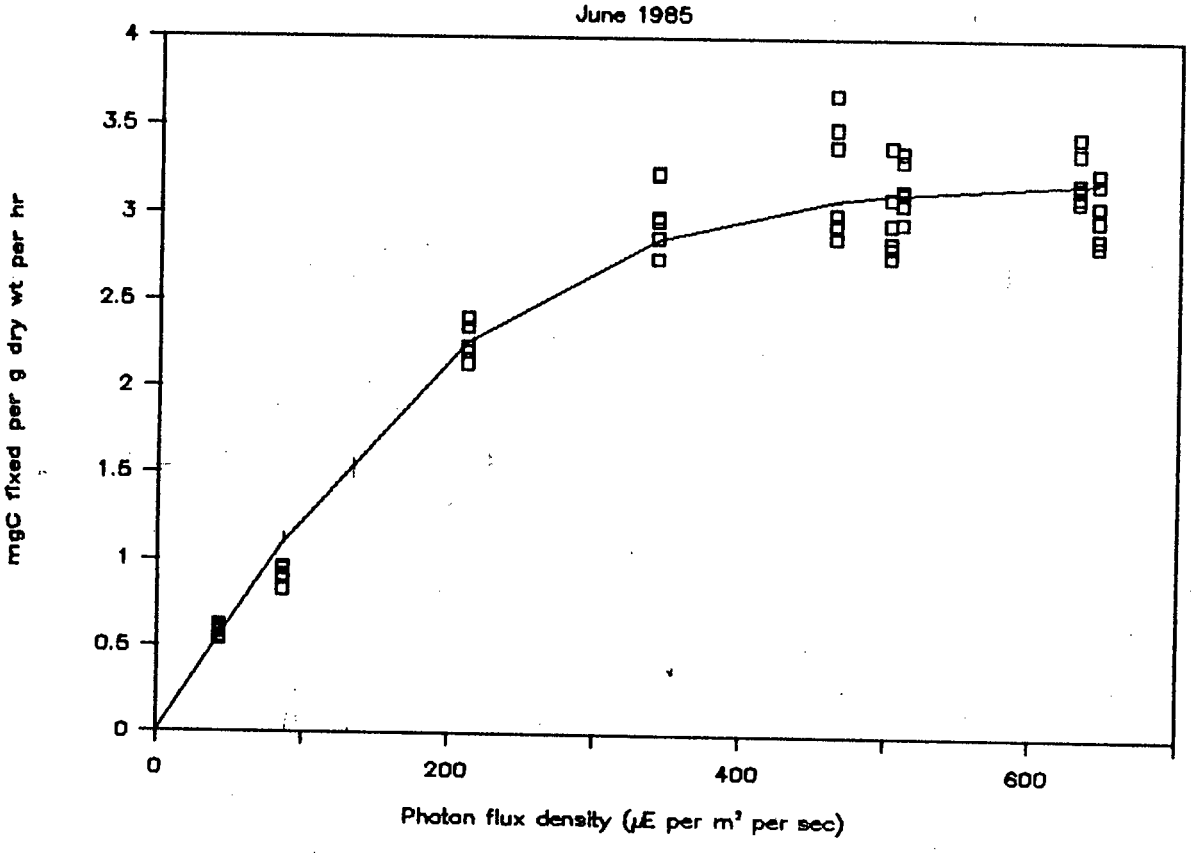


Fig. AP 3g *Gigartina radula*

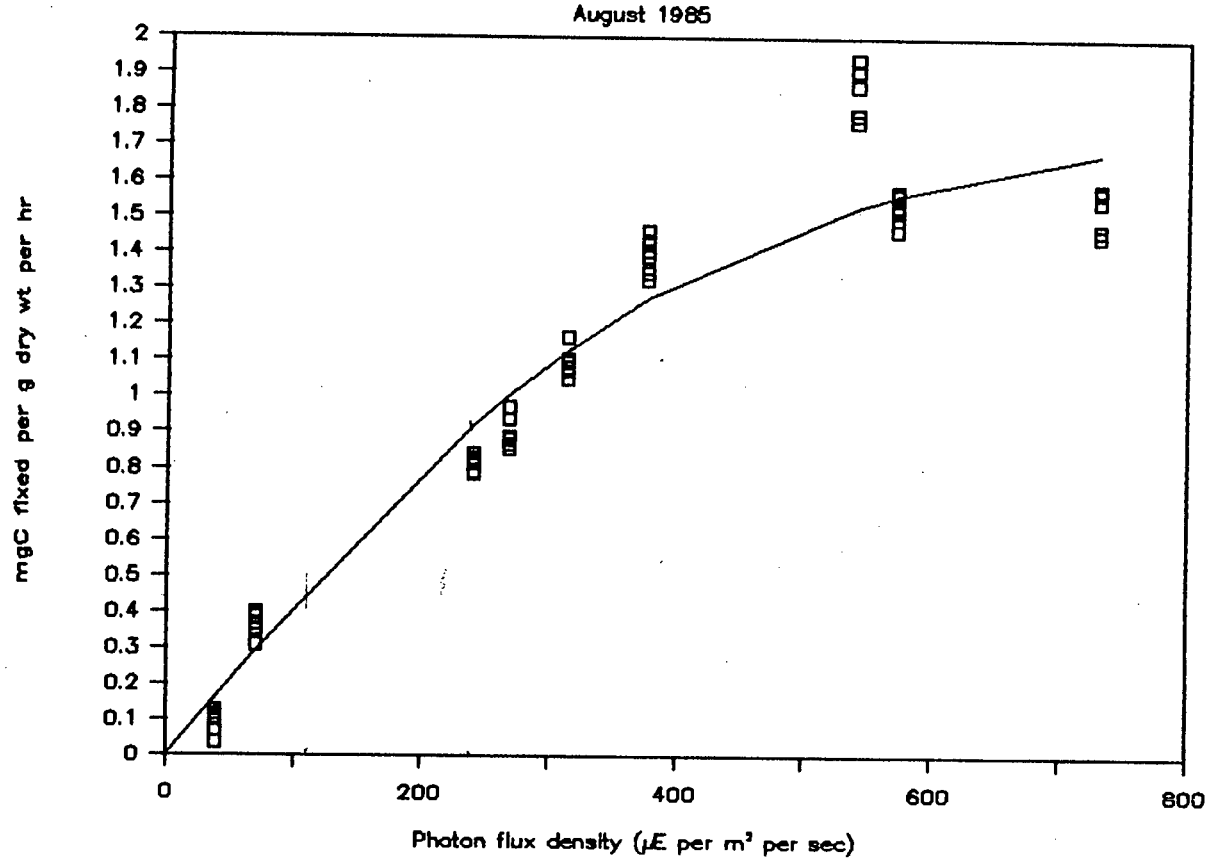


Fig. AP 3h *Gigartina radula*

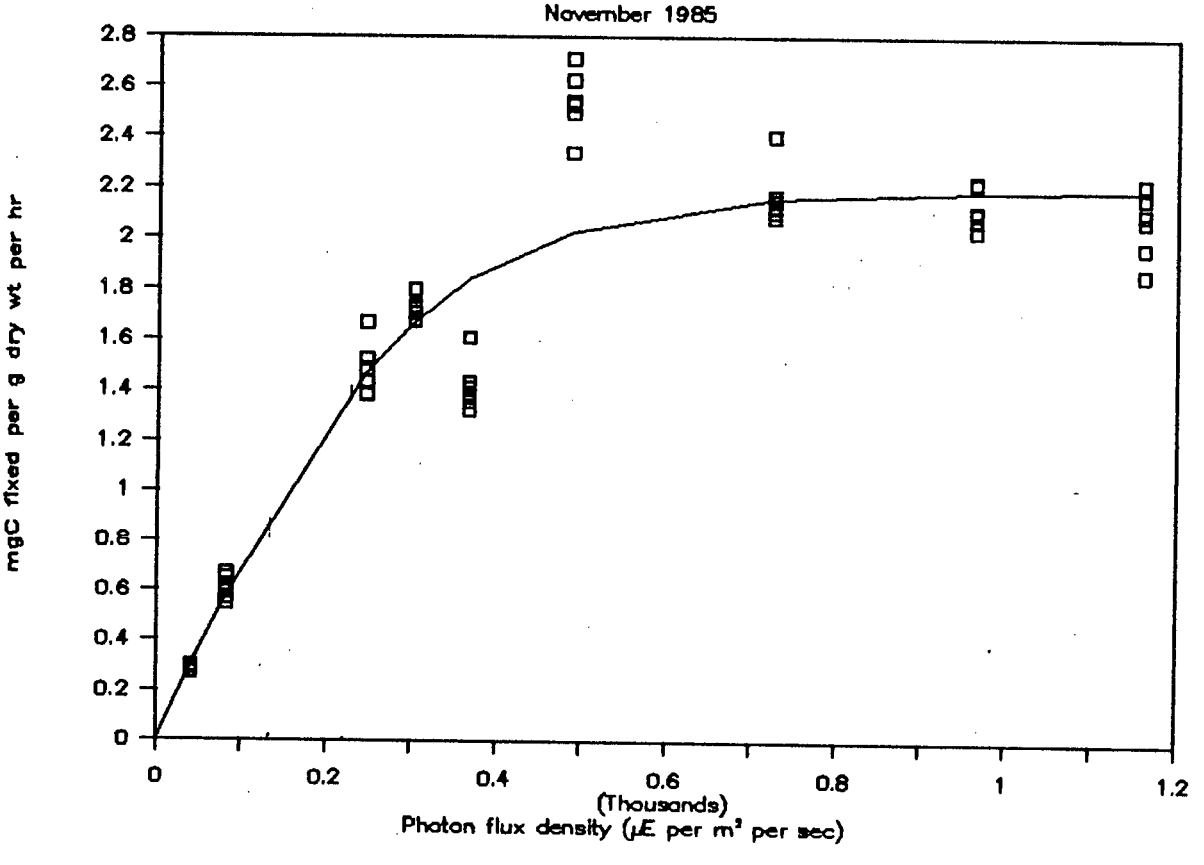


Fig. AP 4a *Splachnidium rugosum*

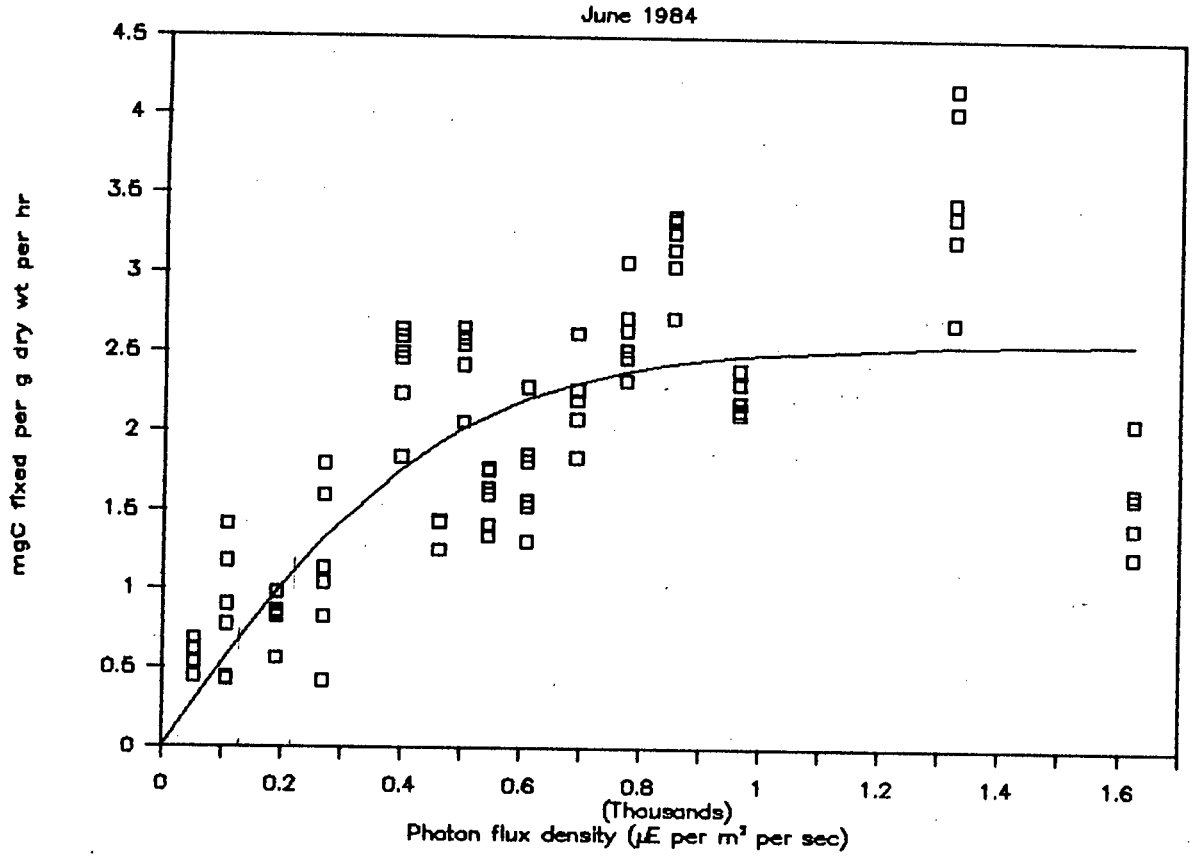


Fig. AP 4b *Splachnidium rugosum*

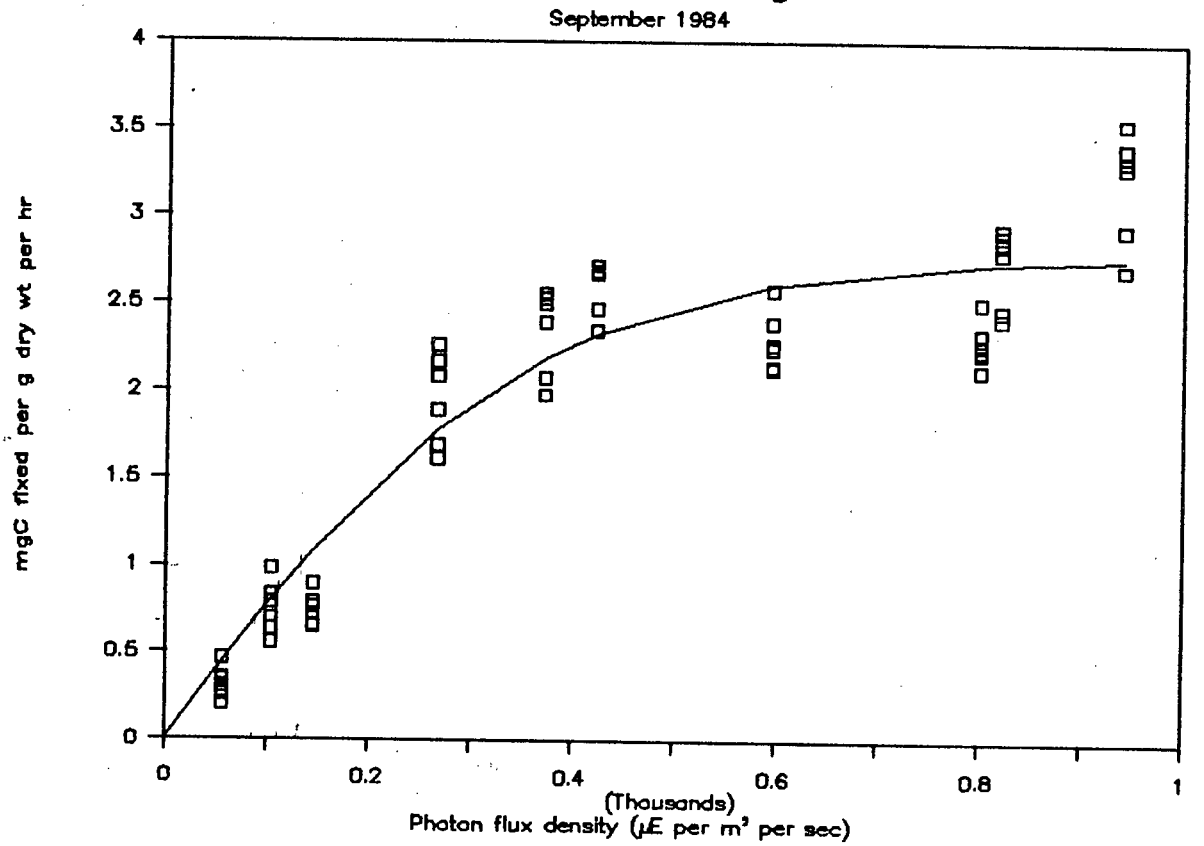


Fig. AP 4c *Splachnidium rugosum*

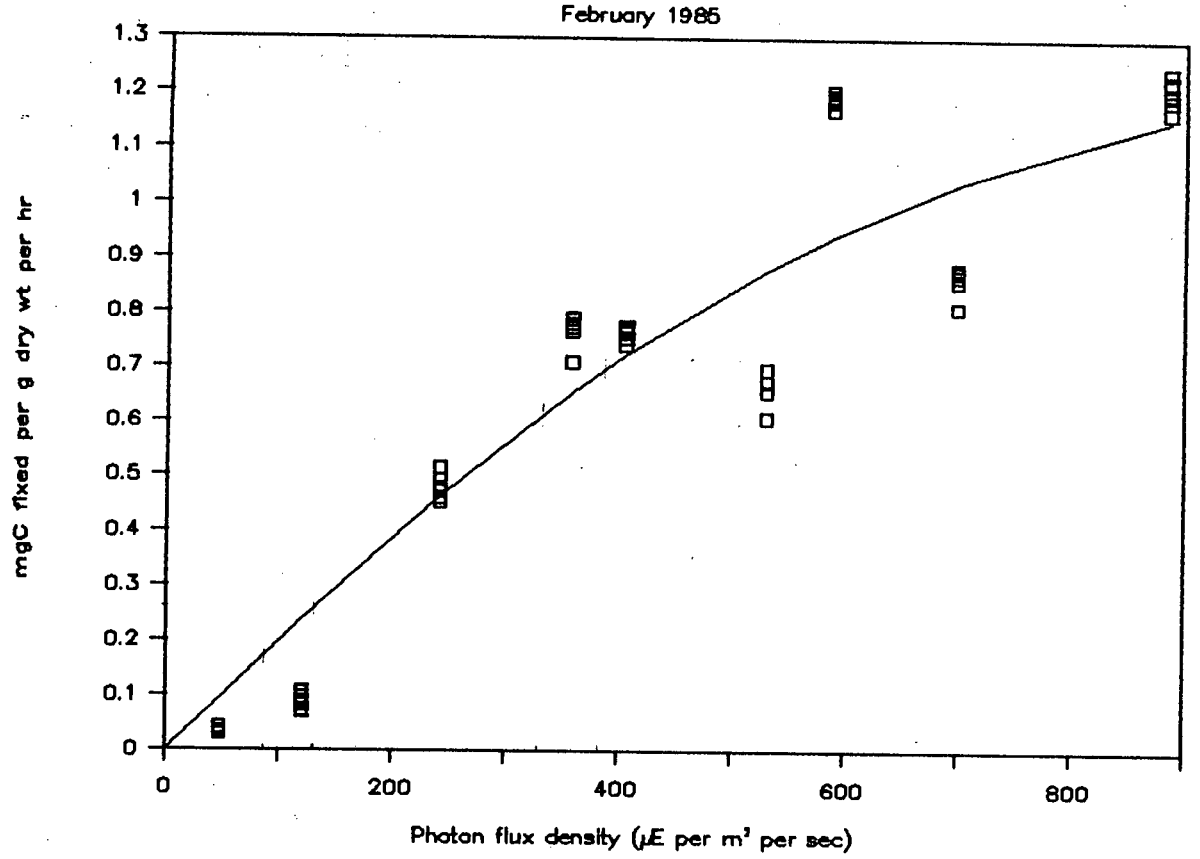


Fig. AP 4d *Splachnidium rugosum*

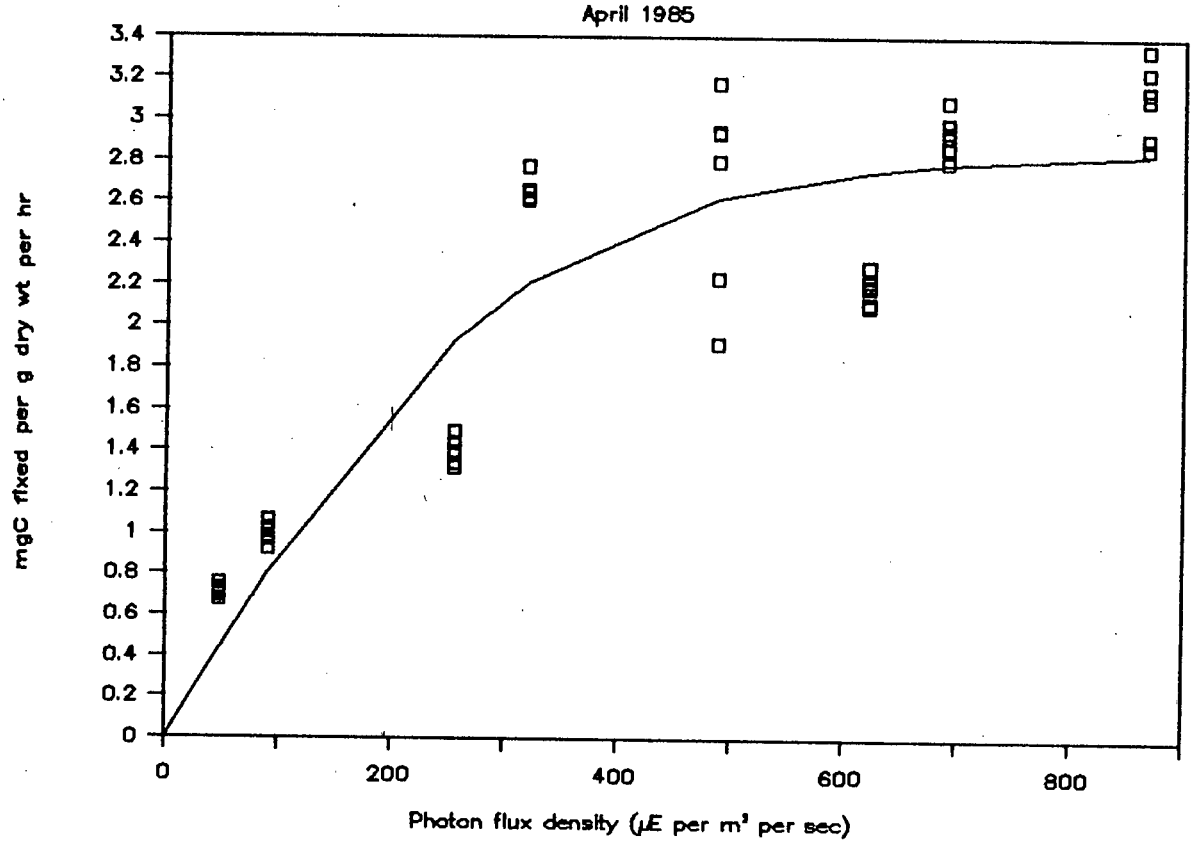


Fig. AP 4e *Splachnidium rugosum*

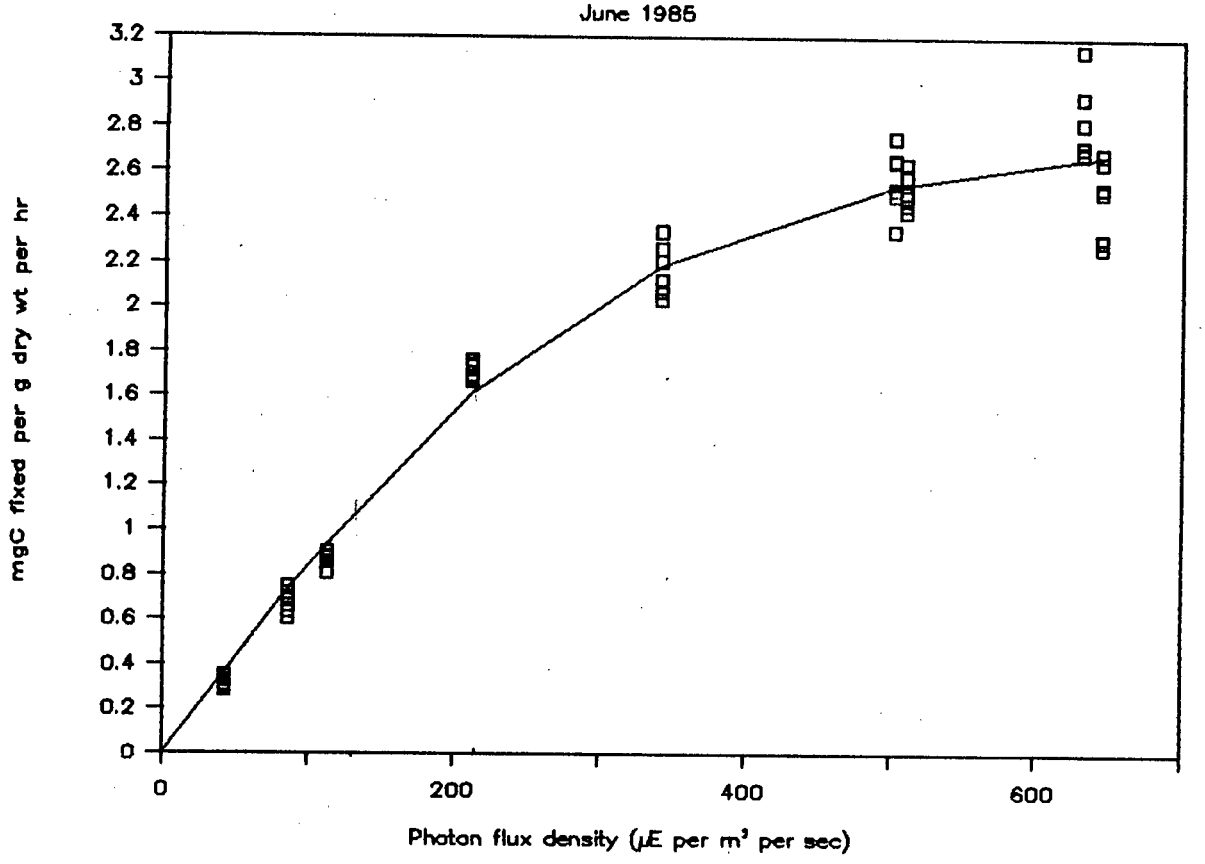


Fig. AP 4f *Splachnidium rugosum*

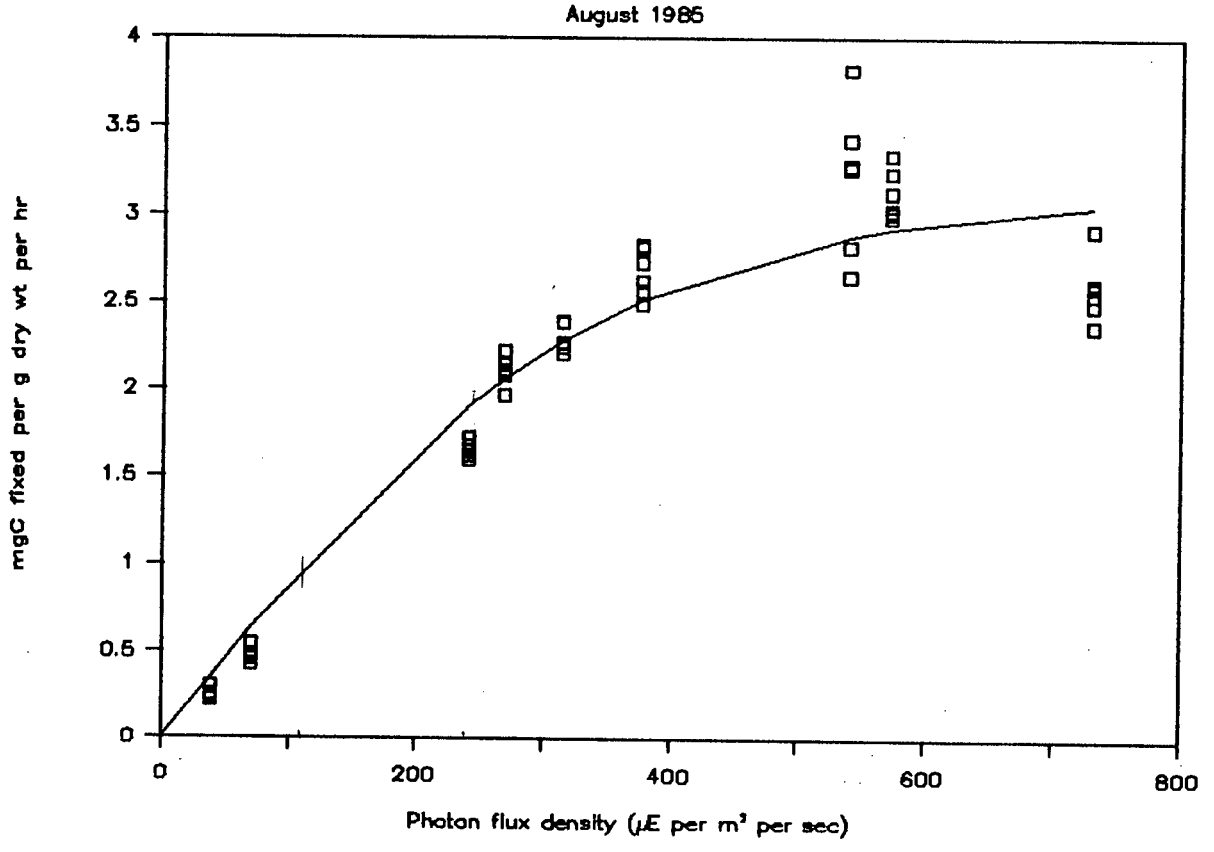


Fig. AP 4g *Splachnidium rugosum*

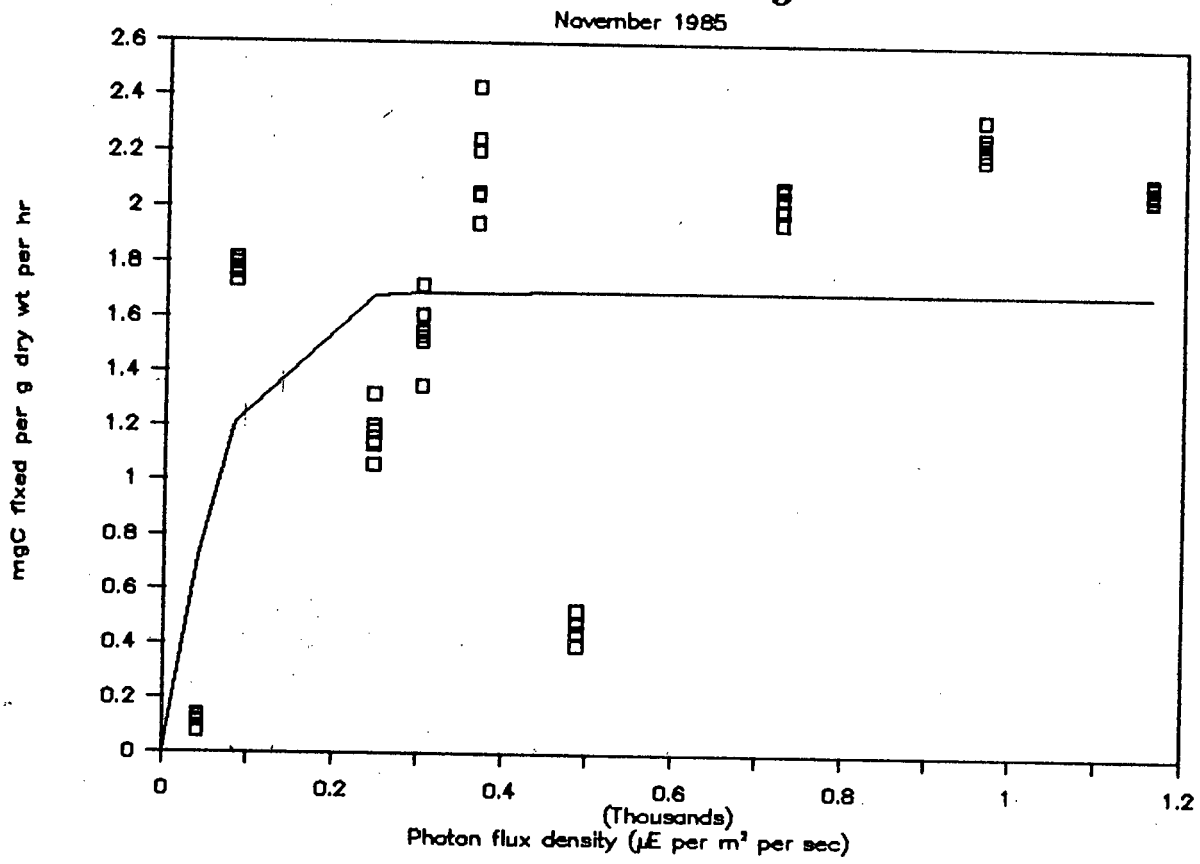


Fig. AP 5a *Bifurcaria brassicaeformis*

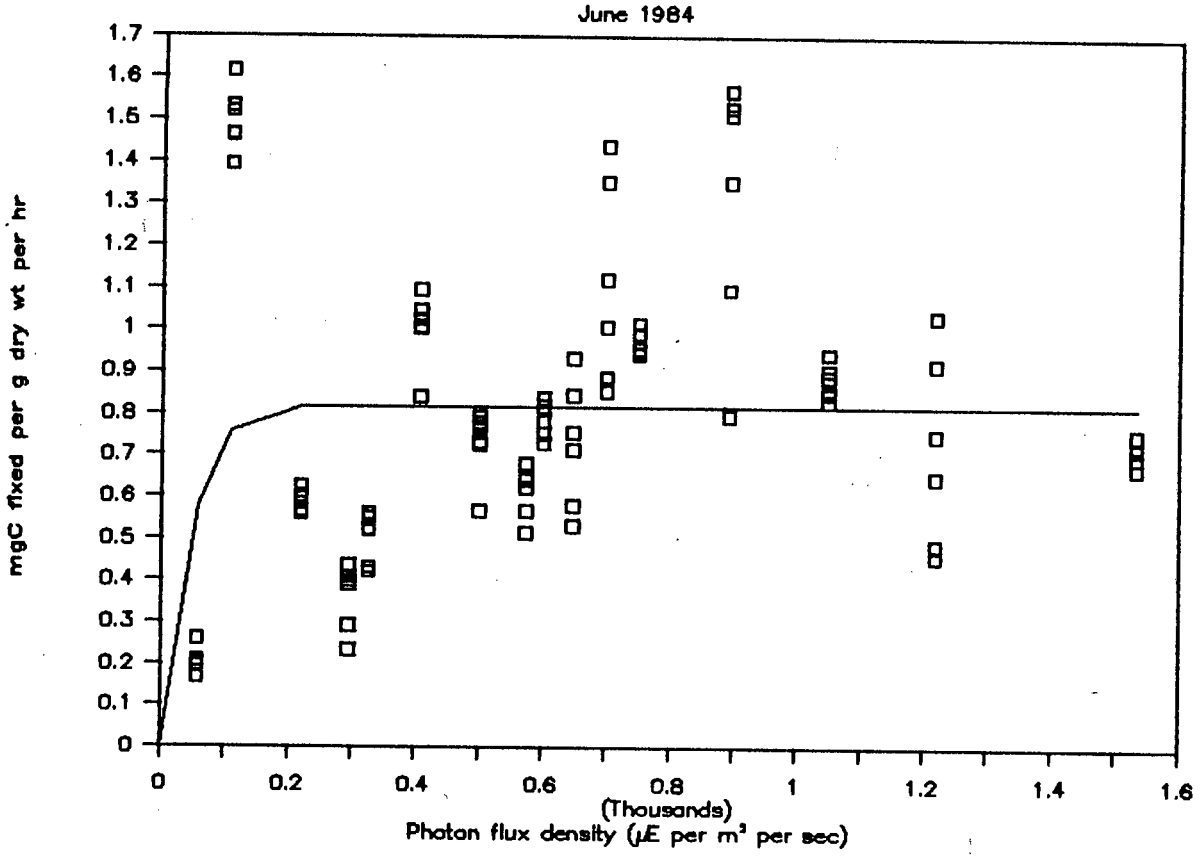


Fig. AP 5b *Bifurcaria brassicaeformis*

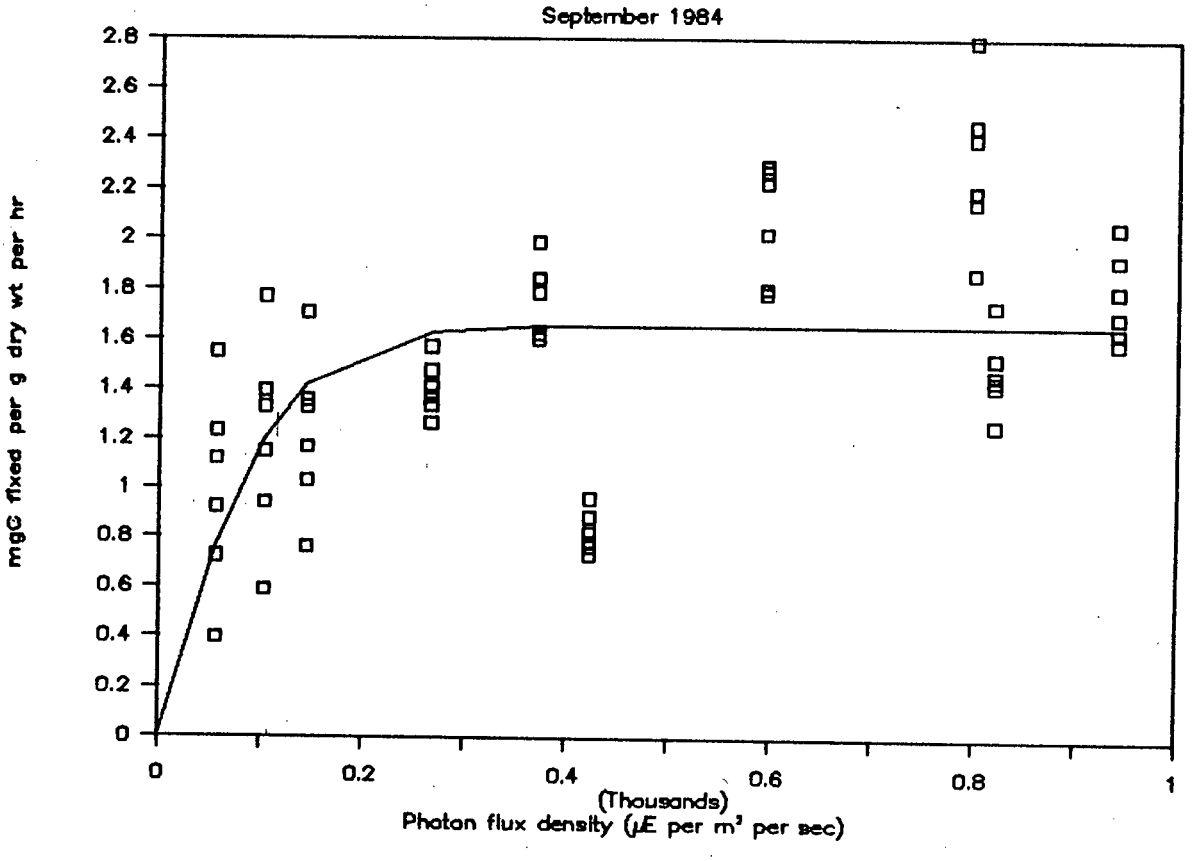


Fig. AP 5c *Bifurcaria brassicaeformis*

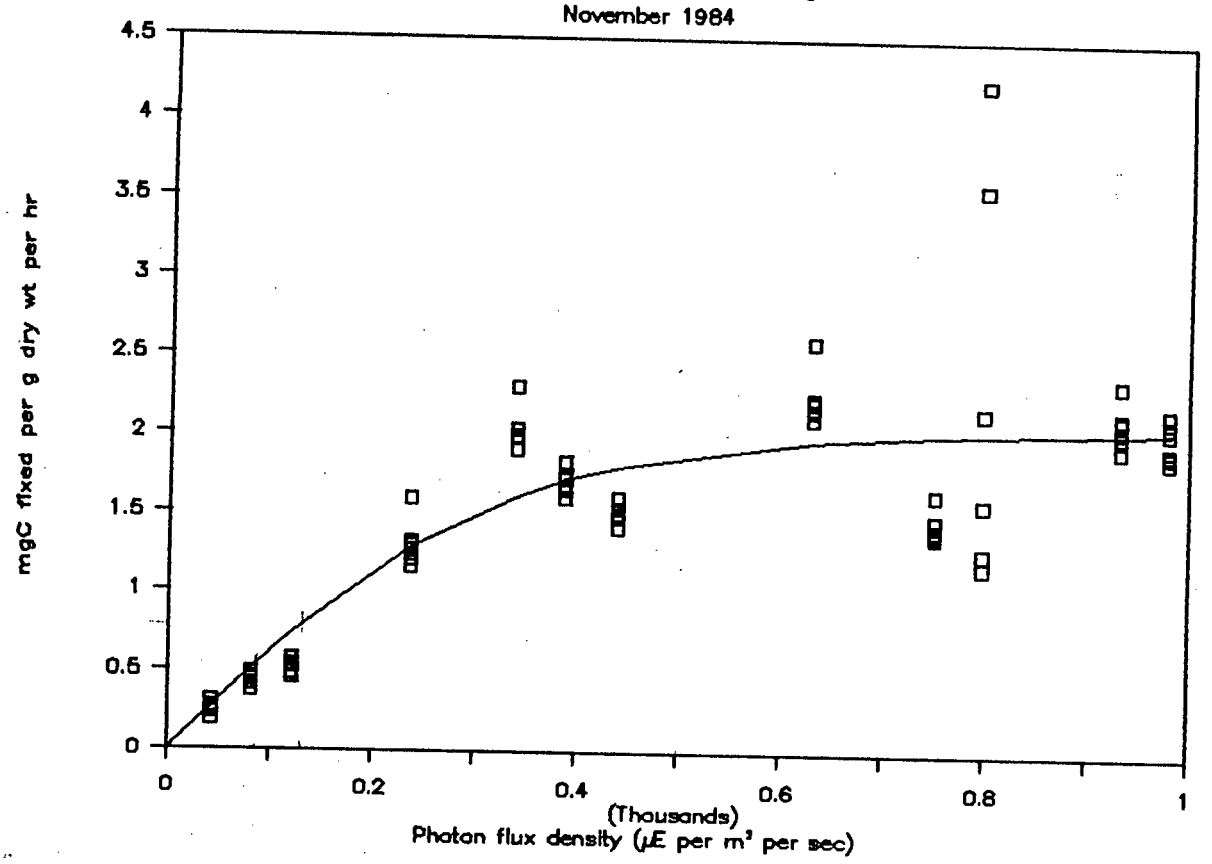


Fig. AP 5d *Bifurcaria brassicaeformis*

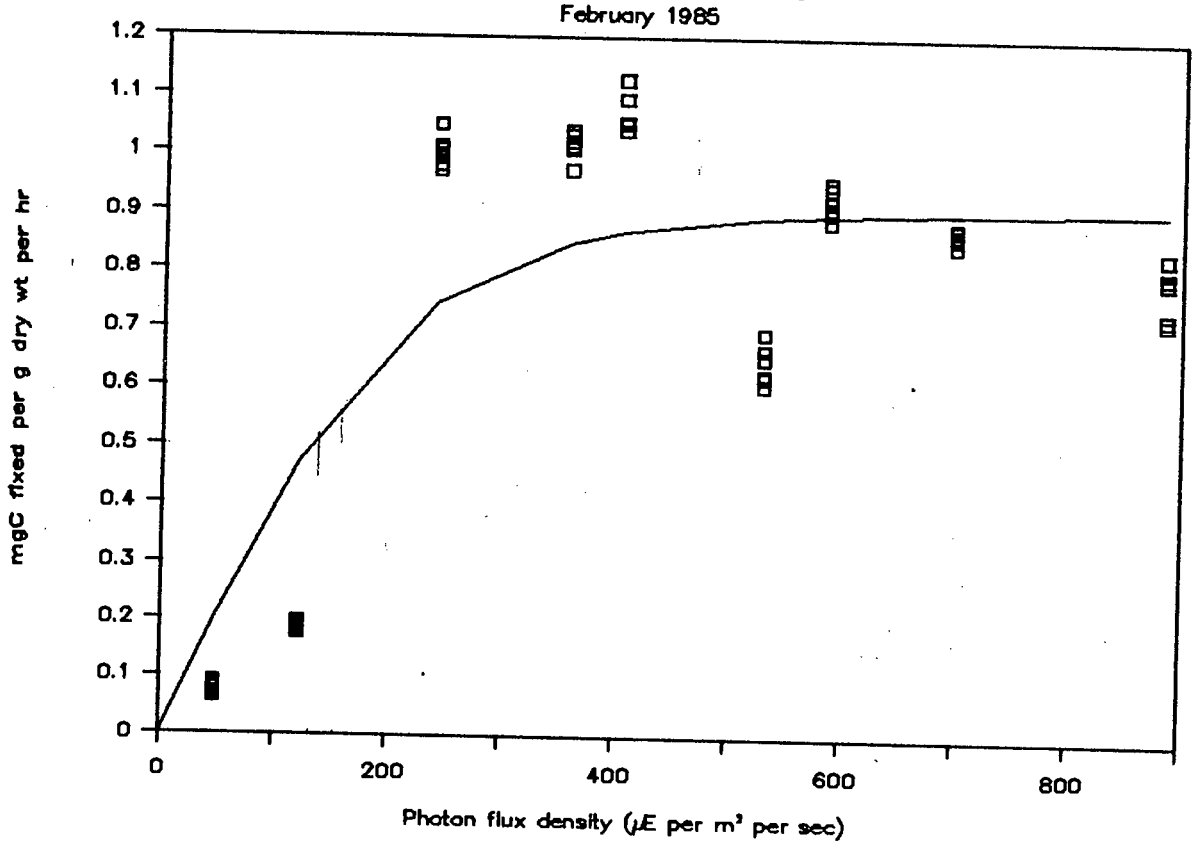


Fig. AP 5e *Bifurcaria brassicaeformis*

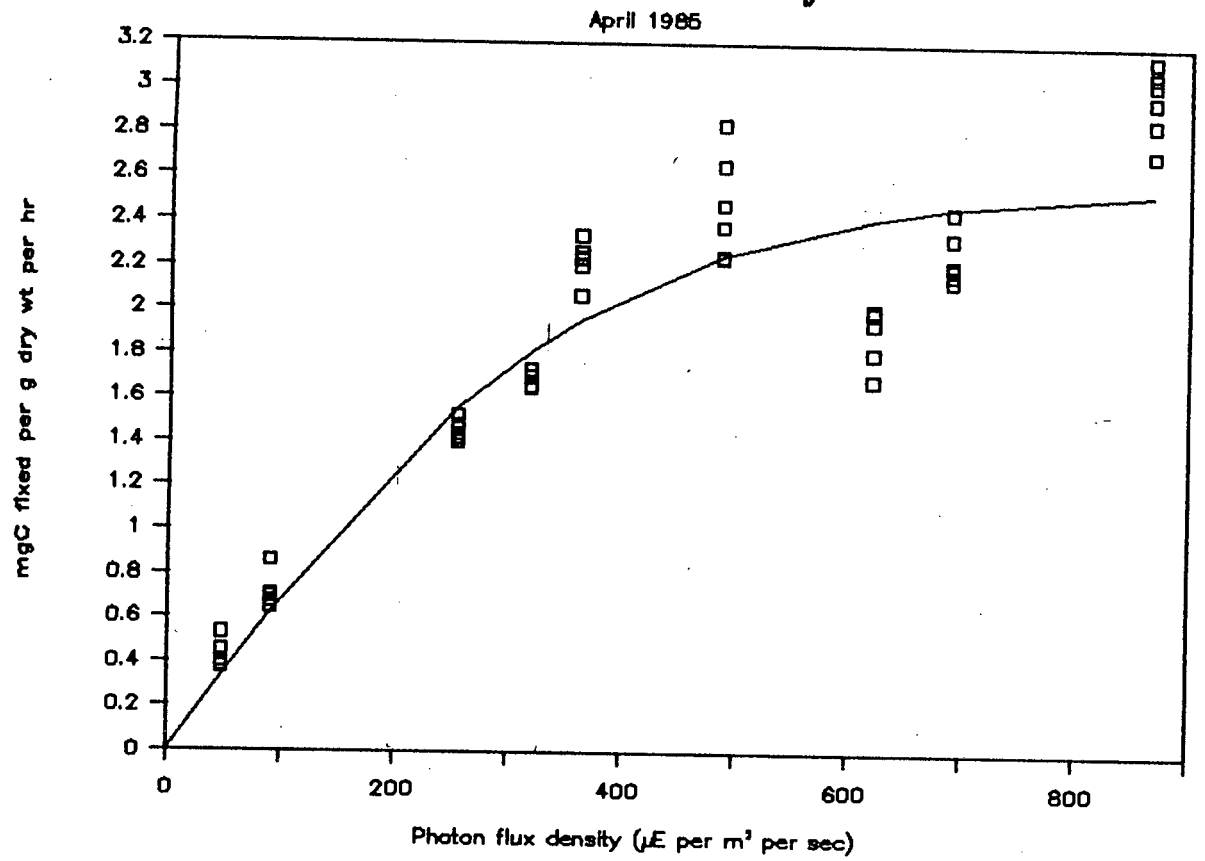


Fig. AP 5f *Bifurcaria brassicaeformis*

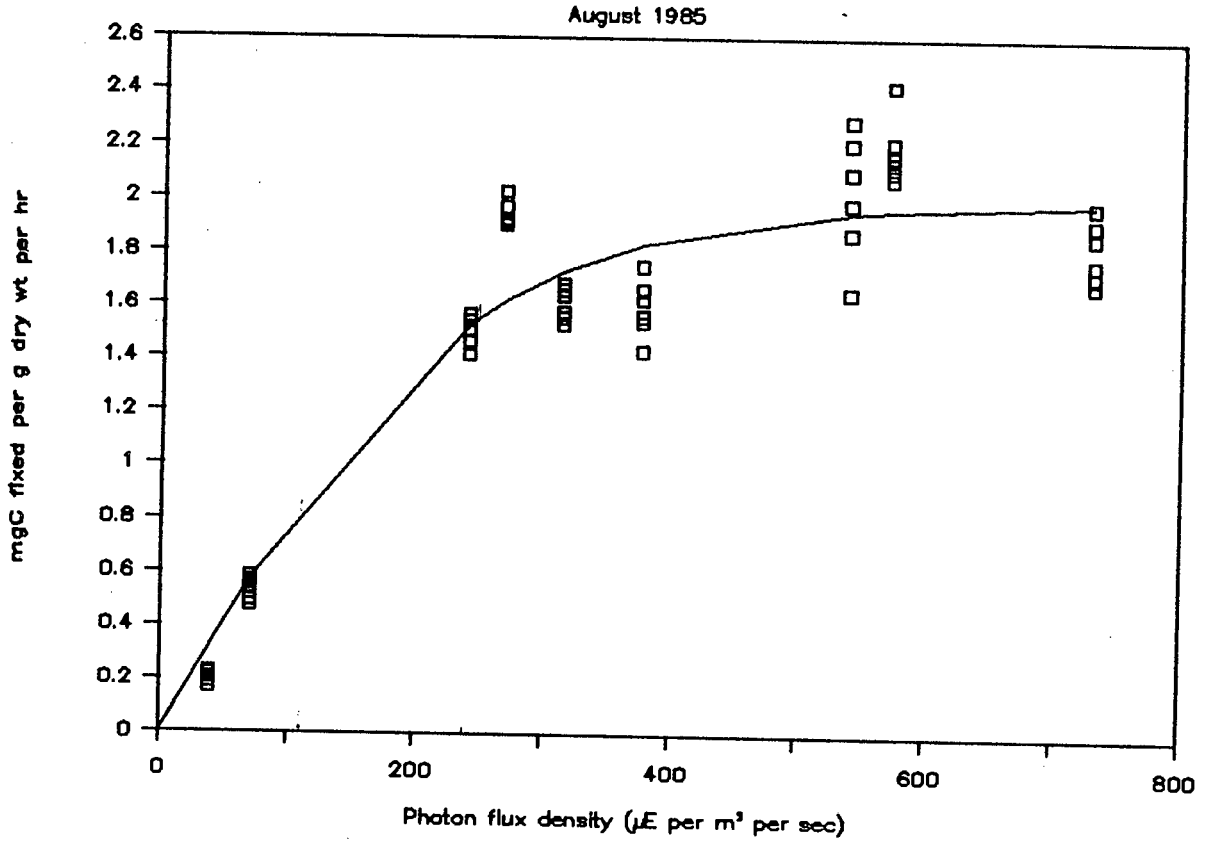
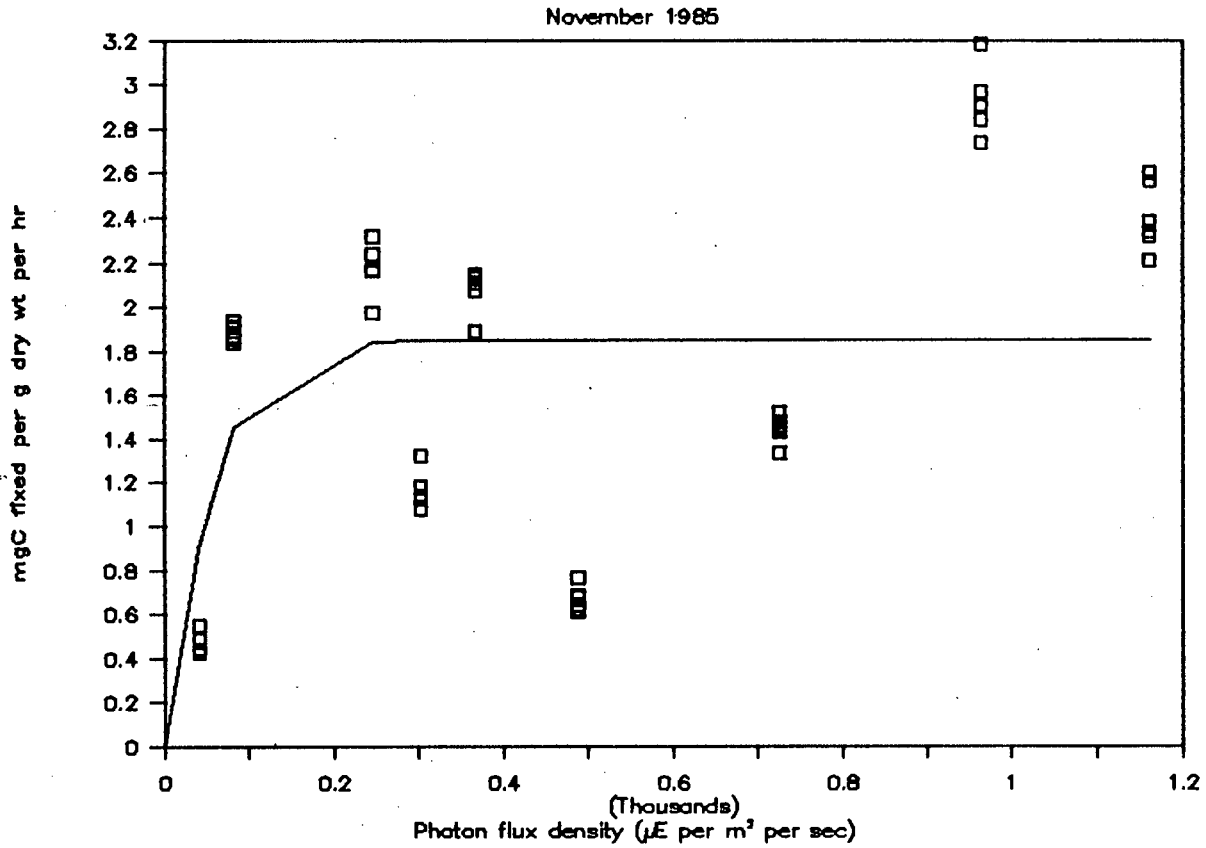


Fig. AP 5g *Bifurcaria brassicaeformis*



APPENDIX IV: SEASONAL PHOTOSYNTHETIC LIGHT CURVES FOR SUBTIDAL SEAWEEDS

This appendix contains the photosynthetic light curves (P-I curves) observed in the three subtidal seaweeds investigated.

The figures are as follows:

Fig. AP 6a, b: Summer and winter photosynthetic light curves for *Botryocarpa prolifera*, mg C fixed per g dry wt per hr versus irradiance ($\mu\epsilon . m^{-2} . sec^{-2}$). Fig. AP 6a = July, 1984; fig AP 6b = January, 1985.

Fig. AP 7a, b: Summer and winter photosynthetic light curves for *Gigartina radula*, mg C fixed per g dry wt per hr versus irradiance ($\mu\epsilon . m^{-2} . sec^{-2}$). Fig. AP 7a = July, 1984; fig AP 7b = January, 1985.

Fig. AP 8a, b: Summer and winter photosynthetic light curves for *Epymenia obtusa*, mg C fixed per g dry wt per hr versus irradiance ($\mu\epsilon . m^{-2} . sec^{-2}$). Fig. AP 8a = July, 1984; fig AP 8b = January, 1985.

Fig. AP 6a *Botryocarpa prolifera*

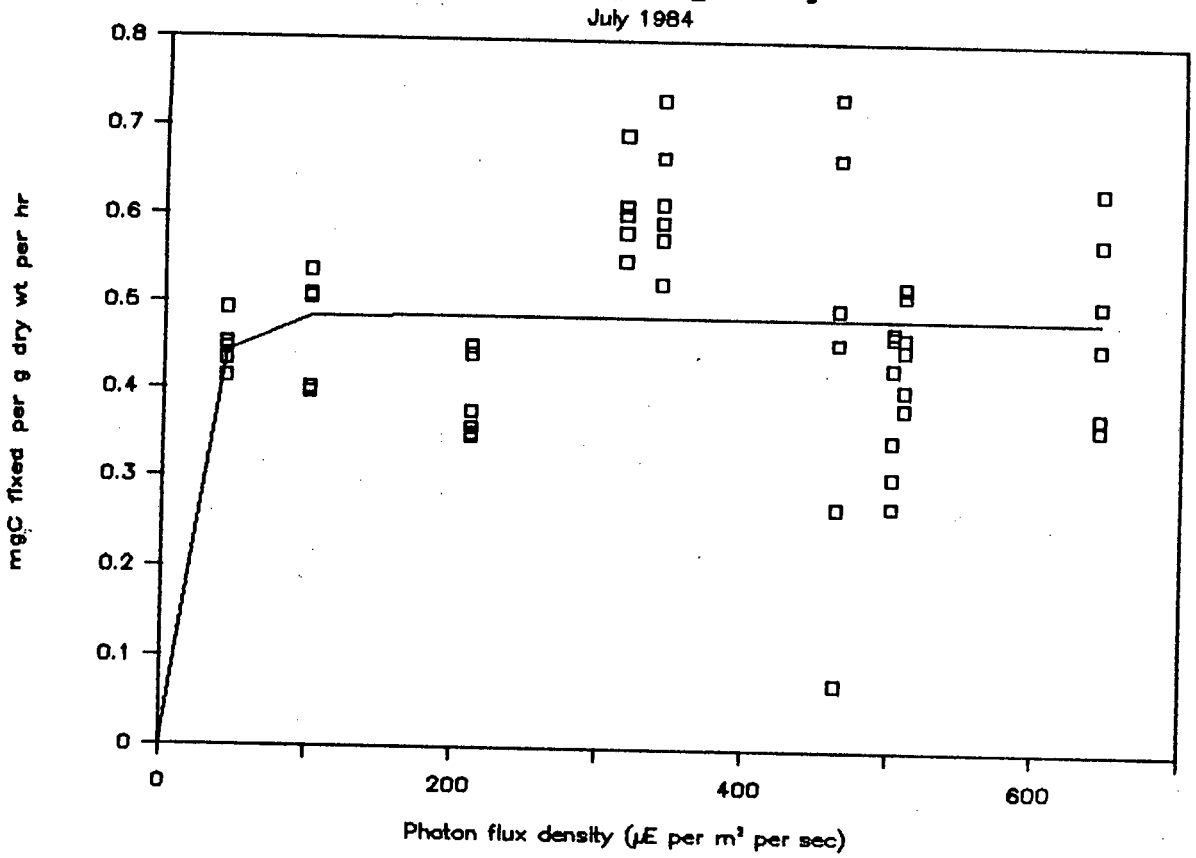


Fig. AP 6b *Botryocarpa prolifera*

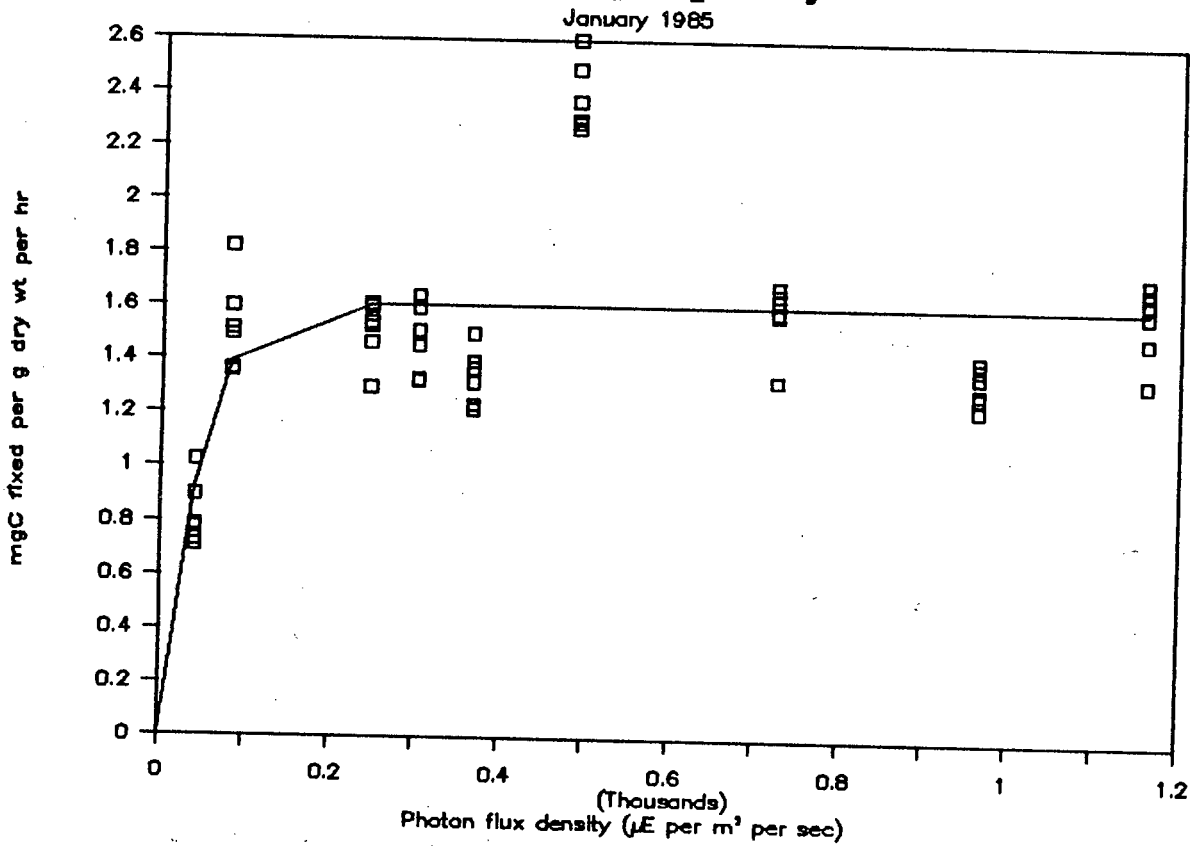


Fig. AP 7a *Gigartina radula*

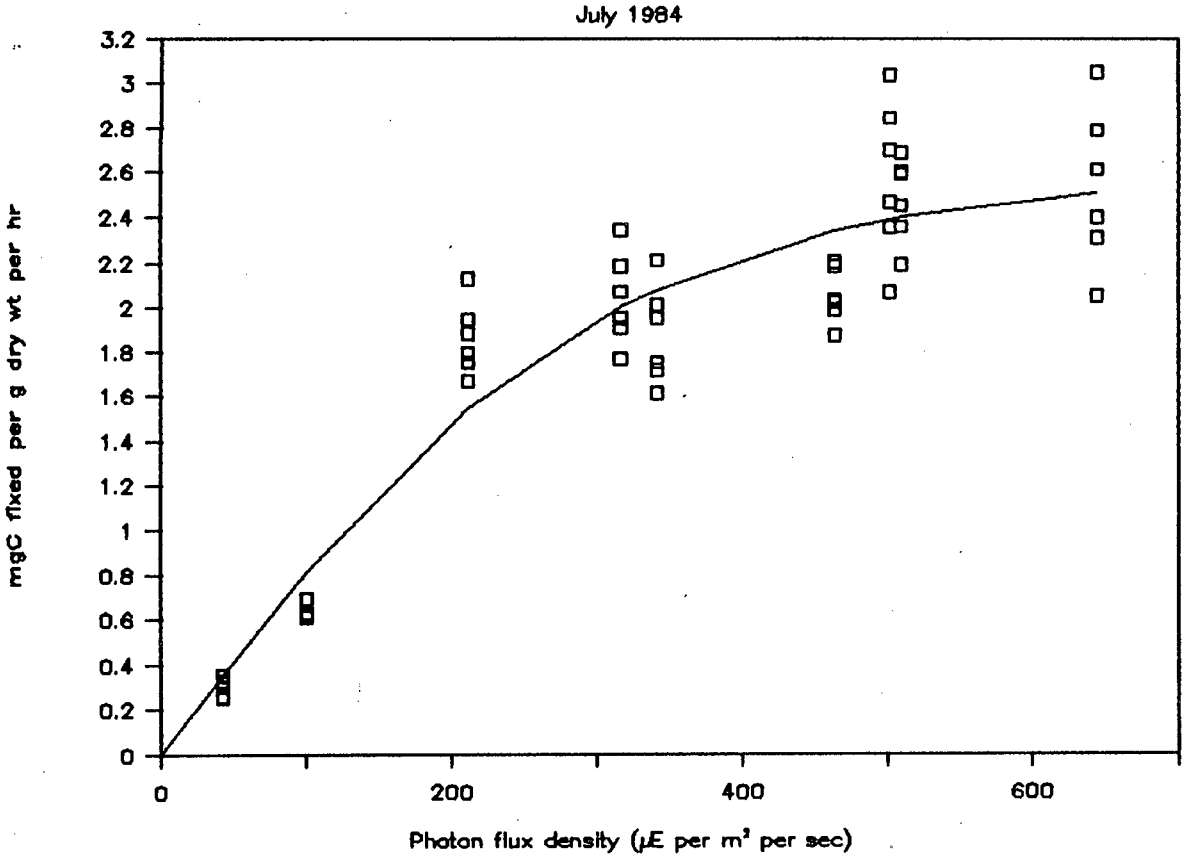


Fig. AP 7b *Gigartina radula*

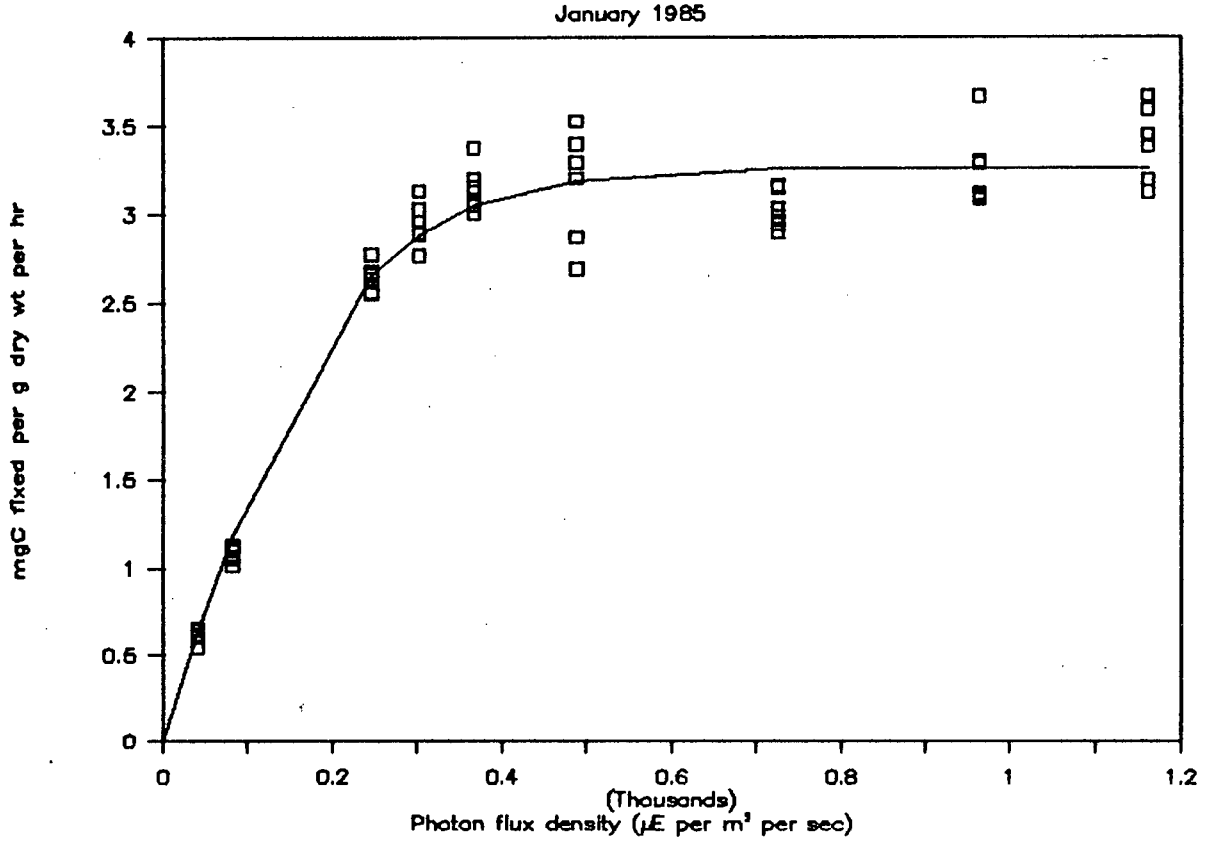


Fig. AP 8a

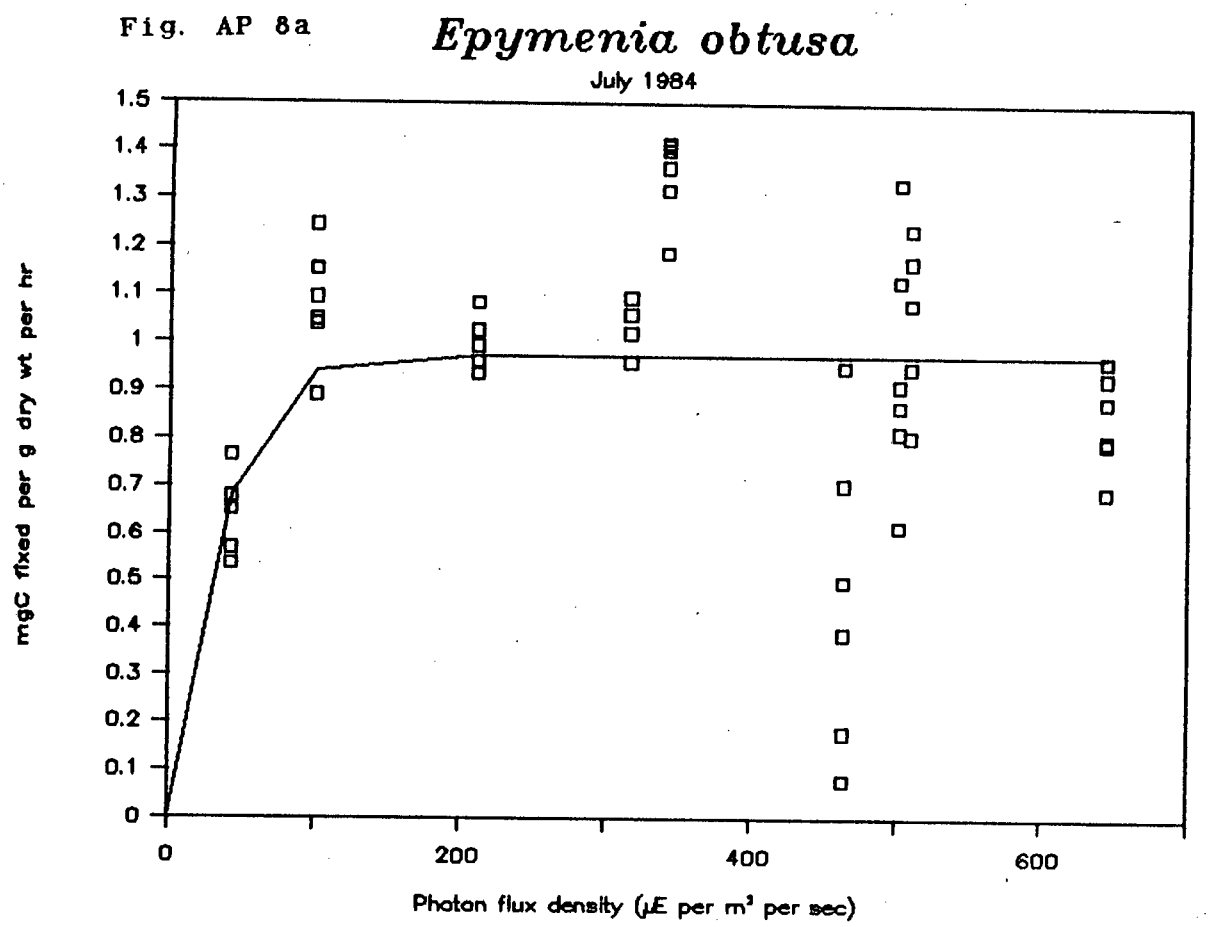
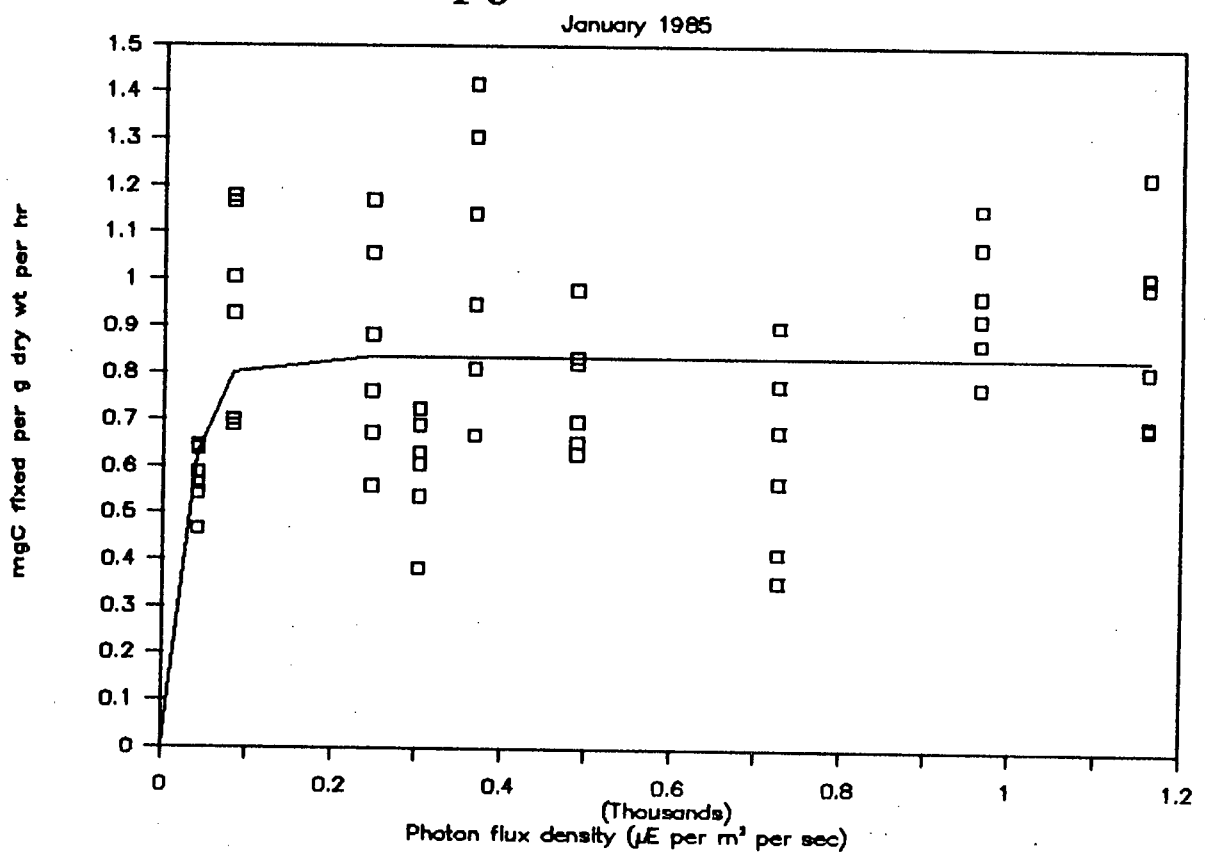


Fig. AP 8b



APPENDIX V: CALCULATIONS OF TOTAL ANNUAL PRIMARY PRODUCTION

1. Intertidal algae - Submersed photosynthesis

a). *Porphyra capensis*

January: Using photosynthesis data from the closest month (February 1985), P_{max} = 3.11mg C fixed per g dw per hr, I_k = 218 $\mu\epsilon.m^{-2}.sec^{-1}$. From the January light data this species will be photosynthetically light-saturated from 6a.m. to 7p.m. (appendix VI), = 13 hrs x 3.11 = 40.43mg C fixed. From 5a.m. to 6a.m. and 7p.m. to 8.pm. at an average irradiance of 152$\mu\epsilon.m^{-2}.sec^{-1}$ (appendix VI), this species will produce 1.85mg C.g $dw^{-1}.hr^{-1}$, which totals 3.70mg C fixed during this period. The total net photosynthesis for the daylight period will therefore be 40.43 + 3.70 = 44.13mg C. This will yield a net production figure of 31 x 44.13 = 1368.03mg C.g dw^{-1} in January. Using a respiration rate of 10.4% of P_{max}, the average respiration rate for this species is 0.32mg C respired g $dw^{-1}.hr^{-1}$. Therefore respiration during the day = 15 x 0.32 = 4.80mg C respired.g dw^{-1}, and respiration at night = 9 x 0.32 = 2.88mg C respired.g dw^{-1}. Therefore total January daytime respiration = 4.80 x 31 = 148.80mg C respired.g dw^{-1}, and total January night time respiration = 2.88 x 31 = 89.28mg C respired.g dw^{-1}. Since photorespiration = 0.92 x the respiration rate, the photorespiration rate will be 0.92 x 0.32 = 0.29mg C respired.g dw^{-1}. The daily amount of photorespiration will therefore be 15 x 0.29 = 4.42mg C respired.g dw^{-1}. The total photorespiration for January will be 4.42 x 31 = 136.90mg C respired.g dw^{-1}. The gross production for *Porphyra capensis* in January will therefore be net production + daytime

respiration - night time respiration + photorespiration = 1368.03 + 148.80 - 89.28 + 136.90 = 1564.45mg C fixed.g dw^{-1}.

February: P_{max} = 3.11mg C fixed.g $dw^{-1}.hr^{-1}$ at 218$\mu E.m^{-2}.sec^{-1}$ (February 1985 data). Light saturated for 13 hours per day, unsaturated for nil hours per day. Gross production is 1267.86mg C fixed.g dw^{-1}. Net production is 1142.15mg C fixed.g dw^{-1}.

March: P_{max} = 2.25mg C fixed.g $dw^{-1}.hr^{-1}$ at 131$\mu E.m^{-2}.sec^{-1}$ (April 1985 data). Light saturated for 13 hours per day, unsaturated for nil hours per day. Gross production is 1005.64mg C fixed.g dw^{-1}. Net production is 906.75mg C fixed.g dw^{-1}.

April: P_{max} = 2.25mg C fixed.g $dw^{-1}.hr^{-1}$ at 131$\mu E.m^{-2}.sec^{-1}$ (April 1985 data). Light saturated for 11 hours per day, unsaturated for nil hours per day. Gross production is 798.00mg C fixed.g dw^{-1}. Net production is 742.50mg C fixed.g dw^{-1}.

May: P_{max} = 4.72mg C fixed.g $dw^{-1}.hr^{-1}$ at 363$\mu E.m^{-2}.sec^{-1}$ (average June 1984 & June 1985 data). Light saturated for 9 hours per day, unsaturated for two hours per day. Gross production is 1563.95mg C fixed.g dw^{-1}. Net production is 1440.88mg C fixed.g dw^{-1}.

June: P_{max} = 4.72mg C fixed.g $dw^{-1}.hr^{-1}$ at 363$\mu E.m^{-2}.sec^{-1}$ (average June 1984 & June 1985 data). Light saturated for 9 hours per day, unsaturated for two hours per day. Gross production is 1470.90mg C fixed.g dw^{-1}. Net production is 1351.80mg C fixed.g dw^{-1}.

July: P_{max} = 4.72mg C fixed.g $dw^{-1}.hr^{-1}$ at 363$\mu E.m^{-2}.sec^{-1}$ (August 1985 data). Light saturated for 9 hours per day,

unsaturated for two hours per day. Gross production is 1514.97mg C fixed.g dw^{-1}. Net production is 1391.90mg C fixed.g dw^{-1}.

August: P_{max} = 4.72mg C fixed.g $dw^{-1}.hr^{-1}$ at 363$\mu E.m^{-2}.sec^{-1}$ (August 1985 data). Light saturated for 9 hours per day, unsaturated for two hours per day. Gross production is 1625.95mg C fixed.g dw^{-1}. Net production is 1502.88mg C fixed.g dw^{-1}.

September: P_{max} = 6.77mg C fixed.g $dw^{-1}.hr^{-1}$ at 220$\mu E.m^{-2}.sec^{-1}$ (September 1984 data). Light saturated for 11 hours per day, unsaturated for two hours per day. Gross production is 2713.50mg C fixed.g dw^{-1}. Net production is 2421.90mg C fixed.g dw^{-1}.

October: P_{max} = 2.68mg C fixed.g $dw^{-1}.hr^{-1}$ at 90$\mu E.m^{-2}.sec^{-1}$ (October 1985 data). Light saturated for 13 hours per day, unsaturated for nil hours per day. Gross production is 1202.18mg C fixed.g dw^{-1}. Net production is 1080.04mg C fixed.g dw^{-1}.

November: P_{max} = 4.19mg C fixed.g $dw^{-1}.hr^{-1}$ at 176$\mu E.m^{-2}.sec^{-1}$ (average of September 1984, February 1985 & October 1985 data). Light saturated for 13 hours per day, unsaturated for two hours per day. Gross production is 2006.10mg C fixed.g dw^{-1}. Net production is 1746.90mg C fixed.g dw^{-1}.

December: P_{max} = 4.19mg C fixed.g $dw^{-1}.hr^{-1}$ at 176$\mu E.m^{-2}.sec^{-1}$ (average of September 1984, February 1985 & October 1985 data). Light saturated for 13 hours per day, unsaturated for two hours per day. Gross production is 2046.93mg C fixed.g dw^{-1}. Net production is 1779.09mg C fixed.g dw^{-1}.

Annual gross production of submersed *Porphyra capensis* is 18780.43mg C fixed.g $dw^{-1}.yr^{-1}$. Annual net production of submersed *Porphyra capensis* is 16874.82mg C fixed.g dw^{-1}. Now since *Porphyra capensis* is exposed for 78.85% of the time, its actual submersed gross photosynthesis will be 0.2115 x the calculated rate. Therefore monthly gross production is: Jan 330.88; Feb 268.15; Mar 212.69; Apr 168.78; May 330.78; Jun 311.10; Jul 320.42; Aug 343.89; Sep 573.91; Oct 254.26; Nov 424.29; Dec 432.93. Annual gross submersed production = 3972.06mg C fixed.g dw^{-1}.

b). ***Ulva rigida***

January: P_{max} = 2.91mg C fixed.g $dw^{-1}.hr^{-1}$ at 298$\mu\epsilon.m^{-2}.sec^{-1}$ (February 1985 data). Light saturated for 13 hours per day, unsaturated for two hours per day. Gross production is 1406.16mg C fixed.g dw^{-1}. Net production is 1238.23mg C fixed.g dw^{-1}.

February: P_{max} = 2.91mg C fixed.g $dw^{-1}.hr^{-1}$ at 298$\mu\epsilon.m^{-2}.sec^{-1}$ (February 1985 data). Light saturated for 13 hours per day, unsaturated for nil hours per day. Gross production is 1218.71mg C fixed.g dw^{-1}. Net production is 1068.70mg C fixed.g dw^{-1}.

March: P_{max} = 3.68mg C fixed.g $dw^{-1}.hr^{-1}$ at 122$\mu\epsilon.m^{-2}.sec^{-1}$ (April 1985 data). Light saturated for 13 hours per day, unsaturated for nil hours per day. Gross production is 1694.77mg C fixed.g dw^{-1}. Net production is 1483.04mg C fixed.g dw^{-1}.

April: P_{max} = 3.68mg C fixed.g $dw^{-1}.hr^{-1}$ at 122$\mu\epsilon.m^{-2}.sec^{-1}$ (April 1985 data). Light saturated for 11 hours per day, unsaturated for nil hours per day. Gross production is

1333.50mg C fixed.g dw^{-1}. Net production is 1214.40mg C fixed.g dw^{-1}.

May: P_{max} = 4.21mg C fixed.g $dw^{-1}.hr^{-1}$ at 178$\mu E.m^{-2}.sec^{-1}$ (average June 1984 & June 1985 data). Light saturated for 9 hours per day, unsaturated for two hours per day. Gross production is 1497.61mg C fixed.g dw^{-1}. Net production is 1355.01mg C fixed.g dw^{-1}.

June: P_{max} = 4.21mg C fixed.g $dw^{-1}.hr^{-1}$ at 178$\mu E.m^{-2}.sec^{-1}$ (average June 1984 & June 1985 data). Light saturated for 9 hours per day, unsaturated for two hours per day. Gross production is 1394.70mg C fixed.g dw^{-1}. Net production is 1256.70mg C fixed.g dw^{-1}.

July: P_{max} = 5.30mg C fixed.g $dw^{-1}.hr^{-1}$ at 103$\mu E.m^{-2}.sec^{-1}$ (August 1985 data). Light saturated for 11 hours per day, unsaturated for nil hours per day. Gross production is 1982.14mg C fixed.g dw^{-1}. Net production is 1807.30mg C fixed.g dw^{-1}.

August: P_{max} = 5.30mg C fixed.g $dw^{-1}.hr^{-1}$ at 103$\mu E.m^{-2}.sec^{-1}$ (August 1985 data). Light saturated for 11 hours per day, unsaturated for nil hours per day. Gross production is 1982.14mg C fixed.g dw^{-1}. Net production is 1807.30mg C fixed.g dw^{-1}.

September: P_{max} = 9.51mg C fixed.g $dw^{-1}.hr^{-1}$ at 92$\mu E.m^{-2}.sec^{-1}$ (September 1984 data). Light saturated for 13 hours per day, unsaturated for nil hours per day. Gross production is 4236.90mg C fixed.g dw^{-1}. Net production is 3708.90mg C fixed.g dw^{-1}.

October: P_{max} = 1.88mg C fixed.g $dw^{-1}.hr^{-1}$ at 53$\mu E.m^{-2}.sec^{-1}$ (October 1985 data). Light saturated for 13 hours per day, unsaturated for nil hours per day. Gross production is

865.83mg C fixed.g dw^{-1}. Net production is 757.64mg C fixed.g dw^{-1}.

November: P_{max} = 4.77mg C fixed.g $dw^{-1}.hr^{-1}$ at 148$\mu\epsilon.m^{-2}.sec^{-1}$ (average of September 1984, February 1985 & October 1985 data). Light saturated for 13 hours per day, unsaturated for two hours per day. Gross production is 2474.10mg C fixed.g dw^{-1}. Net production is 2099.70mg C fixed.g dw^{-1}.

December: P_{max} = 4.77mg C fixed.g $dw^{-1}.hr^{-1}$ at 148$\mu\epsilon.m^{-2}.sec^{-1}$ (average of September 1984, February 1985 & October 1985 data). Light saturated for 13 hours per day, unsaturated for two hours per day. Gross production is 2542.93mg C fixed.g dw^{-1}. Net production is 2156.05mg C fixed.g dw^{-1}.

Annual gross production of submersed *Ulva rigida* is 22629.49mg C fixed.g $dw^{-1}.yr^{-1}$. Annual net production of submersed *Ulva rigida* is 19952.97mg C fixed.g dw^{-1}. Now since *Ulva rigida* is exposed for 51.37% of the time, its actual submersed gross photosynthesis will be 0.4863 x the calculated rate. Therefore monthly gross production is: Jan 683.82; Feb 592.66; Mar 824.17; Apr 648.48; May 728.29; Jun 678.24; Jul 963.91; Aug 963.91; Sep 2060.40; Oct 421.05; Nov 1203.15;Dec 1236.63. Annual gross submersed production = 11004.72mg C fixed.g dw^{-1}.

c). ***Gigartina radula***

January: P_{max} = 1.17mg C fixed.g $dw^{-1}.hr^{-1}$ at 248$\mu\epsilon.m^{-2}.sec^{-1}$ (February 1985 data). Light saturated for 13 hours per day, unsaturated for two hours per day. Gross production is 596.44mg C fixed.g dw^{-1}. Net production is 509.95mg C fixed.g dw^{-1}.

February: P_{max} = 1.17mg C fixed.g $dw^{-1}.hr^{-1}$ at 248$\mu E.m^{-2}.sec^{-1}$ (February 1985 data). Light saturated for 13 hours per day, unsaturated for nil hours per day. Gross production is 485.33mg C fixed.g dw^{-1}. Net production is 429.68mg C fixed.g dw^{-1}.

March: P_{max} = 1.07mg C fixed.g $dw^{-1}.hr^{-1}$ at 222$\mu E.m^{-2}.sec^{-1}$ (April 1985 data). Light saturated for 11 hours per day, unsaturated for two hours per day. Gross production is 465.31mg C fixed.g dw^{-1}. Net production is 408.89mg C fixed.g dw^{-1}.

April: P_{max} = 1.07mg C fixed.g $dw^{-1}.hr^{-1}$ at 222$\mu E.m^{-2}.sec^{-1}$ (April 1985 data). Light saturated for 11 hours per day, unsaturated for nil hours per day. Gross production is 384.90mg C fixed.g dw^{-1}. Net production is 353.10mg C fixed.g dw^{-1}.

May: P_{max} = 2.79mg C fixed.g $dw^{-1}.hr^{-1}$ at 249$\mu E.m^{-2}.sec^{-1}$ (average June 1984 & June 1985 data). Light saturated for 9 hours per day, unsaturated for two hours per day. Gross production is 945.50mg C fixed.g dw^{-1}. Net production 860.87mg C fixed.g dw^{-1}.

June: P_{max} = 2.79mg C fixed.g $dw^{-1}.hr^{-1}$ at 249$\mu E.m^{-2}.sec^{-1}$ (average June 1984 & June 1985 data). Light saturated for 9 hours per day, unsaturated for two hours per day. Gross production is 894.00mg C fixed.g dw^{-1}. Net production 812.10mg C fixed.g dw^{-1}.

July: P_{max} = 1.79mg C fixed.g $dw^{-1}.hr^{-1}$ at 423$\mu E.m^{-2}.sec^{-1}$ (August 1985 data). Light saturated for 9 hours per day, unsaturated for two hours per day. Gross production is 584.11mg C fixed.g dw^{-1}. Net production is 526.69mg C fixed.g dw^{-1}.

August: P_{max} = 1.79mg C fixed.g $dw^{-1}.hr^{-1}$ at 423$\mu\epsilon.m^{-2}.sec^{-1}$ (August 1985 data). Light saturated for 9 hours per day, unsaturated for two hours per day. Gross production is 612.63mg C fixed.g dw^{-1}. Net production is 555.21mg C fixed.g dw^{-1}.

September: P_{max} = 4.60mg C fixed.g $dw^{-1}.hr^{-1}$ at 150$\mu\epsilon.m^{-2}.sec^{-1}$ (September 1984 data). Light saturated for 11 hours per day, unsaturated for two hours per day. Gross production is 1934.40mg C fixed.g dw^{-1}. Net production is 1698.00mg C fixed.g dw^{-1}.

October: P_{max} = 2.19mg C fixed.g $dw^{-1}.hr^{-1}$ at 303$\mu\epsilon.m^{-2}.sec^{-1}$ (October 1985 data). Light saturated for 11 hours per day, unsaturated for two hours per day. Gross production is 943.33mg C fixed.g dw^{-1}. Net production is 830.49mg C fixed.g dw^{-1}.

November: P_{max} = 0.81mg C fixed.g $dw^{-1}.hr^{-1}$ at 82$\mu\epsilon.m^{-2}.sec^{-1}$ (November 1984 data). Light saturated for 15 hours per day, unsaturated for nil hours per day. Gross production is 423.00mg C fixed.g dw^{-1}. Net production is 364.50mg C fixed.g dw^{-1}.

December: P_{max} = 1.39mg C fixed.g $dw^{-1}.hr^{-1}$ at 211$\mu\epsilon.m^{-2}.sec^{-1}$ (average of November 1984, February 1985 & October 1985 data). Light saturated for 13 hours per day, unsaturated for two hours per day. Gross production is 714.55mg C fixed.g dw^{-1}. Net production is 608.53mg C fixed.g dw^{-1}.

Annual gross production of submersed *Gigartina radula* is 8983.50mg C fixed.g $dw^{-1}.yr^{-1}$. Annual net production of *Gigartina radula* is 7958.01mg C fixed.g dw^{-1}. Now since *Gigartina radula* is emersed for 21.15% of the time, its

actual submersed gross photosynthesis will be 0.7885 x the calculated rate. Therefore monthly gross production is: Jan 470.29; Feb 382.68; Mar 366.90; Apr 303.49; May 745.53; Jun 704.92; Jul 460.57; Aug 483.06; Sep 1525.27; Oct 743.82; Nov 333.54; Dec 563.42. Annual gross submersed production = 7083.49mg C fixed.g dw^{-1}.

d). ***Splachnidium rugosum***

January: P_{max} = 1.32mg C fixed.g $dw^{-1}.hr^{-1}$ at 661$\mu\epsilon.m^{-2}.sec^{-1}$ (February 1985 data). Light saturated for 11 hours per day, unsaturated for four hours per day. Gross production is 573.19mg C fixed.g dw^{-1}. Net production is 458.80mg C fixed.g dw^{-1}.

February: P_{max} = 1.32mg C fixed.g $dw^{-1}.hr^{-1}$ at 661$\mu\epsilon.m^{-2}.sec^{-1}$ (February 1985 data). Light saturated for 11 hours per day, unsaturated for two hours per day. Gross production is 483.56mg C fixed.g dw^{-1}. Net production is 444.09mg C fixed.g dw^{-1}.

March: P_{max} = 2.85mg C fixed.g $dw^{-1}.hr^{-1}$ at 311$\mu\epsilon.m^{-2}.sec^{-1}$ (April 1985 data). Light saturated for 11 hours per day, unsaturated for two hours per day. Gross production is 1227.60mg C fixed.g dw^{-1}. Net production is 1053.69mg C fixed.g dw^{-1}.

April: P_{max} = 2.85mg C fixed.g $dw^{-1}.hr^{-1}$ at 311$\mu\epsilon.m^{-2}.sec^{-1}$ (April 1985 data). Light saturated for 11 hours per day, unsaturated for nil hours per day. Gross production is 1038.60mg C fixed.g dw^{-1}. Net production is 940.50mg C fixed.g dw^{-1}.

May: P_{max} = 2.67mg C fixed.g $dw^{-1}.hr^{-1}$ at 397$\mu\epsilon.m^{-2}.sec^{-1}$ (average June 1984 & June 1985 data). Light saturated for 9 hours per day, unsaturated for two hours per day. Gross

production is 894.04mg C fixed.g dw^{-1}. Net production 798.15mg C fixed.g dw^{-1}.

June: P_{max} = 2.67mg C fixed.g $dw^{-1}.hr^{-1}$ at 397$\mu\epsilon.m^{-2}.sec^{-1}$ (average June 1984 & June 1985 data). Light saturated for 7 hours per day, unsaturated for four hours per day. Gross production is 814.20mg C fixed.g dw^{-1}. Net production 721.50mg C fixed.g dw^{-1}.

July: P_{max} = 3.13mg C fixed.g $dw^{-1}.hr^{-1}$ at 341$\mu\epsilon.m^{-2}.sec^{-1}$ (August 1985 data). Light saturated for 9 hours per day, unsaturated for two hours per day. Gross production is 1038.81mg C fixed.g dw^{-1}. Net production is 929.69mg C fixed.g dw^{-1}.

August: P_{max} = 3.13mg C fixed.g $dw^{-1}.hr^{-1}$ at 341$\mu\epsilon.m^{-2}.sec^{-1}$ (August 1985 data). Light saturated for 9 hours per day, unsaturated for two hours per day. Gross production is 1099.57mg C fixed.g dw^{-1}. Net production is 990.45mg C fixed.g dw^{-1}.

September: P_{max} = 2.78mg C fixed.g $dw^{-1}.hr^{-1}$ at 352$\mu\epsilon.m^{-2}.sec^{-1}$ (September 1984 data). Light saturated for 11 hours per day, unsaturated for two hours per day. Gross production is 1132.20mg C fixed.g dw^{-1}. Net production is 968.40mg C fixed.g dw^{-1}.

October: P_{max} = 1.69mg C fixed.g $dw^{-1}.hr^{-1}$ at 91$\mu\epsilon.m^{-2}.sec^{-1}$ (October 1985 data). Light saturated for 13 hours per day, unsaturated for nil hours per day. Gross production is 784.61mg C fixed.g dw^{-1}. Net production is 681.07mg C fixed.g dw^{-1}.

November: P_{max} = 1.93mg C fixed.g $dw^{-1}.hr^{-1}$ at 368$\mu\epsilon.m^{-2}.sec^{-1}$ (average of September 1984, February 1985 & October 1985 data). Light saturated for 13 hours per day,

unsaturated for two hours per day. Gross production is 955.80mg C fixed.g dw^{-1}. Net production is 794.70mg C fixed.g dw^{-1}.

December: P_{max} = 1.93mg C fixed.g $dw^{-1}.hr^{-1}$ at 368$\mu\epsilon.m^{-2}.sec^{-1}$ (average of September 1984, February 1985 & October 1985 data). Light saturated for 13 hours per day, unsaturated for two hours per day. Gross production is 998.20mg C fixed.g dw^{-1}. Net production is 831.73mg C fixed.g dw^{-1}.

Annual gross production of submersed *Splachnidium rugosum* is 11040.38mg C fixed.g $dw^{-1}.yr^{-1}$. Annual net production of submersed *Splachnidium rugosum* is 9612.77mg C fixed.g dw^{-1}. Now since *Splachnidium rugosum* is emersed for 36.26% of the time, its actual submersed gross photosynthesis will be 0.6374 x the calculated rate. Therefore monthly gross production is: Jan 365.35; Feb 308.22; Mar 782.47; Apr 662.00; May 569.86; Jun 518.97; Jul 662.14; Aug 700.87; Sep 721.66; Oct 500.11; Nov 609.23; Dec 636.25. Annual gross submersed production = 7037.14mg C fixed.g dw^{-1}.

e). ***Bifurcaria brassicaeformis***

January: P_{max} = 0.90mg C fixed.g $dw^{-1}.hr^{-1}$ at 208$\mu\epsilon.m^{-2}.sec^{-1}$ (February 1985 data). Light saturated for 13 hours per day, unsaturated for two hours per day. Gross production is 483.29mg C fixed.g dw^{-1}. Net production is 396.80mg C fixed.g dw^{-1}.

February: P_{max} = 0.90mg C fixed.g $dw^{-1}.hr^{-1}$ at 208$\mu\epsilon.m^{-2}.sec^{-1}$ (February 1985 data). Light saturated for 13 hours per day, unsaturated for nil hours per day. Gross production is 386.18mg C fixed.g dw^{-1}. Net production is 330.53mg C fixed.g dw^{-1}.

March: P_{max} = 2.58mg C fixed.g $dw^{-1}.hr^{-1}$ at 367$\mu\epsilon.m^{-2}.sec^{-1}$ (April 1985 data). Light saturated for 11 hours per day, unsaturated for two hours per day. Gross production is 1135.84mg C fixed.g dw^{-1}. Net production is 957.28mg C fixed.g dw^{-1}.

April: P_{max} = 2.58mg C fixed.g $dw^{-1}.hr^{-1}$ at 367$\mu\epsilon.m^{-2}.sec^{-1}$ (April 1985 data). Light saturated for 9 hours per day, unsaturated for two hours per day. Gross production is 907.80mg C fixed.g dw^{-1}. Net production is 807.00mg C fixed.g dw^{-1}.

May: P_{max} = 0.82mg C fixed.g $dw^{-1}.hr^{-1}$ at 66$\mu\epsilon.m^{-2}.sec^{-1}$ (June 1984 data). Light saturated for 11 hours per day, unsaturated for nil hours per day. Gross production is 312.48mg C fixed.g dw^{-1}. Net production is 279.62mg C fixed.g dw^{-1}.

June: P_{max} = 0.82mg C fixed.g $dw^{-1}.hr^{-1}$ at 66$\mu\epsilon.m^{-2}.sec^{-1}$ (June 1984 data). Light saturated for 11 hours per day, unsaturated for nil hours per day. Gross production is 302.40mg C fixed.g dw^{-1}. Net production is 270.60mg C fixed.g dw^{-1}.

July: P_{max} = 1.99mg C fixed.g $dw^{-1}.hr^{-1}$ at 238$\mu\epsilon.m^{-2}.sec^{-1}$ (August 1985 data). Light saturated for 9 hours per day, unsaturated for two hours per day. Gross production is 683.86mg C fixed.g dw^{-1}. Net production is 604.81mg C fixed.g dw^{-1}.

August: P_{max} = 1.79mg C fixed.g $dw^{-1}.hr^{-1}$ at 423$\mu\epsilon.m^{-2}.sec^{-1}$ (August 1985 data). Light saturated for 9 hours per day, unsaturated for two hours per day. Gross production is 729.12mg C fixed.g dw^{-1}. Net production is 650.07mg C fixed.g dw^{-1}.

September: P_{max} = 1.66mg C fixed.g $dw^{-1}.hr^{-1}$ at 114$\mu E.m^{-2}.sec^{-1}$ (September 1984 data). Light saturated for 11 hours per day, unsaturated for two hours per day. Gross production is 737.10mg C fixed.g dw^{-1}. Net production is 623.40mg C fixed.g dw^{-1}.

October: P_{max} = 1.85mg C fixed.g $dw^{-1}.hr^{-1}$ at 77$\mu E.m^{-2}.sec^{-1}$ (October 1985 data). Light saturated for 13 hours per day, unsaturated for nil hours per day. Gross production is 876.99mg C fixed.g dw^{-1}. Net production is 745.55mg C fixed.g dw^{-1}.

November: P_{max} = 2.05mg C fixed.g $dw^{-1}.hr^{-1}$ at 323$\mu E.m^{-2}.sec^{-1}$ (November 1984 data). Light saturated for 13 hours per day, unsaturated for two hours per day. Gross production is 1025.59mg C fixed.g dw^{-1}. Net production is 830.70mg C fixed.g dw^{-1}.

December: P_{max} = 1.60mg C fixed.g $dw^{-1}.hr^{-1}$ at 203$\mu E.m^{-2}.sec^{-1}$ (average of November 1984, February 1985 & October 1985 data). Light saturated for 13 hours per day, unsaturated for two hours per day. Gross production is 860.84mg C fixed.g dw^{-1}. Net production is 703.70mg C fixed.g dw^{-1}.

Annual gross production of submersed *Bifurcaria brassicaeformis* is 8441.49mg C fixed.g $dw^{-1}.yr^{-1}$. Annual net production of submersed *Bifurcaria brassicaeformis* is 7200.06mg C fixed.g dw^{-1}. Now since *Bifurcaria brassicaeformis* is emersed for 8.79% of the time, its actual submersed gross photosynthesis will be 0.9121 x the calculated rate. Therefore monthly gross production is: Jan 367.84; Feb 352.23; Mar 1036.00; Apr 828.00; May 285.01; Jun 275.82; Jul 623.75; Aug 665.03; Sep 672.31; Oct 799.90; Nov

935.44;Dec 785.17. Annual gross submersed production = 7699.48mg C fixed.g dw^{-1}.

2. Intertidal algae - Emersed photosynthesis

a). ***Porphyra capensis***

Percentage of time exposed = 78.85%. Minutes exposed per day = 1136; minutes exposed per tidal cycle = 568. Since one tidal cycle is during the day, the plant will be exposed and photosynthesising for one continuous period of 568 mins. day^{-1}.

Net photosynthesis will therefore be 0.9219mg C fixed.g dw^{-1} in the first half hour, 0.7758mg C fixed.g dw^{-1} in the second half hour. From 1-2 hrs 1.2110mg C fixed.g dw^{-1}, 2-3 hrs 1.0805mg C fixed.g dw^{-1}, 3-4 hrs 0.8819mg C fixed.g dw^{-1}, 4-5 hrs 0.5466mg C fixed.g dw^{-1}, 5-6 hrs 0.2160mg C fixed, 6-7 hrs approx. 0.075mg C fixed.g dw^{-1}, 7-8hrs 0.0375mg C fixed.g dw^{-1}; 8-9hrs approximately 0.0187mg C fixed.g dw^{-1}; 9-10 hrs approximately 0.0094mg C fixed.g dw^{-1}. Total net production per emersed cycle 5.7743mg C.g dw^{-1}. Daylight respiration = 10.4% of net production, therefore respiration = 0.6005mg C respired.g dw^{-1}. Assuming day and night are of equal length (appendix VI), day and night respiration will cancel each other out and will have no overall effect on calculations of gross production. Photorespiration = 0.92 x 0.60 = 0.5525mg C respired.g dw^{-1}. Gross emersed production = net production + daylight respiration - night respiration + photorespiration = 5.7743 + 0.6005 - 0.6005 + 0.5525 = 6.3268mg C fixed.g $dw^{-1}.day^{-1}$. Therefore monthly gross production is: Jan 196.13; Feb 178.73; Mar 196.13; Apr 189.80; May 196.13; Jun 189.80; Jul 196.13; Aug 196.13; Sep 189.80; Oct 196.13; Nov 189.80;Dec

196.13. Annual gross emersed production = 2310.84mg C fixed.g dw^{-1}.

b). ***Ulva rigida***

Minutes exposed per tidal cycle (i.e. per daylight period) = 370. Net photosynthesis: 1st half hour 0.7772mg C fixed.g dw^{-1}; 2nd half hour 0.6216mg C fixed.g dw^{-1}; 1-2hrs 0.7004mg C fixed.g dw^{-1}; 2-3hrs 0.2799mg C fixed.g dw^{-1}; 3-4hrs 0.0864mg C fixed.g dw^{-1}; 4-5hrs 0.0648mg C fixed.g dw^{-1}; 5-6hrs 0.0134mg C fixed.g dw^{-1}. Total net production per emersed cycle 2.5437mg C fixed.g dw^{-1}. In *Ulva rigida*, respiration is 13.2% of production, therefore amount respired is 0.3358mg C respired.g $dw^{-1}.day^{-1}$. However, since the assumption is that day and night are on average of equal length, daylight and night-time respiration will have no net effect on gross production. Photorespiration = 0.92 x respiration rate, therefore photorespiration = 0.92 x 0.3358 = 0.3089mg C fixed.g $dw^{-1}.day^{-1}$. Gross production of *Ulva rigida* is therefore 2.5437 + 0.3358 - 0.3358 + 0.3089 = 2.8526mg C fixed.g $dw^{-1}.day^{-1}$. Therefore monthly gross production is: Jan 88.43; Feb 80.58; Mar 88.43; Apr 85.58; May 88.43; Jun 85.58; Jul 88.43; Aug 88.43; Sep 85.58; Oct 88.43; Nov 85.58;Dec 88.43. Annual gross emersed production = 1054.61mg C fixed.g dw^{-1}.

c). ***Gigartina radula***

Minutes exposed per tidal cycle (i.e. per daylight period) = 153. Net photosynthesis: 1st half hour 0.7493mg C fixed.g dw^{-1}; 2nd half hour 0.6356mg C fixed.g dw^{-1}; 1-2hrs 0.6502mg C fixed.g dw^{-1}; 2-2.5hrs 0.1337mg C fixed.g dw^{-1}. Total net production per emersed cycle 2.1688mg C fixed.g dw^{-1}. In *Gigartina radula*, respiration is 12.1% of

production, therefore amount respired is 0.2624mg C respired.g dw^{-1}.day^{-1}. However, since the assumption is that day and night are on average of equal length, daylight and night-time respiration will have no net effect on gross production. Photorespiration = 0.92 x respiration rate, therefore photorespiration = 0.92 x 0.2624 = 0.2414mg C fixed.g dw^{-1}.day^{-1}. Gross production of *Gigartina radula* is therefore 2.1688 + 0.2624 - 0.2624 + 0.2414 = 2.4102mg C fixed.g dw^{-1}.day^{-1}. Therefore monthly gross production is: Jan 74.72; Feb 68.09; Mar 74.72; Apr 72.31; May 74.72; Jun 72.31; Jul 74.72; Aug 74.72; Sep 72.31; Oct 74.72; Nov 72.31;Dec 74.72. Annual gross emersed production = 880.37mg C fixed.g dw^{-1}.

d). ***Splachnidium rugosum***

Minutes exposed per tidal cycle (i.e. per daylight period) = 261. Net photosynthesis: 1st half hour 0.7122mg C fixed.g dw^{-1}; 2nd half hour 0.5419mg C fixed.g dw^{-1}; 1-2hrs 0.2487mg C fixed.g dw^{-1}; 2-3hrs 0.0751mg C fixed.g dw^{-1}; 3-4hrs 0.0262mg C fixed.g dw^{-1}; 4-4.33hrs -0.0005mg C fixed.g dw^{-1}. Total net production per emersed cycle 1.6036mg C fixed.g dw^{-1}. In *Splachnidium rugosum*, respiration is 14.1% of production, therefore amount respired is 0.2261mg C respired.g dw^{-1}.day^{-1}. However, since the assumption is that day and night are on average of equal length, daylight and night-time respiration will have no net effect on gross production. Photorespiration = 0.92 x respiration rate, therefore photorespiration = 0.92 x 0.2261 = 0.2080mg C fixed.g dw^{-1}.day^{-1}. Gross production of *Splachnidium rugosum* is therefore 1.6036 + 0.2261 - 0.2261 + 0.2080 = 1.8116mg C fixed.g dw^{-1}.day^{-1}. Therefore monthly gross

production is: Jan 56.16; Feb 51.18; Mar 56.16; Apr 54.35; May 56.16; Jun 54.35; Jul 56.16; Aug 56.16; Sep 54.35; Oct 56.16; Nov 54.35; Dec 56.16. Annual gross emersed production = 661.70mg C fixed.g dw^{-1}.

e). ***Bifurcaria brassicaeformis***

Minutes exposed per tidal cycle (i.e. per daylight period) = 63. Net photosynthesis: 1st half hour 0.5516mg C fixed.g dw^{-1}; 2nd half hour 0.4188mg C fixed.g dw^{-1}. Total net production per emersed cycle 0.9704mg C fixed.g dw^{-1}. In *Bifurcaria brassicaeformis*, respiration is 16.0% of production, therefore amount respired is 0.1553mg C respired.g $dw^{-1}.day^{-1}$. However, since the assumption is that day and night are on average of equal length, daylight and night-time respiration will have no net effect on gross production. Photorespiration = 0.92 x respiration rate, therefore photorespiration = 0.92 x 0.1553 = 0.1428mg C fixed.g $dw^{-1}.day^{-1}$. Gross production of *Bifurcaria brassicaeformis* is therefore 0.9704 + 0.1553 - 0.1553 + 0.1428 = 1.1132mg C fixed.g $dw^{-1}.day^{-1}$. Therefore monthly gross production is: Jan 34.51; Feb 31.45; Mar 34.51; Apr 33.40; May 34.51; Jun 33.40; Jul 34.51; Aug 34.51; Sep 33.40; Oct 34.51; Nov 33.40; Dec 34.51. Annual gross emersed production = 411.06mg C fixed.g dw^{-1}.

3. Subtidal algae

a). ***Botryocarpa prolifera***

January: Using photosynthesis data from January 1985 P = 0.86mg C fixed per g dw per hr. From the January light data this species will be photosynthetically active from 5a.m. to 8p.m. (appendix VI), = 15 hrs x 0.86 (the mean rate of net photosynthesis observed in January) = 12.90mg C fixed.g

$dw^{-1}.day^{-1}$. This will yield a net production figure of 31 x 12.90 = 399.90mg C.g dw^{-1} in January. Using the measured January respiration rate of 0.55mg C respired g $dw^{-1}.hr^{-1}$, amount of daylight respiration is 15 x 0.55 = 8.25mg C respired.g $dw^{-1}.day^{-1}$ which equals 31 x 8.25 = 255.75mg C respired.g $dw^{-1}.month^{-1}$, and respiration at night is 9 x 0.55 = 4.95mg C respired per g $dw^{-1}.day^{-1}$ which equals 153.45mg C respired.g $dw^{-1}.month^{-1}$. The gross production for *Botryocarpa prolifera* in January will therefore be net production + daytime respiration - night time respiration= 399.90 + 255.75 - 153.45 = 502.20mg C fixed.g dw^{-1}.

February: Net production is = 0.52mg C fixed.g $dw^{-1}.hr$ x 13 hrs x 28.25 days = 190.97mg C fixed.g $dw^{-1}.month^{-1}$. Daylight respiration = 0.28mg C respired.g $dw^{-1}.hr^{-1}$ x 13 hrs x 28.25 days = 102.83mg C respired.g $dw^{-1}.month^{-1}$. Night-time respiration = 0.28mg C respired.g $dw^{-1}.hr^{-1}$ x 11 hrs x 28.25 days = 206.79mg C respired.g $dw^{-1}.month^{-1}$. The gross February production will therefore be 206.79mg C fixed.g $dw^{-1}.month^{-1}$.

March: Net production is = 0.39mg C fixed.g $dw^{-1}.hr$ x 13 hrs x 31 days = 157.17mg C fixed.g $dw^{-1}.month^{-1}$. Daylight respiration = 0.19mg C respired.g $dw^{-1}.hr^{-1}$ x 13 hrs x 31 days = 76.57mg C respired.g $dw^{-1}.month^{-1}$. Night-time respiration = 0.19mg C respired.g $dw^{-1}.hr^{-1}$ x 11 hrs x 31 days = 64.79mg C respired.g $dw^{-1}.month^{-1}$. The gross March production will therefore be 168.95mg C, fixed.g $dw^{-1}.month^{-1}$.

April: Net production is = 0.24mg C fixed.g $dw^{-1}.hr$ x 11 hrs x 30 days = 79.20mg C fixed.g $dw^{-1}.month^{-1}$. Daylight respiration = 0.09mg C respired.g $dw^{-1}.hr^{-1}$ x 11 hrs x 30

days = 29.70mg C respired.g dw^{-1}.$month^{-1}$. Night-time respiration = 0.09mg C respired.g dw^{-1}.hr^{-1} x 13 hrs x 30 days = 35.10mg C respired.g dw^{-1}.$month^{-1}$. The gross April production will therefore be 73.80mg C fixed.g dw^{-1}.$month^{-1}$. May: Net production is = 0.20mg C fixed.g dw^{-1}.hr x 11 hrs x 31 days = 68.20mg C fixed.g dw^{-1}.$month^{-1}$. Daylight respiration = 0.07mg C respired.g dw^{-1}.hr^{-1} x 11 hrs x 31 days = 23.87mg C respired.g dw^{-1}.$month^{-1}$. Night-time respiration = 0.07mg C respired.g dw^{-1}.hr^{-1} x 13 hrs x 31 days = 28.21mg C respired.g dw^{-1}.$month^{-1}$. The gross May production will therefore be 63.86mg C fixed.g dw^{-1}.$month^{-1}$. June: Net production is = 0.15mg C fixed.g dw^{-1}.hr x 11 hrs x 30 days = 49.50mg C fixed.g dw^{-1}.$month^{-1}$. Daylight respiration = 0.01mg C respired.g dw^{-1}.hr^{-1} x 11 hrs x 30 days = 3.30mg C respired.g dw^{-1}.$month^{-1}$. Night-time respiration = 0.01mg C respired.g dw^{-1}.hr^{-1} x 13 hrs x 30 days = 3.90mg C respired.g dw^{-1}.$month^{-1}$. The gross June production will therefore be 48.90mg C fixed.g dw^{-1}.$month^{-1}$. July:Net production is = 0.59mg C fixed.g dw^{-1}.hr x 11 hrs x 31 days = 201.19mg C fixed.g dw^{-1}.$month^{-1}$. Daylight respiration = 0.06mg C respired.g dw^{-1}.hr^{-1} x 11 hrs x 31 days = 20.46mg C respired.g dw^{-1}.$month^{-1}$. Night-time respiration = 0.06mg C respired.g dw^{-1}.hr^{-1} x 13 hrs x 31 days = 24.18mg C respired.g dw^{-1}.$month^{-1}$. The gross July production will therefore be 197.47mg C fixed.g dw^{-1}.$month^{-1}$.

August:Net production is = 0.86mg C fixed.g dw^{-1}.hr x 11 hrs x 31 days = 293.26mg C fixed.g dw^{-1}.$month^{-1}$. Daylight respiration = 0.41mg C respired.g dw^{-1}.hr^{-1} x 11 hrs x 31 days = 139.81mg C respired.g dw^{-1}.$month^{-1}$. Night-time

respiration = 0.41mg C respired.g $dw^{-1}.hr^{-1}$ x 13 hrs x 31 days = 165.23mg C respired.g $dw^{-1}.month^{-1}$. The gross August production will therefore be 267.84mg C fixed.g $dw^{-1}.month^{-1}$.

September:Net production is = 0.92mg C fixed.g $dw^{-1}.hr$ x 13 hrs x 30 days = 358.80mg C fixed.g $dw^{-1}.month^{-1}$. Daylight respiration = 0.33mg C respired.g $dw^{-1}.hr^{-1}$ x 13 hrs x 30 days = 128.70mg C respired.g $dw^{-1}.month^{-1}$. Night-time respiration = 0.33mg C respired.g $dw^{-1}.hr^{-1}$ x 11 hrs x 30 days = 108.90mg C respired.g $dw^{-1}.month^{-1}$. The gross September production will therefore be 378.60mg C fixed.g $dw^{-1}.month^{-1}$.

October:Net production is = 1.72mg C fixed.g $dw^{-1}.hr$ x 13 hrs x 31 days = 691.15mg C fixed.g $dw^{-1}.month^{-1}$. Daylight respiration = 0.52mg C respired.g $dw^{-1}.hr^{-1}$ x 13 hrs x 31 days = 209.56mg C respired.g $dw^{-1}.month^{-1}$. Night-time respiration = 0.52mg C respired.g $dw^{-1}.hr^{-1}$ x 11 hrs x 31 days = 177.32mg C respired.g $dw^{-1}.month^{-1}$. The gross October production will therefore be 723.39mg C fixed.g $dw^{-1}.month^{-1}$.

November:Net production is = 1.14mg C fixed.g $dw^{-1}.hr$ x 15 hrs x 30 days = 513.00mg C fixed.g $dw^{-1}.month^{-1}$. Daylight respiration = 0.40mg C respired.g $dw^{-1}.hr^{-1}$ x 15 hrs x 30 days = 180.00mg C respired.g $dw^{-1}.month^{-1}$. Night-time respiration = 0.40mg C respired.g $dw^{-1}.hr^{-1}$ x 9 hrs x 30 days = 108.00mg C respired.g $dw^{-1}.month^{-1}$. The gross November production will therefore be 585.00mg C fixed.g $dw^{-1}.month^{-1}$.

December:Net production is = 0.93mg C fixed.g $dw^{-1}.hr$ x 15 hrs x 31 days = 432.45mg C fixed.g $dw^{-1}.month^{-1}$. Daylight

respiration = 0.24mg C respired.g $dw^{-1}.hr^{-1}$ x 15 hrs x 31 days = 111.60mg C respired.g $dw^{-1}.month^{-1}$. Night-time respiration = 0.24mg C respired.g $dw^{-1}.hr^{-1}$ x 9 hrs x 31 days = 66.96mg C respired.g $dw^{-1}.month^{-1}$. The gross December production will therefore be 477.09mg C fixed.g $dw^{-1}.month^{-1}$.

Annual gross production of sublittoral *Botryocarpa prolifera* is 3693.89mg C fixed.g $dw^{-1}.yr^{-1}$.

b). ***Gigartina radula***

January: Net production is = 0.39mg C fixed.g $dw^{-1}.hr$ x 15 hrs x 31 days = 181.35mg C fixed.g $dw^{-1}.month^{-1}$. Daylight respiration = 0.32mg C respired.g $dw^{-1}.hr^{-1}$ x 15 hrs x 31 days = 148.80mg C respired.g $dw^{-1}.month^{-1}$. Night-time respiration = 0.32mg C respired.g $dw^{-1}.hr^{-1}$ x 9 hrs x 31 days = 89.28mg C respired.g $dw^{-1}.month^{-1}$. The gross January production will therefore be 240.87mg C fixed.g $dw^{-1}.month^{-1}$.

February: Net production is = 0.33mg C fixed.g $dw^{-1}.hr$ x 13 hrs x 28.25 days = 121.19mg C fixed.g $dw^{-1}.month^{-1}$. Daylight respiration = 0.17mg C respired.g $dw^{-1}.hr^{-1}$ x 13 hrs x 28.25 days = 62.43mg C respired.g $dw^{-1}.month^{-1}$. Night-time respiration = 0.17mg C respired.g $dw^{-1}.hr^{-1}$ x 11 hrs x 28.25 days = 52.83mg C respired.g $dw^{-1}.month^{-1}$. The gross February production will therefore be 130.79mg C fixed.g $dw^{-1}.month^{-1}$.

March: Net production is = 0.32mg C fixed.g $dw^{-1}.hr$ x 13 hrs x 31 days = 128.96mg C fixed.g $dw^{-1}.month^{-1}$. Daylight respiration = 0.07mg C respired.g $dw^{-1}.hr^{-1}$ x 13 hrs x 31 days = 28.21mg C respired.g $dw^{-1}.month^{-1}$. Night-time respiration = 0.07mg C respired.g $dw^{-1}.hr^{-1}$ x 11 hrs x 31

days = 23.87mg C respired.g dw^{-1}.$month^{-1}$. The gross March production will therefore be 133.30mg C fixed.g dw^{-1}.$month^{-1}$.

April: Net production is = 0.27mg C fixed.g dw^{-1}.hr x 11 hrs x 30 days = 89.10mg C fixed.g dw^{-1}.$month^{-1}$. Daylight respiration = 0.06mg C respired.g dw^{-1}.hr^{-1} x 11 hrs x 30 days = 19.80mg C respired.g dw^{-1}.$month^{-1}$. Night-time respiration = 0.06mg C respired.g dw^{-1}.hr^{-1} x 13 hrs x 30 days = 23.40mg C respired.g dw^{-1}.$month^{-1}$. The gross April production will therefore be 85.50mg C fixed.g dw^{-1}.$month^{-1}$.

May: Net production is = 0.25mg C fixed.g dw^{-1}.hr x 11 hrs x 31 days = 85.25mg C fixed.g dw^{-1}.$month^{-1}$. Daylight respiration = 0.06mg C respired.g dw^{-1}.hr^{-1} x 11 hrs x 31 days = 20.46mg C respired.g dw^{-1}.$month^{-1}$. Night-time respiration = 0.06mg C respired.g dw^{-1}.hr^{-1} x 13 hrs x 31 days = 24.18mg C respired.g dw^{-1}.$month^{-1}$. The gross May production will therefore be 81.53mg C fixed.g dw^{-1}.$month^{-1}$.

June: Net production is = 0.24mg C fixed.g dw^{-1}.hr x 11 hrs x 30 days = 47.20mg C fixed.g dw^{-1}.$month^{-1}$. Daylight respiration = 0.16mg C respired.g dw^{-1}.hr^{-1} x 11 hrs x 30 days = 52.80mg C respired.g dw^{-1}.$month^{-1}$. Night-time respiration = 0.16mg C respired.g dw^{-1}.hr^{-1} x 13 hrs x 30 days = 62.40mg C respired.g dw^{-1}.$month^{-1}$. The gross June production will therefore be 69.60mg C fixed.g dw^{-1}.$month^{-1}$.

July:Net production is = 0.67mg C fixed.g dw^{-1}.hr x 11 hrs x 31 days = 228.47mg C fixed.g dw^{-1}.$month^{-1}$. Daylight respiration = 0.23mg C respired.g dw^{-1}.hr^{-1} x 11 hrs x 31 days = 78.43mg C respired.g dw^{-1}.$month^{-1}$. Night-time respiration = 0.23mg C respired.g dw^{-1}.hr^{-1} x 13 hrs x 31 days = 92.69mg C respired.g dw^{-1}.$month^{-1}$. The gross July

production will therefore be 214.21mg C fixed.g dw^{-1}. $month^{-1}$.

August:Net production is = 1.04mg C fixed.g dw^{-1}.hr x 11 hrs x 31 days = 354.64mg C fixed.g dw^{-1}.$month^{-1}$. Daylight respiration = 0.18mg C respired.g dw^{-1}.hr^{-1} x 11 hrs x 31 days = 61.38mg C respired.g dw^{-1}.$month^{-1}$. Night-time respiration = 0.18mg C respired.g dw^{-1}.hr^{-1} x 13 hrs x 31 days = 72.54mg C respired.g dw^{-1}.$month^{-1}$. The gross August production will therefore be 343.48mg C fixed.g dw^{-1}. $month^{-1}$.

September:Net production is = 1.24mg C fixed.g dw^{-1}.hr x 13 hrs x 30 days = 483.60mg C fixed.g dw^{-1}.$month^{-1}$. Daylight respiration = 0.28mg C respired.g dw^{-1}.hr^{-1} x 13 hrs x 30 days = 109.20mg C respired.g dw^{-1}.$month^{-1}$. Night-time respiration = 0.28mg C respired.g dw^{-1}.hr^{-1} x 11 hrs x 30 days = 92.40mg C respired.g dw^{-1}.$month^{-1}$. The gross September production will therefore be 500.40mg C fixed.g dw^{-1}.$month^{-1}$.

October:Net production is = 1.66mg C fixed.g dw^{-1}.hr x 13 hrs x 31 days = 666.97mg C fixed.g dw^{-1}.$month^{-1}$. Daylight respiration = 0.13mg C respired.g dw^{-1}.hr^{-1} x 13 hrs x 31 days = 50.38mg C respired.g dw^{-1}.$month^{-1}$. Night-time respiration = 0.13mg C respired.g dw^{-1}.hr^{-1} x 11 hrs x 31 days = 42.63mg C respired.g dw^{-1}.$month^{-1}$. The gross October production will therefore be 674.72mg C fixed.g dw^{-1}. $month^{-1}$.

November:Net production is = 1.06mg C fixed.g dw^{-1}.hr x 15 hrs x 30 days = 477.00mg C fixed.g dw^{-1}.$month^{-1}$. Daylight respiration = 0.34mg C respired.g dw^{-1}.hr^{-1} x 15 hrs x 30 days = 153.00mg C respired.g dw^{-1}.$month^{-1}$. Night-time

respiration = 0.34mg C respired.g $dw^{-1}.hr^{-1}$ x 9 hrs x 30 days = 91.80mg C respired.g $dw^{-1}.month^{-1}$. The gross November production will therefore be 538.20mg C fixed.g $dw^{-1}.month^{-1}$.

December:Net production is = 1.17mg C fixed.g $dw^{-1}.hr$ x 15 hrs x 31 days = 544.05mg C fixed.g $dw^{-1}.month^{-1}$. Daylight respiration = 0.21mg C respired.g $dw^{-1}.hr^{-1}$ x 15 hrs x 31 days = 97.65mg C respired.g $dw^{-1}.month^{-1}$. Night-time respiration = 0.21mg C respired.g $dw^{-1}.hr^{-1}$ x 9 hrs x 31 days = 58.59mg C respired.g $dw^{-1}.month^{-1}$. The gross December production will therefore be 583.11mg C fixed.g $dw^{-1}.month^{-1}$.

Annual gross production of sublittoral *Gigartina radula* is 3595.71mg C fixed.g $dw^{-1}.yr^{-1}$.

c). ***Epymenia obtusa***

January: Net production is = 0.60mg C fixed.g $dw^{-1}.hr$ x 15 hrs x 31 days = 279.35mg C fixed.g $dw^{-1}.month^{-1}$. Daylight respiration = 0.16mg C respired.g $dw^{-1}.hr^{-1}$ x 15 hrs x 31 days = 74.40mg C respired.g $dw^{-1}.month^{-1}$. Night-time respiration = 0.16mg C respired.g $dw^{-1}.hr^{-1}$ x 9 hrs x 31 days = 44.64mg C respired.g $dw^{-1}.month^{-1}$. The gross January production will therefore be 308.76mg C fixed.g $dw^{-1}.month^{-1}$.

February: Net production is = 0.89mg C fixed.g $dw^{-1}.hr$ x 13 hrs x 28.25 days = 326.85mg C fixed.g $dw^{-1}.month^{-1}$. Daylight respiration = 0.35mg C respired.g $dw^{-1}.hr^{-1}$ x 13 hrs x 28.25 days = 128.54mg C respired.g $dw^{-1}.month^{-1}$. Night-time respiration = 0.35mg C respired.g $dw^{-1}.hr^{-1}$ x 11 hrs x 28.25 days = 108.76mg C respired.g $dw^{-1}.month^{-1}$. The gross

February production will therefore be 346.63mg C fixed.g dw^{-1}.$month^{-1}$.

March: Net production is = 0.56mg C fixed.g dw^{-1}.hr x 13 hrs x 31 days = 225.68mg C fixed.g dw^{-1}.$month^{-1}$. Daylight respiration = 0.23mg C respired.g dw^{-1}.hr^{-1} x 13 hrs x 31 days = 92.69mg C respired.g dw^{-1}.$month^{-1}$. Night-time respiration = 0.23mg C respired.g dw^{-1}.hr^{-1} x 11 hrs x 31 days = 78.43mg C respired.g dw^{-1}.$month^{-1}$. The gross March production will therefore be 239.94mg C fixed.g dw^{-1}.$month^{-1}$.

April: Net production is = 0.25mg C fixed.g dw^{-1}.hr x 11 hrs x 30 days = 82.50mg C fixed.g dw^{-1}.$month^{-1}$. Daylight respiration = 0.10mg C respired.g dw^{-1}.hr^{-1} x 11 hrs x 30 days = 33.00mg C respired.g dw^{-1}.$month^{-1}$. Night-time respiration = 0.10mg C respired.g dw^{-1}.hr^{-1} x 13 hrs x 30 days = 39.00mg C respired.g dw^{-1}.$month^{-1}$. The gross April production will therefore be 76.50mg C fixed.g dw^{-1}.$month^{-1}$.

May: Net production is = 0.16mg C fixed.g dw^{-1}.hr x 11 hrs x 31 days = 54.56mg C fixed.g dw^{-1}.$month^{-1}$. Daylight respiration = 0.06mg C respired.g dw^{-1}.hr^{-1} x 11 hrs x 31 days = 20.46mg C respired.g dw^{-1}.$month^{-1}$. Night-time respiration = 0.06mg C respired.g dw^{-1}.hr^{-1} x 13 hrs x 31 days = 24.18mg C respired.g dw^{-1}.$month^{-1}$. The gross May production will therefore be 50.84mg C fixed.g dw^{-1}.$month^{-1}$.

June: Net production is = 0.03mg C fixed.g dw^{-1}.hr x 11 hrs x 30 days = 9.90mg C fixed.g dw^{-1}.$month^{-1}$. Daylight respiration = 0.02mg C respired.g dw^{-1}.hr^{-1} x 11 hrs x 30 days = 6.60mg C respired.g dw^{-1}.$month^{-1}$. Night-time respiration = 0.02mg C respired.g dw^{-1}.hr^{-1} x 13 hrs x 30

days = 7.80mg C respired.g dw^{-1}.$month^{-1}$. The gross June production will therefore be 8.70mg C fixed.g dw^{-1}.$month^{-1}$.

July:Net production is = 0.03mg C fixed.g dw^{-1}.hr x 11 hrs x 31 days = 10.23mg C fixed.g dw^{-1}.$month^{-1}$. Daylight respiration = 0.01mg C respired.g dw^{-1}.hr^{-1} x 11 hrs x 31 days = 3.41mg C respired.g dw^{-1}.$month^{-1}$. Night-time respiration = 0.01mg C respired.g dw^{-1}.hr^{-1} x 13 hrs x 31 days = 4.03mg C respired.g dw^{-1}.$month^{-1}$. The gross July production will therefore be 9.61mg C fixed.g dw^{-1}.$month^{-1}$.

August:Net production is = 0.52mg C fixed.g dw^{-1}.hr x 11 hrs x 31 days = 177.32mg C fixed.g dw^{-1}.$month^{-1}$. Daylight respiration = 0.13mg C respired.g dw^{-1}.hr^{-1} x 11 hrs x 31 days = 44.33mg C respired.g dw^{-1}.$month^{-1}$. Night-time respiration = 0.13mg C respired.g dw^{-1}.hr^{-1} x 13 hrs x 31 days = 52.39mg C respired.g dw^{-1}.$month^{-1}$. The gross August production will therefore be 169.26mg C fixed.g dw^{-1}.$month^{-1}$.

September:Net production is = 0.58mg C fixed.g dw^{-1}.hr x 13 hrs x 30 days = 226.20mg C fixed.g dw^{-1}.$month^{-1}$. Daylight respiration = 0.24mg C respired.g dw^{-1}.hr^{-1} x 13 hrs x 30 days = 93.60mg C respired.g dw^{-1}.$month^{-1}$. Night-time respiration = 0.24mg C respired.g dw^{-1}.hr^{-1} x 11 hrs x 30 days = 79.20mg C respired.g dw^{-1}.$month^{-1}$. The gross September production will therefore be 240.60mg C fixed.g dw^{-1}.$month^{-1}$.

October:Net production is = 0.90mg C fixed.g dw^{-1}.hr x 13 hrs x 31 days = 360.69mg C fixed.g dw^{-1}.$month^{-1}$. Daylight respiration = 0.34mg C respired.g dw^{-1}.hr^{-1} x 13 hrs x 31 days = 135.01mg C respired.g dw^{-1}.$month^{-1}$. Night-time respiration = 0.34mg C respired.g dw^{-1}.hr^{-1} x 11 hrs x 31

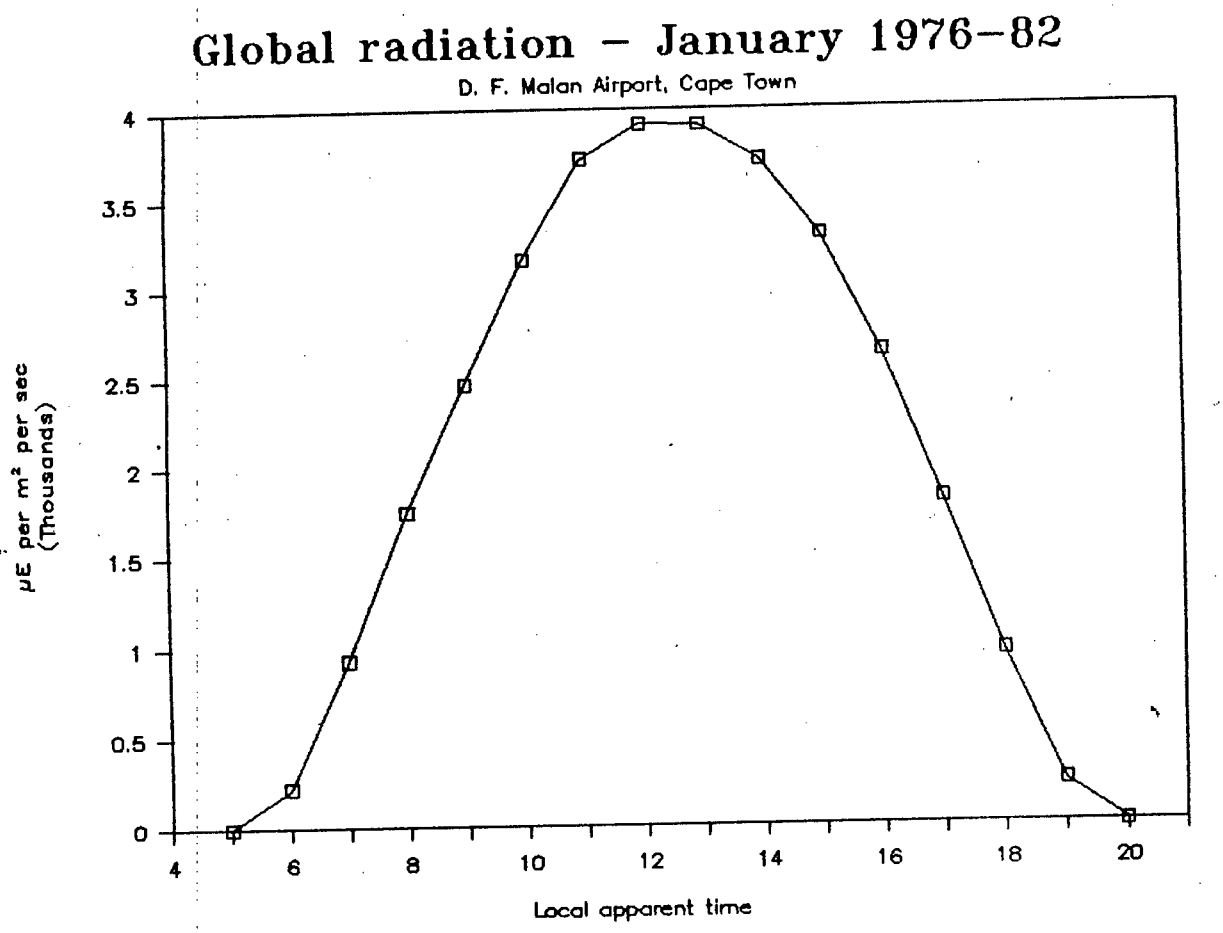
days = 114.24mg C respired. g dw^{-1}. $month^{-1}$. The gross October production will therefore be 381.46mg C fixed. g dw^{-1}. $month^{-1}$.

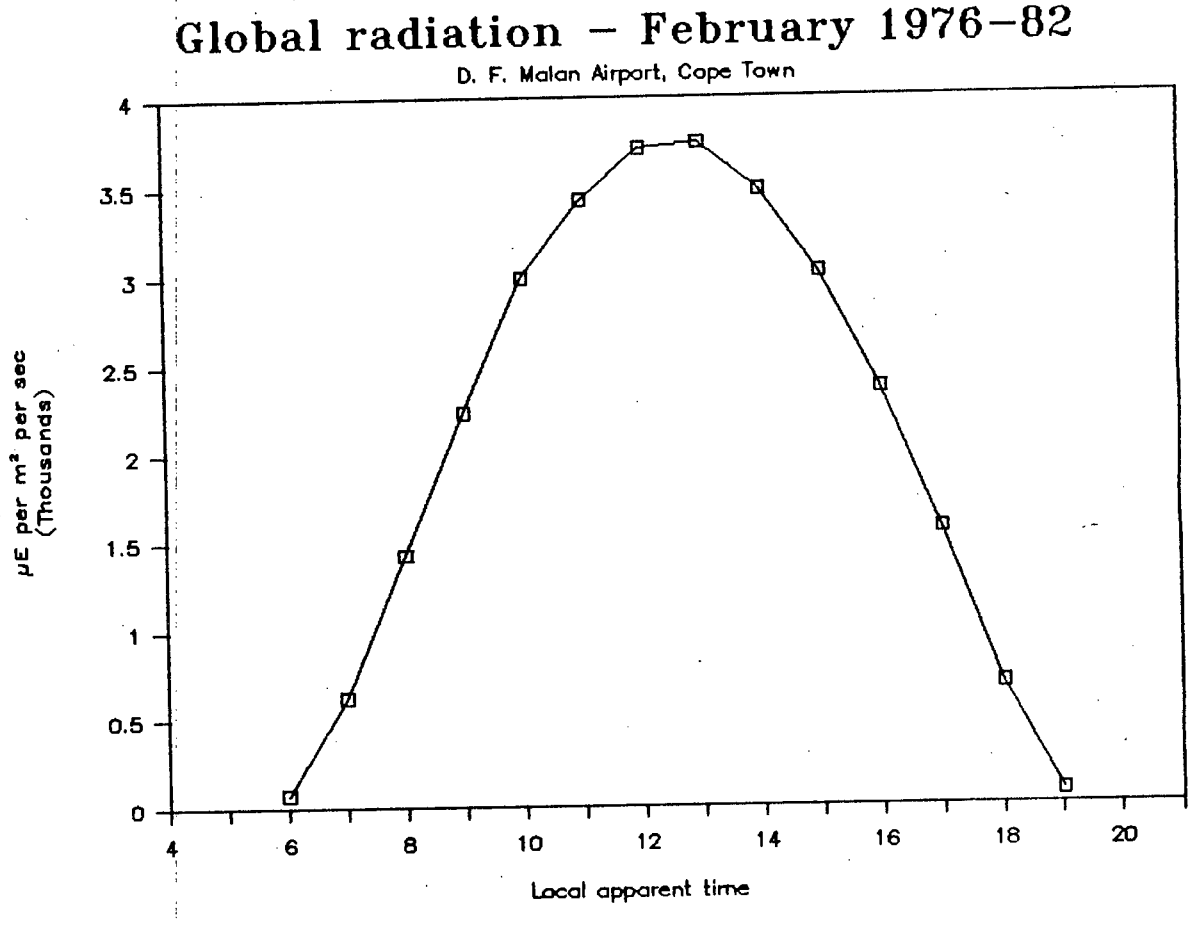
November: Net production is = 0.63mg C fixed. g dw^{-1}. hr x 15 hrs x 30 days = 283.50mg C fixed. g dw^{-1}. $month^{-1}$. Daylight respiration = 0.50mg C respired. g dw^{-1}. hr^{-1} x 15 hrs x 30 days = 225.00mg C respired. g dw^{-1}. $month^{-1}$. Night-time respiration = 0.50mg C respired. g dw^{-1}. hr^{-1} x 9 hrs x 30 days = 135.00mg C respired. g dw^{-1}. $month^{-1}$. The gross November production will therefore be 373.50mg C fixed. g dw^{-1}. $month^{-1}$.

December: Net production is = 0.75mg C fixed. g dw^{-1}. hr x 15 hrs x 31 days = 348.75mg C fixed. g dw^{-1}. $month^{-1}$. Daylight respiration = 0.31mg C respired. g dw^{-1}. hr^{-1} x 15 hrs x 31 days = 144.15mg C respired. g dw^{-1}. $month^{-1}$. Night-time respiration = 0.31mg C respired. g dw^{-1}. hr^{-1} x 9 hrs x 31 days = 103.23mg C respired. g dw^{-1}. $month^{-1}$. The gross December production will therefore be 389.67mg C fixed. g dw^{-1}. $month^{-1}$.

Annual gross production of sublittoral *Epymenia obtusa* is 2595.47mg C fixed. g dw^{-1}. yr^{-1}.

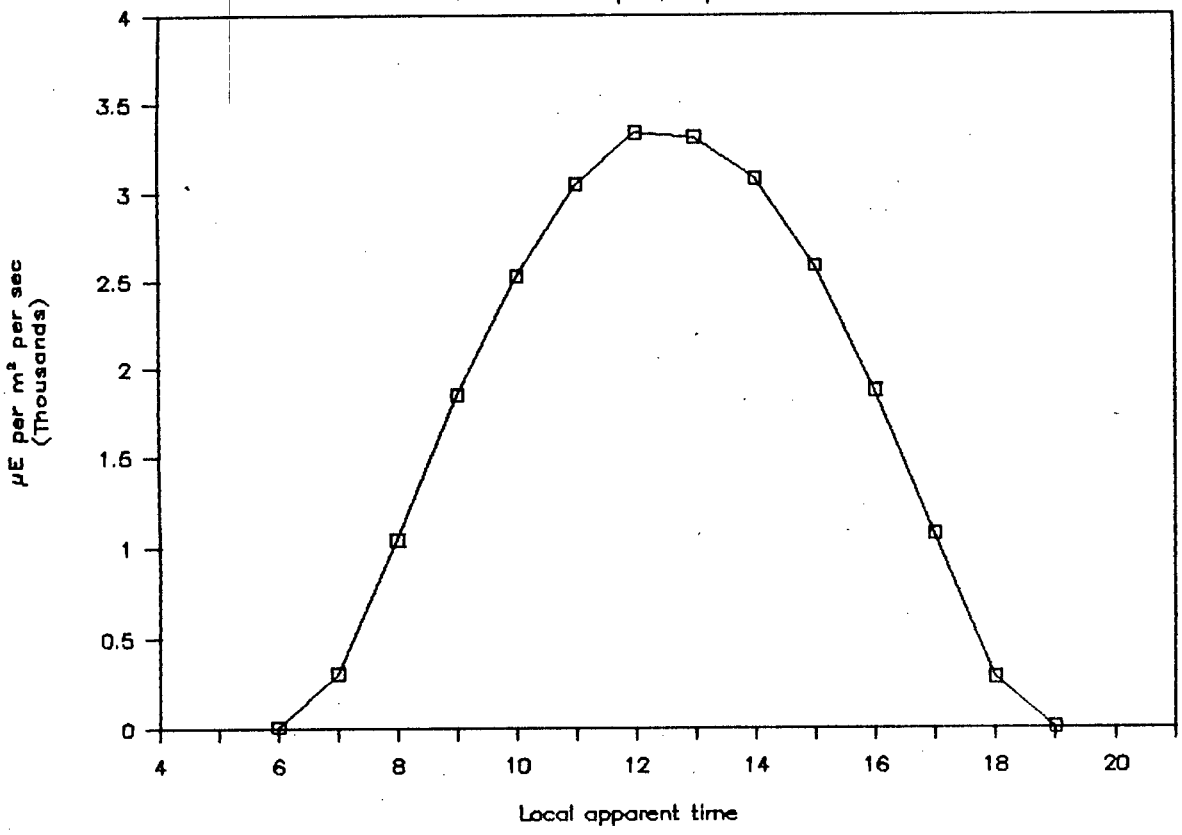
APPENDIX VI: AVERAGE SEASONAL HOURLY GLOBAL RADIATION AT D. F. MALAN AIRPORT, NEAR CAPE TOWN.





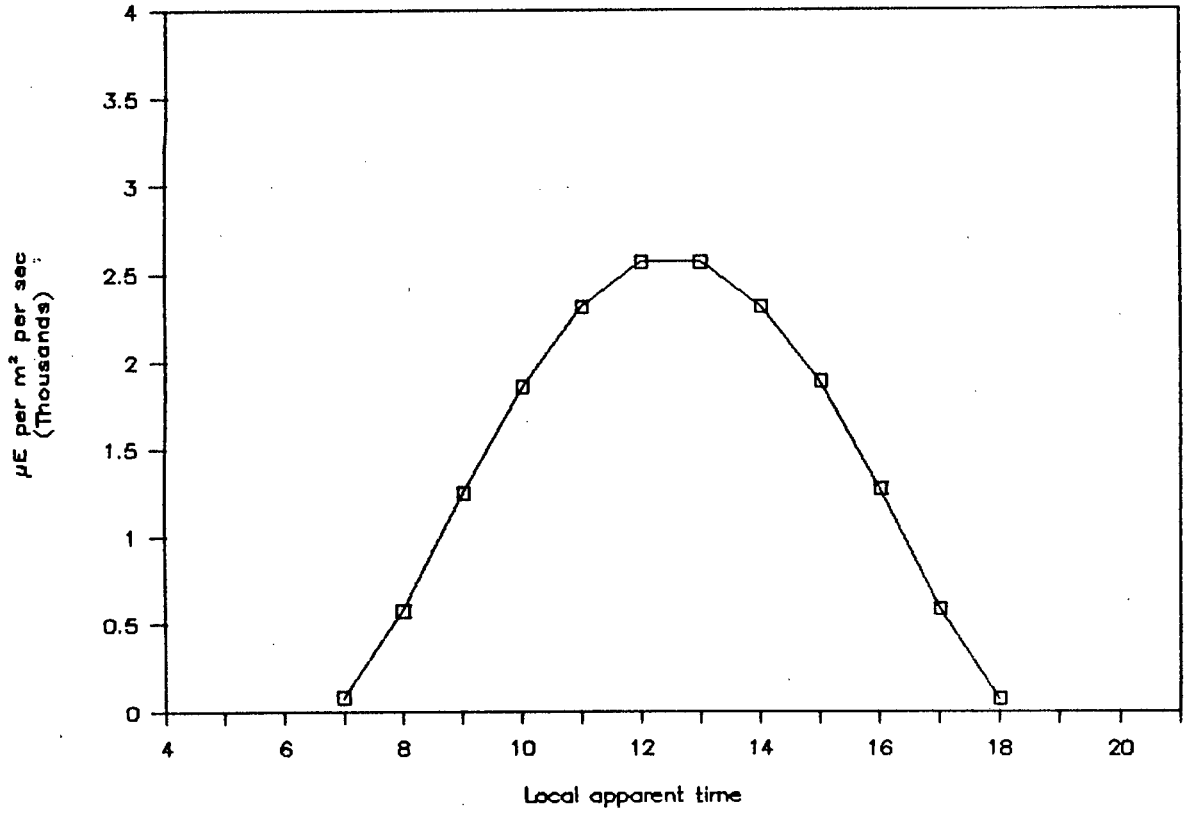
Global radiation – March 1976–82

D. F. Malan Airport, Cape Town



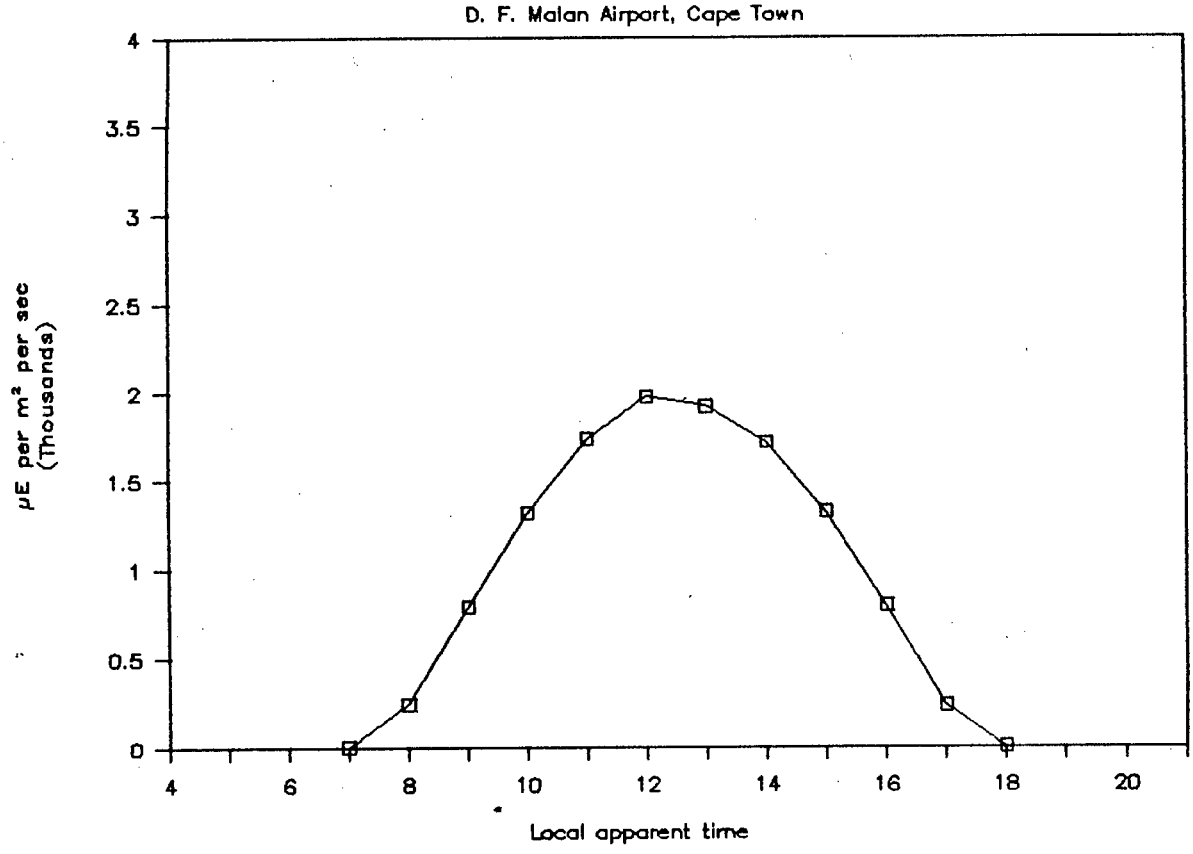
Global radiation – April 1976–82

D. F. Malan Airport, Cape Town



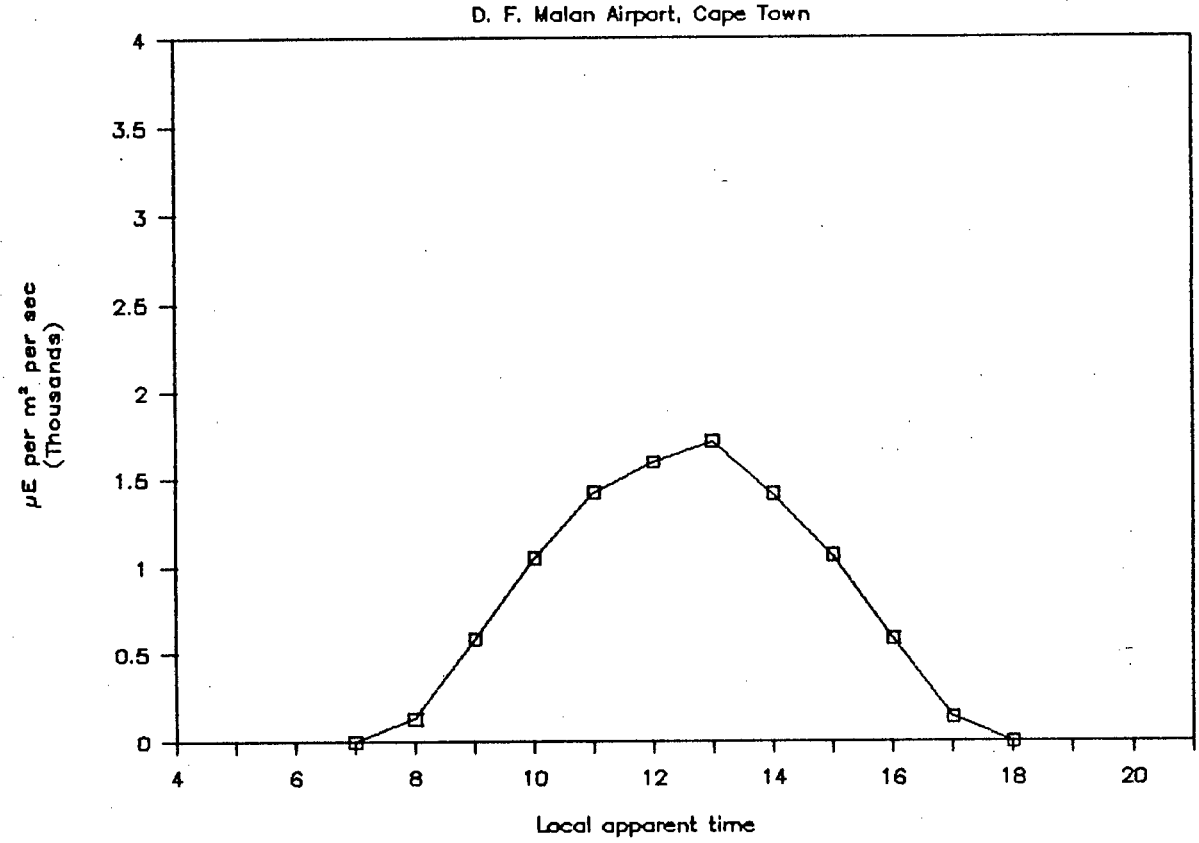
Global radiation – May 1976–82

D. F. Malan Airport, Cape Town



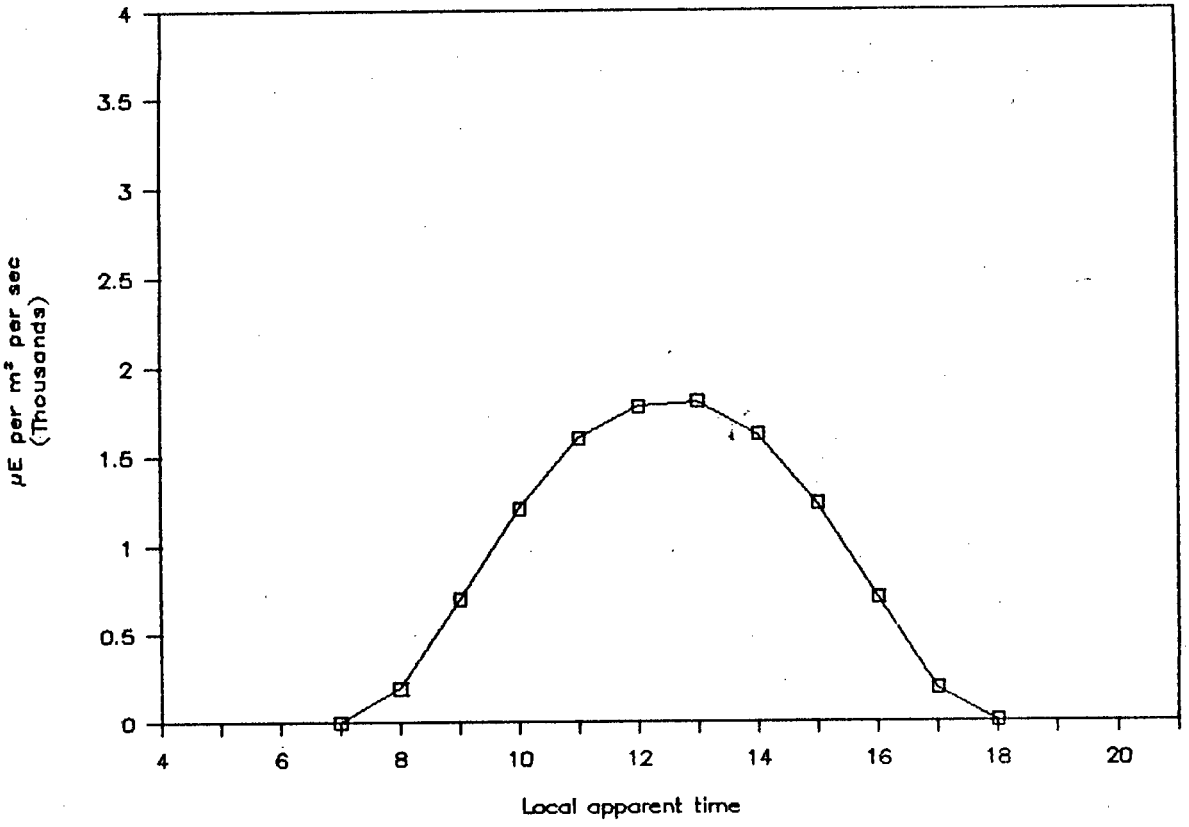
Global radiation – June 1976–82

D. F. Malan Airport, Cape Town



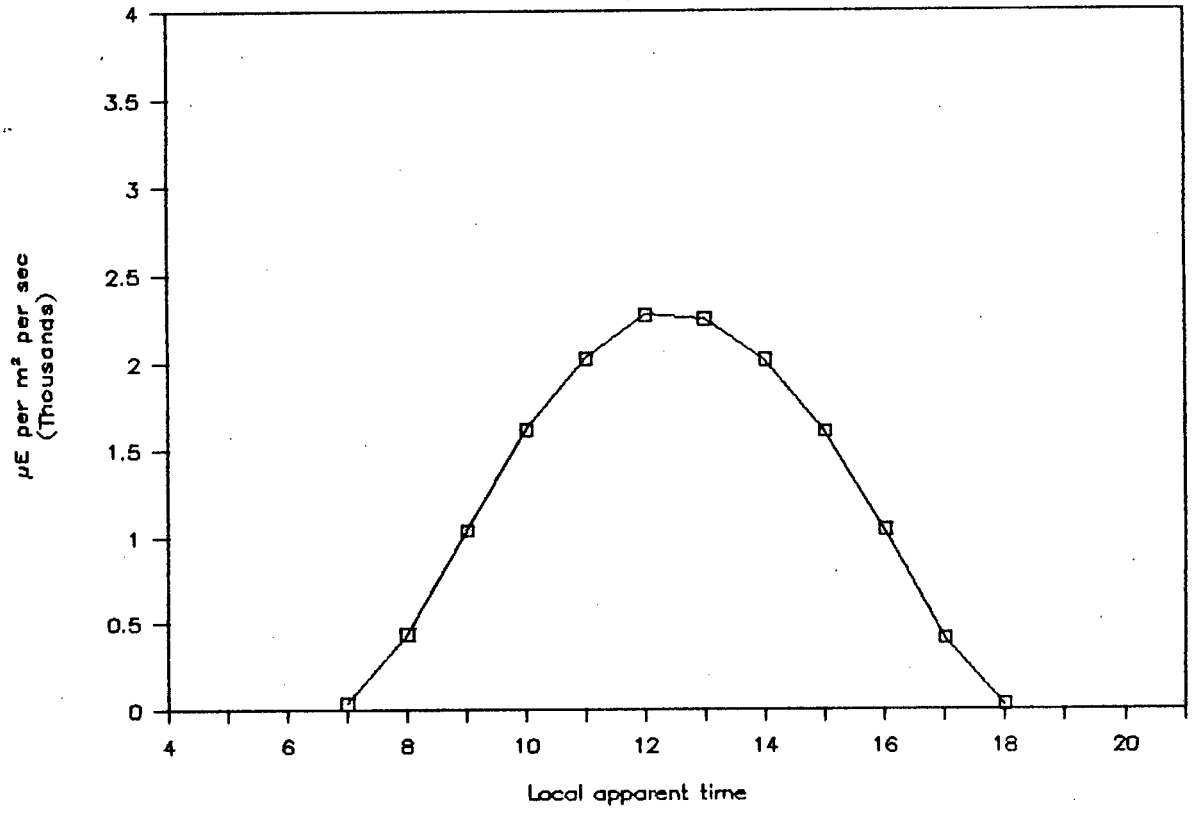
Global radiation – July 1976–82

D. F. Malan Airport, Cape Town



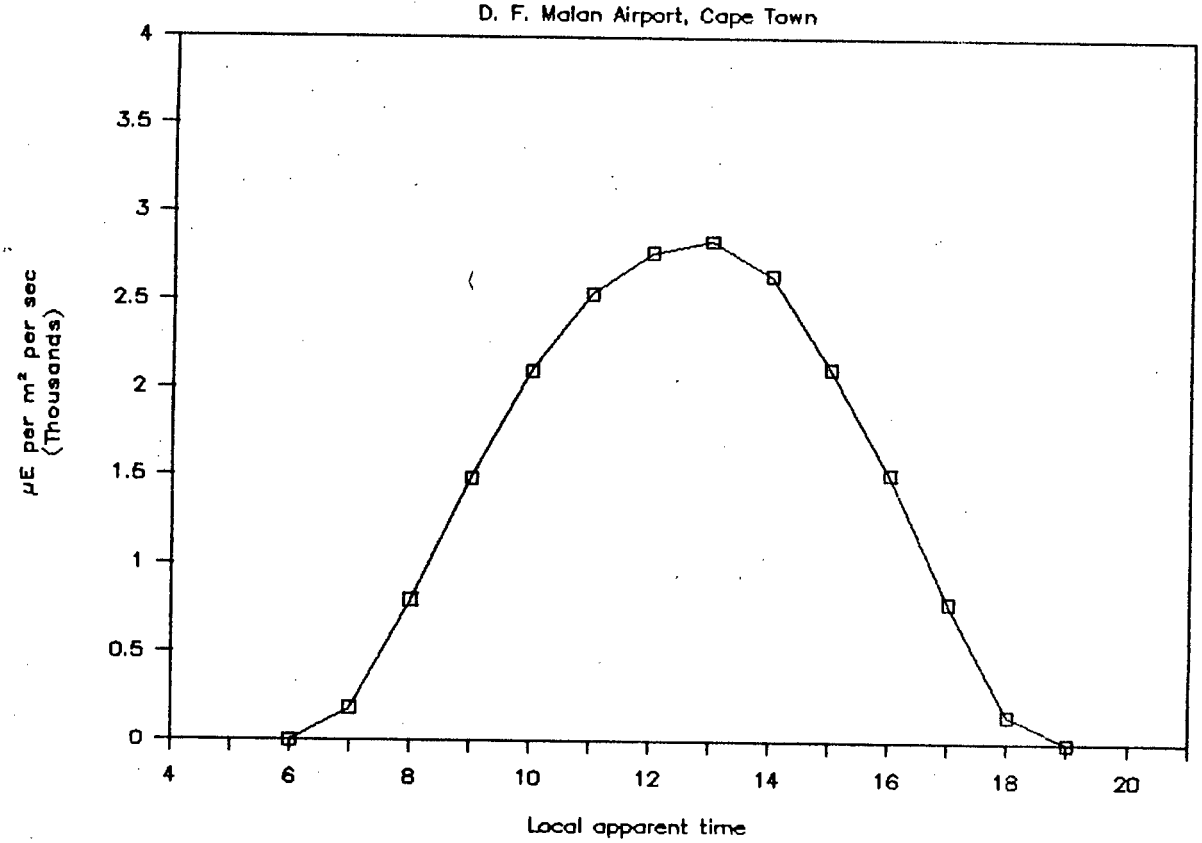
Global radiation – August 1976–82

D. F. Malan Airport, Cape Town



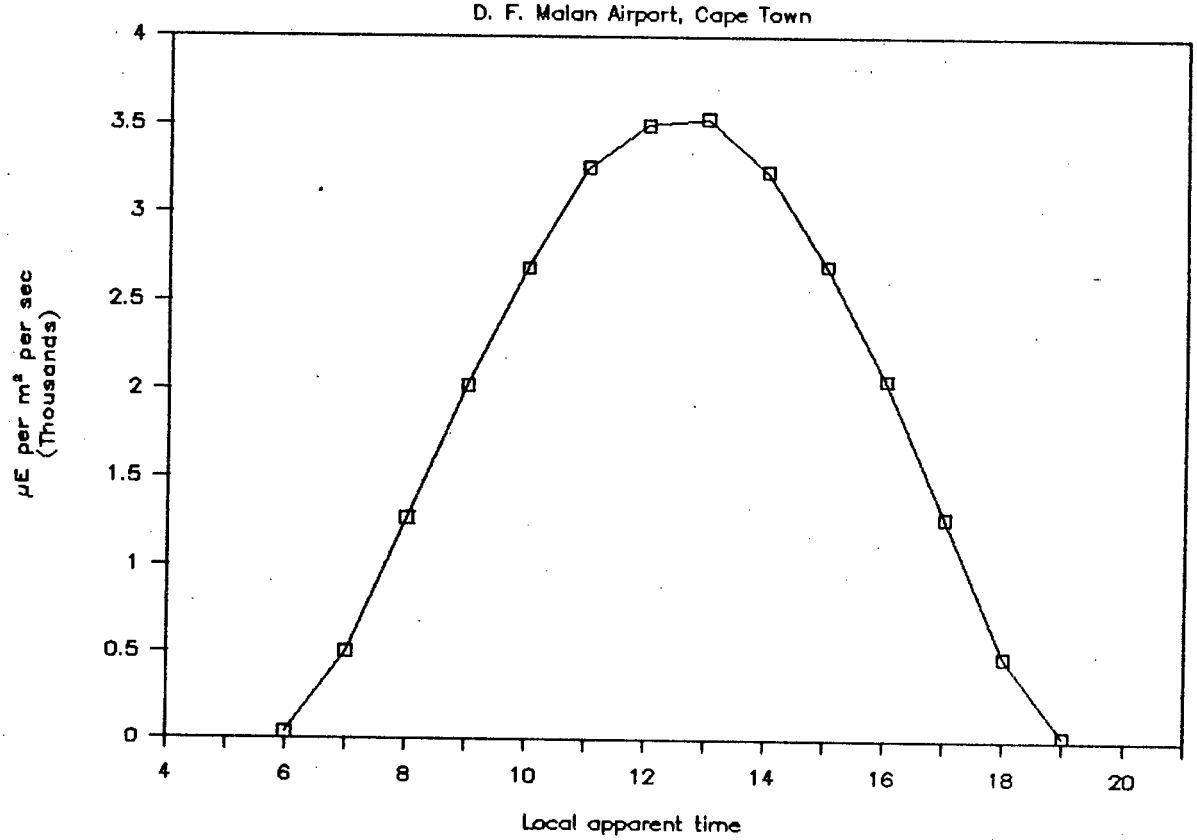
Global radiation – September 1976–82

D. F. Malan Airport, Cape Town



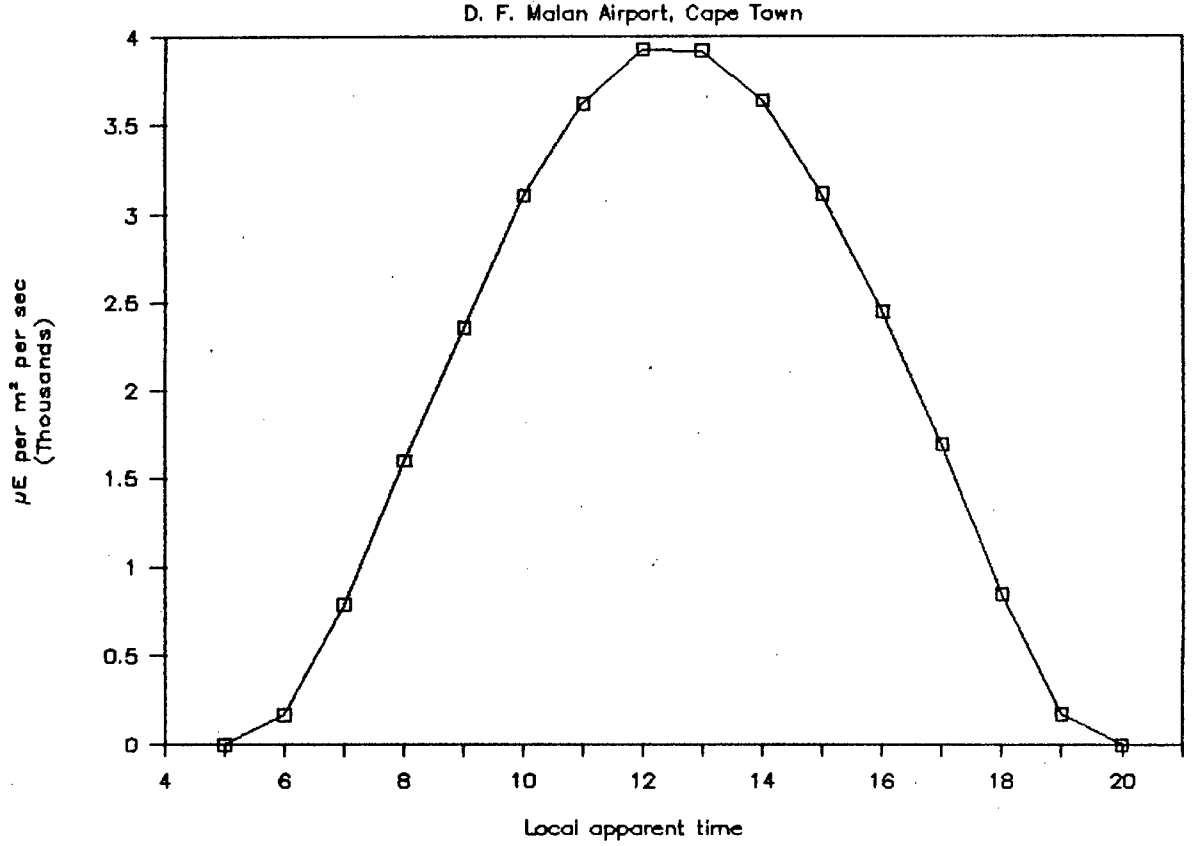
Global radiation – October 1976–82

D. F. Malan Airport, Cape Town



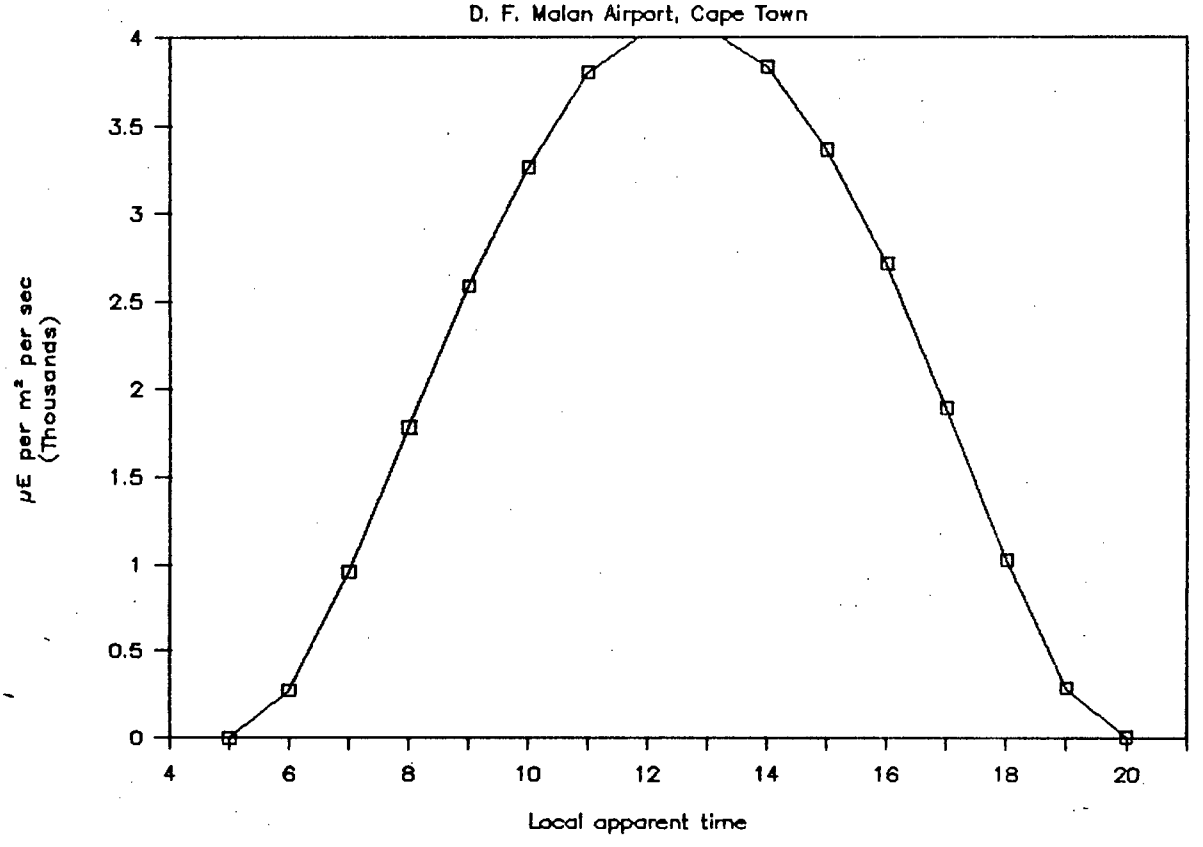
Global radiation – November 1976–82

D. F. Malan Airport, Cape Town

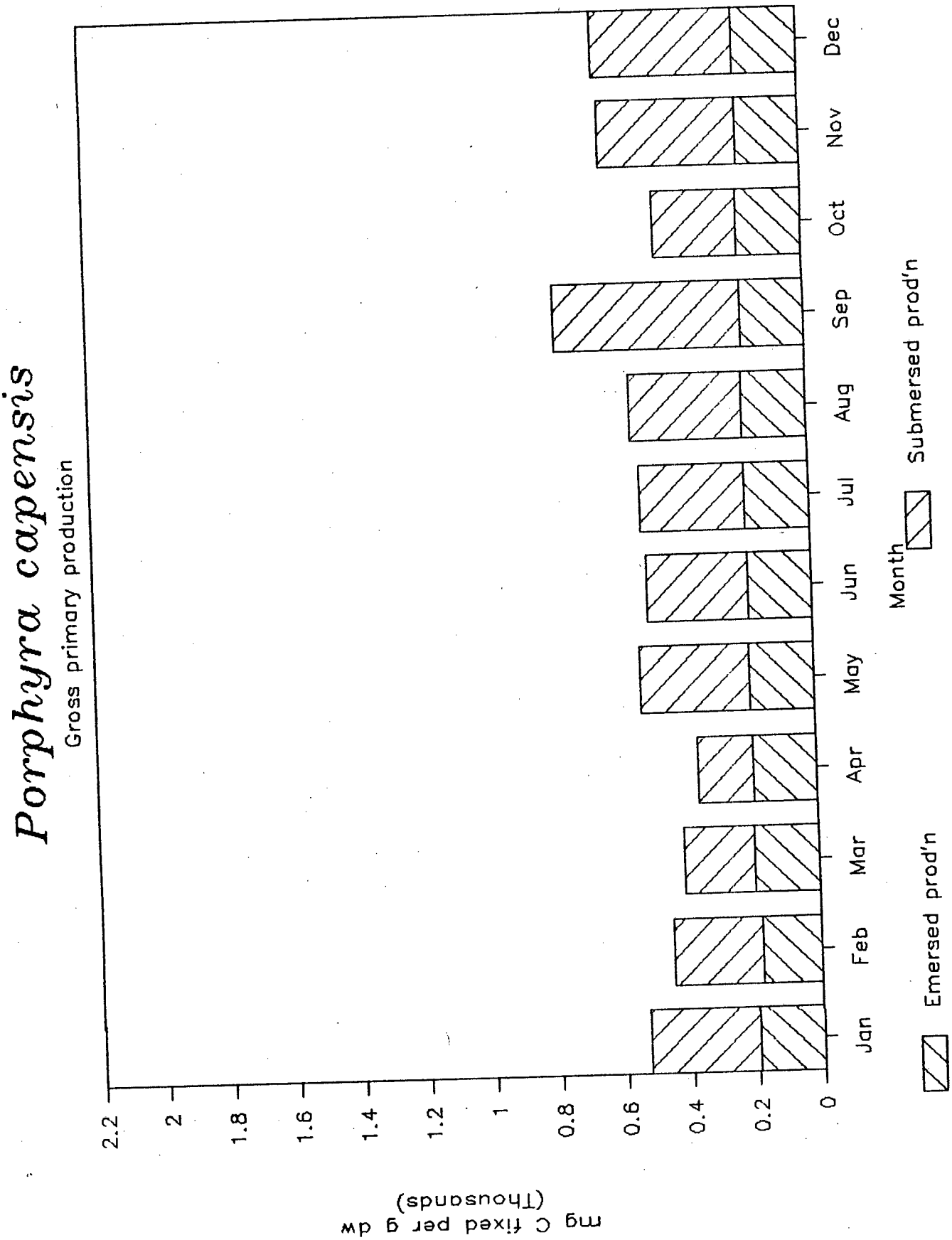


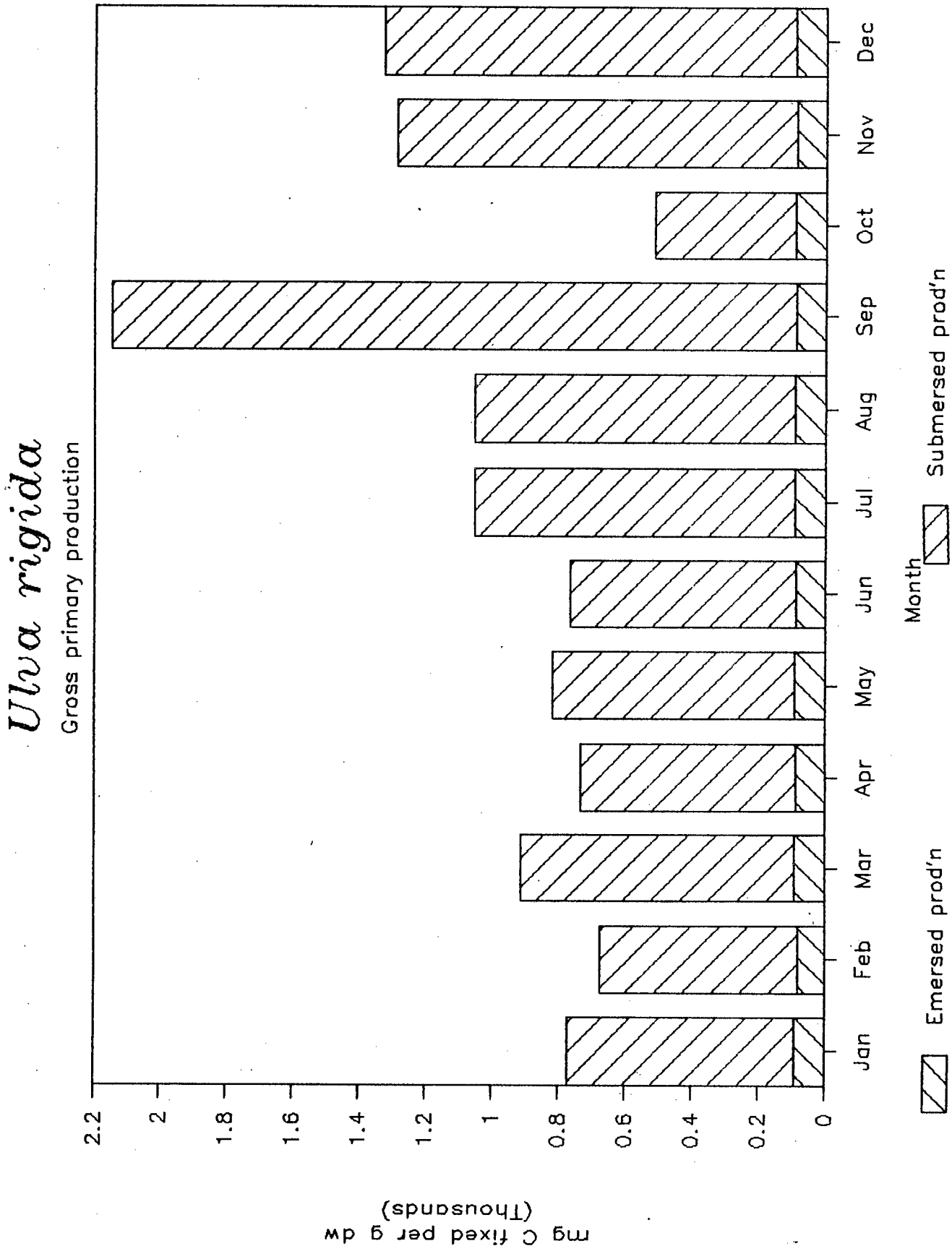
Global radiation – December 1976–82

D. F. Malan Airport, Cape Town

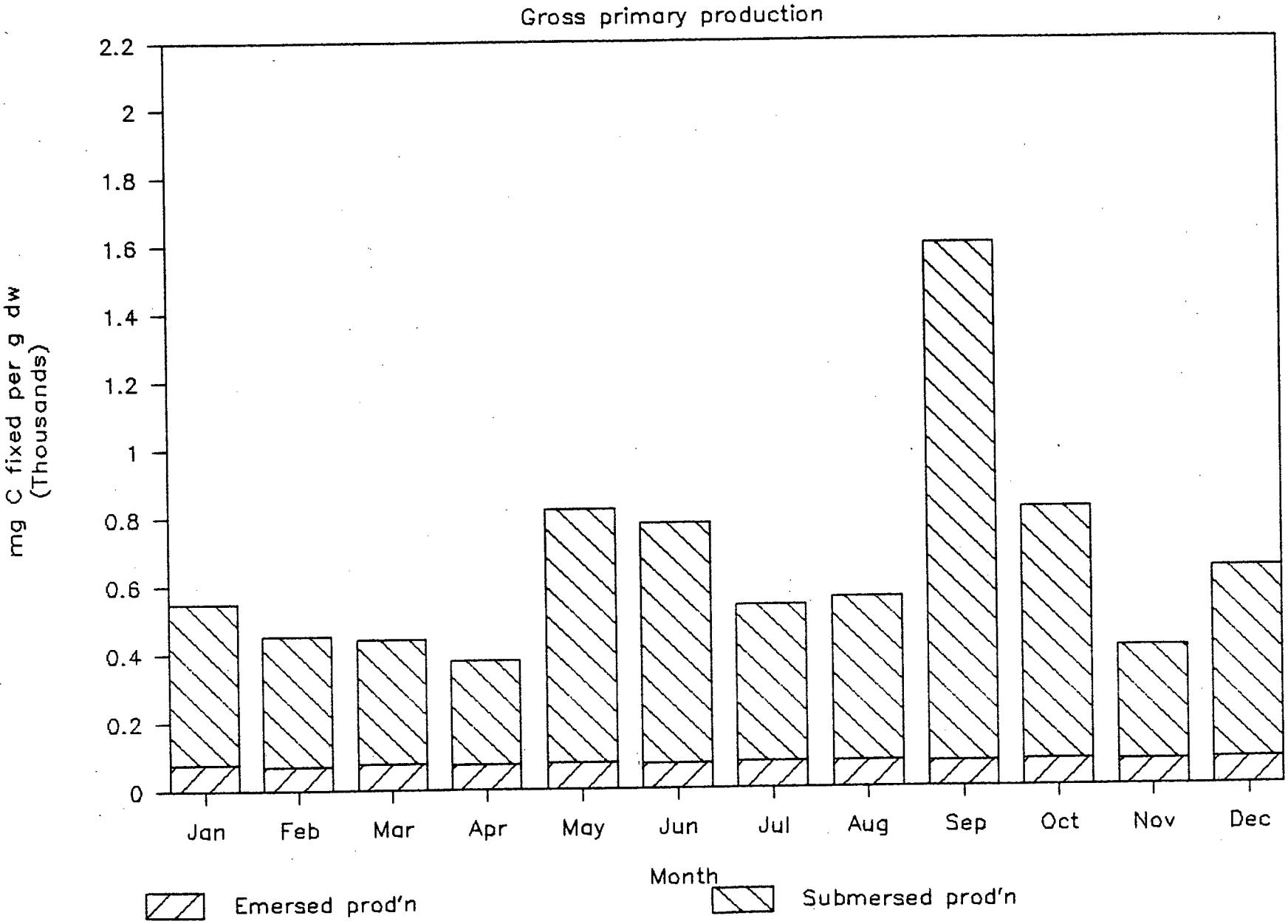


APPENDIX VII: SEASONAL PATTERNS OF GROSS CARBON FIXATION FOR INTERTIDAL SEAWEEDS AT DALEBROOK AND SUBLITTORAL SEAWEEDS AT OUDEKRAAL.

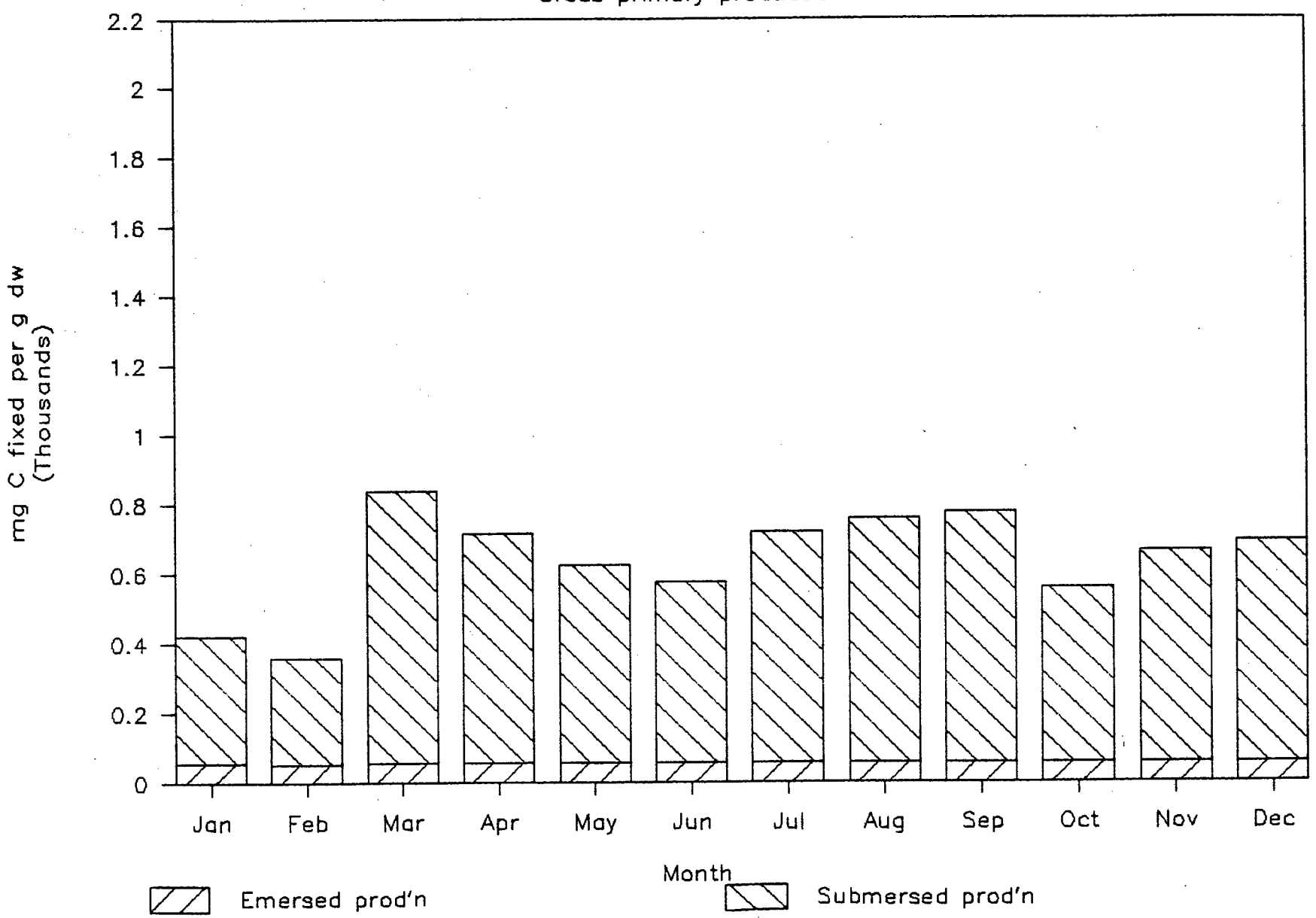


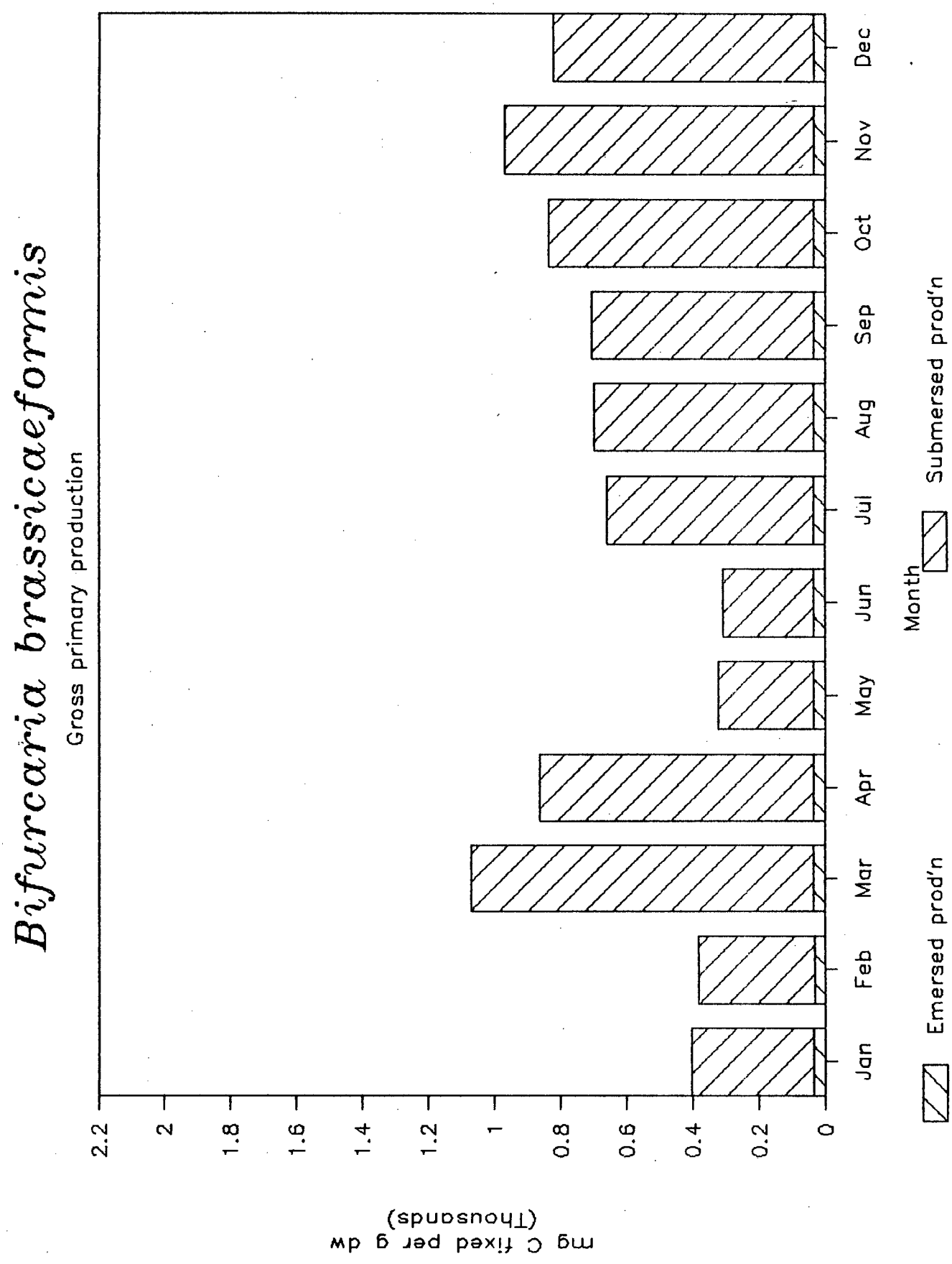

Ulva rigida
Gross primary production
mg C fixed per g dw
(Thousands)
2.2
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month
Emersed prod'n
Submersed prod'n

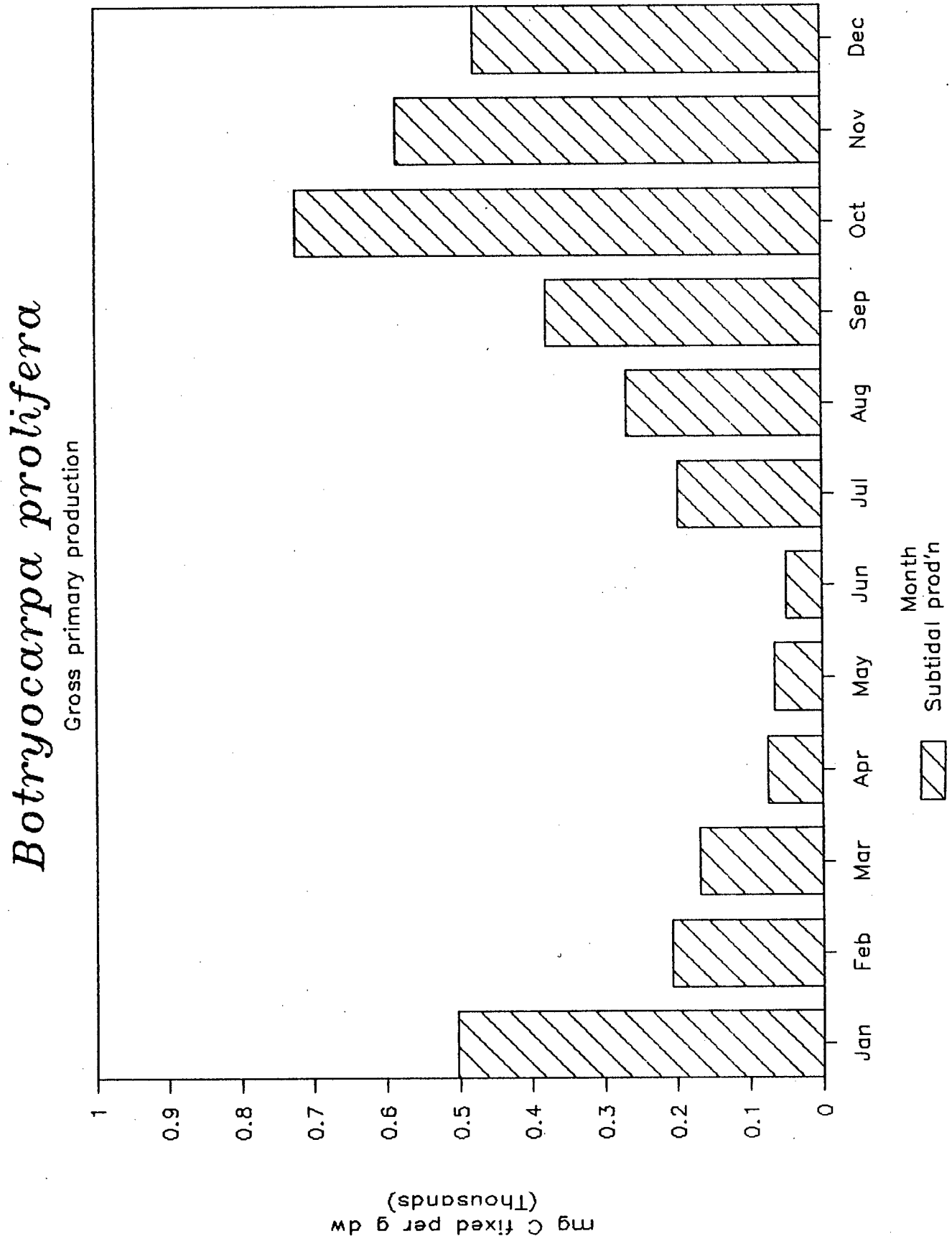
Gigartina radula



Splachnidium rugosum

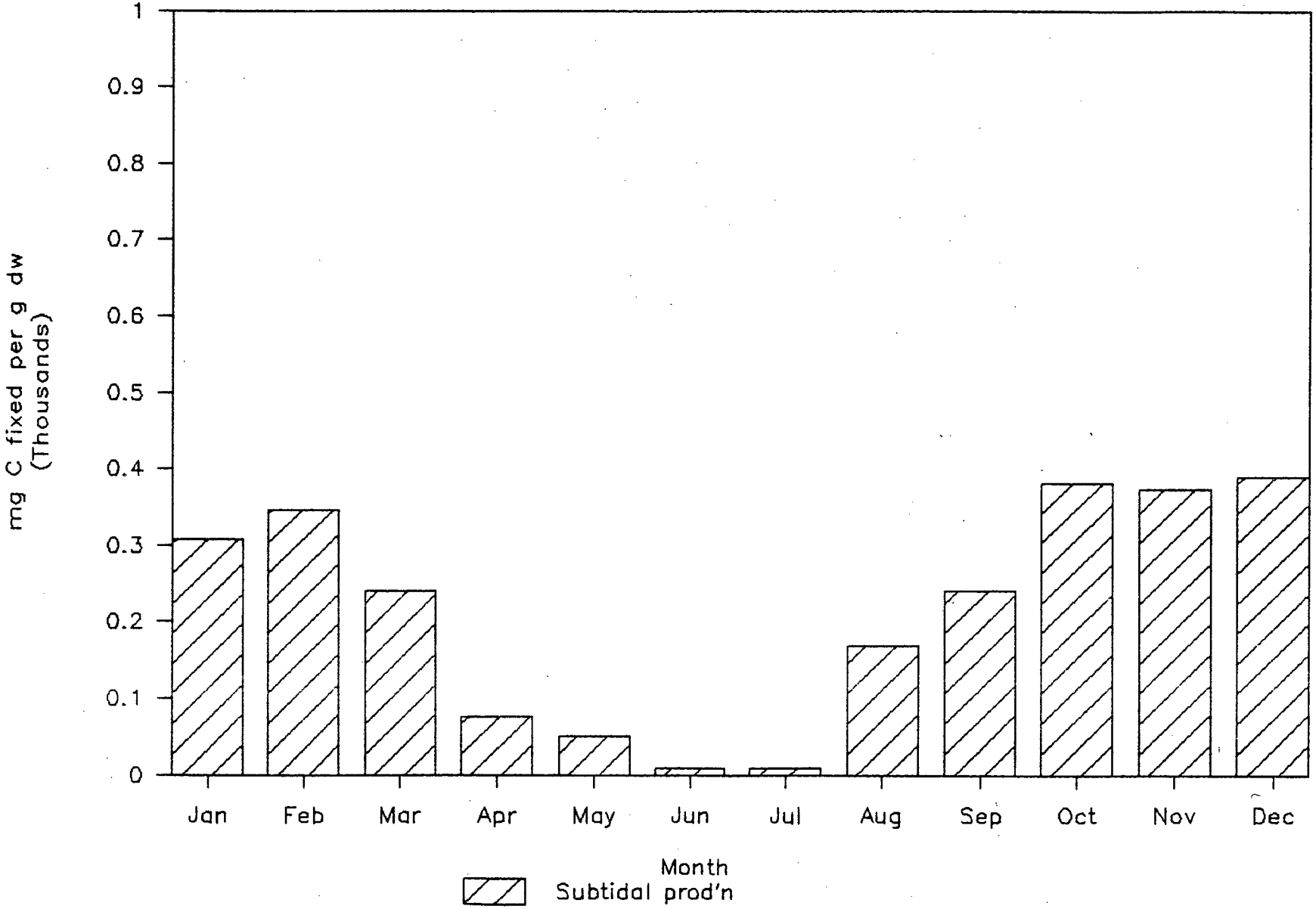



Bifurcaria brassicaefomis
Gross primary production
mg C fixed per g dw
(Thousands)
2.2
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month
Emersed prod'n
Submersed prod'n


Botryocarpa prolifera
Gross primary production
mg C fixed per g dw
(Thousands)
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month
Subtidal prod'n

Epymenia obtusa

Gross primary production



Gigartina radula