Ecklonia radiata

The ecophysiology and production ecology of the kelp

Ecklonia radiata (C.Agardh) J.Agardh,

at West Island, South Australia

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List of Abbreviations

Pm_{gross} Maximum gross photosynthesis

Pm_{net} Maximum net photosynthesis

Ik Sub-saturating photon irradiance

Rd Dark respiration rate

Ic Compensation photon irradiance

$I_{0.95}$ Photon irradiance at which gross photosynthesis is 95% of Pm_{gross}

α Photosynthetic efficiency

I_{max} Maximum photon irradiance

LHCI Light harvesting complex I

LHCII Light harvesting complex II

PSI Photosystem I

PSII Photosystem II

RC Reaction centre

σ_{PSII} the functional absorption cross-section of PSII

PAM Pulse amplitude modulation

PAR Photosynthetically active radiation (400-700nm)

UV Ultraviolet radiation (285-400nm)

BA Biomass accumulation

RBA Relative biomass accumulation

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Abstract

Ecklonia radiata (C.Agardh) J.Agardh is an important component of the macroalgal flora in temperate regions of the southern hemisphere. This work has focused on the ecophysiology of *E. radiata* and has quantified the carbon contribution of this species to further elucidate *E. radiata*'s ecological role in the nearshore marine environment.

The photosynthesis-irradiance response of *E. radiata* was investigated *in situ* throughout the year and across the depth profile. A clear seasonal change in photokinetic parameters was detected and provided strong evidence of a seasonal acclimation response. During winter an increase in the efficiency of light utilisation at low irradiance (α) was accompanied by a decrease in both the irradiance required for sub-saturation of photosynthesis (*Ik*) and that required for photosynthetic compensation (*Ic*). Photosynthetic capacity (*Pm*) also increased during the winter and autumn months and respiratory requirements (*Rd*) decreased.

Changes in photokinetic parameters across the depth profile were less pronounced and a significant decline in productivity occurred at deeper depths. The acclimation state of *E. radiata* did, however, alter across the depth profile. When deeper plants were exposed to the shallow irradiance environment they displayed characteristics of photodamage and chronic photoinhibition. The photoprotective and/or photosynthetic capacity of these plants improved after two weeks at shallow depths but the acclimation response was not completed by that time. The time scale for changes in the pigment suite appears to be longer than two weeks.

The ecological advantage of the seasonal acclimation response was demonstrated by the finding that productivity rates at any one depth remained similar throughout the year. Rates of net daily productivity were maintained at a depth of 3 m at ~ 1300 μmolO$_2$ g^{-1}dwt d^{-1} (0.016 gC g^{-1}dwt d^{-1}) and at ~ 400 μmolO$_2$ g^{-1}dwt d^{-1} (0.005 gC g^{-1}dwt d^{-1}) at a depth of 10 m.

By contrast, the growth rate of *E. radiata* is highly seasonal, with low rates of growth occurring in autumn (0.002 gdwt g^{-1}dwt d^{-1} at both 3 and 10 m) and summer (0.007 and 0.004 gdwt g^{-1}dwt d^{-1} at 3 and 10 m respectively) and higher rates in spring (0.016 and 0.007 gdwt g^{-1}dwt d^{-1}) and winter (0.015 and 0.008 gdwt g^{-1}dwt d^{-1}).

When the results of this study are placed in context with previous work, a schema of the carbon flow through an *E. radiata* forest can be constructed. The rates of biomass accumulation represented only a small proportion of the amount of carbon assimilated annually. At 3 m the gross annual production was 7561 gC m^{-2} y^{-1}, of which 863 gC m^{-2} y^{-1} was incorporated into biomass, 2091 gC m^{-2} y^{-1} respired, 216 gC m^{-2} y^{-1} utilised for reproduction and 4391 gC m^{-2} y^{-1} was exuded. The equivalent amounts for 10 m were 1904 gC m^{-2} y^{-1} gross production, 307 gC m^{-2} y^{-1} incorporated into biomass, 983 gC m^{-2} y^{-1} respired, 77 gC m^{-2} y^{-1} incorporated into reproductive tissue and 537 gC m^{-2} y^{-1} exuded.

Declaration

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by any other person, except where due reference has been made in the text.

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Acknowledgments

Chapter 1 : General Introduction

Rationale

Temperate benthic macroalgae are highly productive members of the nearshore marine community (Mann 1973, Gao and McKinley 1994). The Laminariales is an important benthic order and includes some of the most productive species in the subtidal zone (Mann 1972, Mann 1973, Mann and Kirkman 1981, Kirkman 1984, Hatcher *et al.* 1987, Duggins *et al.* 1989). The Laminariales (or "kelps") dominate many temperate and sub-temperate rocky shorelines in both the northern and southern hemispheres, providing habitat for diverse ranges of animals and smaller algae and produce an important energy source for marine food chains (e.g. Brown 1964, Griffiths *et al.* 1983, Brown *et al.* 1989, Duggins *et al.* 1989, Duggins and Eckman 1994, Vetter 1994, Bustamante *et al.* 1995, Bustamante and Branch 1996, Polis and Hurd 1996, Jennings and Steinberg 1997, Soares *et al.* 1997, Harrold *et al.* 1998). A knowledge of the factors affecting kelp productivity is important for an understanding of the dynamics of nearshore benthic ecosystems.

Over the past few decades a large amount of research on productivity in marine systems has focused on members of the Laminariales. The bulk of this work has been conducted on the genera *Laminaria* and *Macrocystis* in the temperate and arctic regions of the northern hemisphere (e.g. Delf 1932, Parke 1948, John 1969, King and Schramm 1976a, Hatcher *et al.* 1977, Chapman and Craigie 1978, Gerard and Mann 1979, Kain 1979, Lüning 1979, Wheeler 1980a, Wheeler and North 1981, Gagné *et al.* 1982, Drew 1983, Druehl 1984, Gerard 1984, Dunton and Schell 1986, Gerard 1986, Wheeler and Druehl 1986, Davison 1987, Gendron 1989, Dunton 1990, Sakanishi *et al.* 1990, Dring *et al.* 1994, Henley and Dunton 1995, Machalek *et al.* 1996, Henley and Dunton 1997, Hurd and Stevens 1997, Hanelt 1998, Sjøtun *et al.* 1998, Makarov and Vosoboinikov 2001). In the southern hemisphere it is species from the Laminarialean genus *Ecklonia* that are common, and often dominant or co-dominant, over many parts of the mid to upper sublittoral zones in temperate waters (Stephanson 1939, Shepherd and Womersley 1970, Shepherd and Womersley 1971, Shepherd and Womersley 1976, Kirkman 1981, May and Larkum 1981, Choat and Schiel 1982, Novaczek 1984c, Womersley 1987, Sanderson 1997, Soares *et al.* 1997). The genus is represented in Australia by *Ecklonia radiata* (C.Agardh) J.Agardh, which is distributed over much of the southern Australian coastline, including Tasmania, and also around New Zealand (Womersley 1987). Sublittoral forests dominated by *E. radiata* support productive understorey algal populations which depend upon the presence of the kelp canopy to exclude competitors (Kennelly 1987 b,c). *E. radiata* also provides energy to the wide variety of secondary producers which exist

within the forest (Edmonds and Francesconi 1981, Robertson and Lenanton 1984, Kennelly 1991, Kennelly and Underwood 1992, Kennelly and Underwood 1993).

Rocky shorelines in the temperate and arctic northern hemisphere support a diverse range of both subtidal and intertidal kelps from over 20 genera (Chapman and Chapman 1973, Kain 1979, Lobban and Harrison 1994). The relative diversity of kelps throughout the entire southern hemisphere remains much lower (3-4 genera) than that found in comparable northern hemisphere locations (Bolton 1996). For much of its wide distribution *E. radiata* is the sole representative of the order Laminariales (Womersley 1987). Other species of kelp in Australian waters are *Macrocystis pyrifera* (Linnaeus) C.Agardh, *M. angustifolia* Bory and *Lessonia corrugata* Lucas, which have a more restricted geographical distribution than *E. radiata* (Womersley 1987, Sanderson 1997). The invasive kelp *Undaria pinnatifida* (Harvey) Suringar was introduced to Australian waters in the late 1980's and is currently distributed in parts of Tasmania and Victoria (Campbell *et al.* 1999). One population of vegetatively reproducing *Ecklonia* has also been recorded in south-western Australia, and has been assigned to *Ecklonia brevipes* J.Agardh (Huisman 2000). Kelps are largely restricted to the subtidal in the southern hemisphere (Womersley 1987), whereas they are abundant in many littoral regions of the northern hemisphere (Taylor 1957, Chapman and Chapman 1973, Abbott and Hollenberg 1976). Despite this low species diversity the Laminariales remain dominant (in terms of both cover and biomass) on rocky coasts throughout much of southern Australia, with *E. radiata* often occurring as the habitat dominant (Shepherd and Womersley 1970, Shepherd and Womersley 1976, Kirkman 1981, Kennelly 1983, Larkum 1986, Kennelly 1987b, Collings 1996).

The obvious dominance of *E. radiata* has meant it has been the subject of numerous investigations in both Australia and New Zealand. These include work on the light and temperature response of the sporophyte and gametophyte generations (Novaczek 1980, Novaczek 1984b, Novaczek 1984c, Wood 1987), on growth and development (Kirkman 1981, Mann and Kirkman 1981, Kirkman 1984, Novaczek 1984a, Larkum 1986, Hatcher *et al.* 1987, Kirkman 1989), secondary metabolite production and its effect on epiphytes and herbivores (Jennings and Steinberg 1994, Steinberg 1994, Steinberg 1995, Jennings and Steinberg 1997), recruitment processes (Kennelly 1983, Kennelly 1987a, Kennelly 1987b, Kennelly and Underwood 1992), interactions with understorey algae (Kennelly 1987c, Kennelly 1989, Kendrick *et al.* 1999), interactions with herbivores (Choat and Schiel 1982, Andrew and Jones 1990, Choat and Clements 1992), and ecotoxicological investigations of

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the effects of sewage effluent (Burridge *et al.* 1996, Bidwell *et al.* 1998, Ajani *et al.* 1999, Burridge *et al.* 1999).

Research on the primary productivity of *E. radiata* has focussed on growth rate estimates based on length increments (Mann and Kirkman 1981, Kirkman 1984, Novaczek 1984a, Larkum 1986, Hatcher *et al.* 1987, Kirkman 1989). This method provides useful information about biomass accumulation rates and enables investigation of growth strategies, but it does not, however, allow accurate quantification of primary production. Carbon losses through processes such as exudation, herbivory and respiration remain unaccounted for (Larkum 1986) and therefore this approach cannot provide a measure of carbon assimilation rates. No study has yet been published which quantifies *in situ* the net primary productivity of *E. radiata*, information which is vital in order to fully understand the ecological role of this widespread species.

The macroalgal flora in southern Australia is amongst the most diverse on the planet (Womersley 1990). A major treatise is nearing completion which documents this flora and provides taxonomic keys (Womersley 1984, 1987, 1994, 1996, 1998). Ecological research is sparse, although the work of Shepherd and Womersley (1970, 1971, 1976, 1981) has provided a picture of distributional patterns in relation to depth and water motion at numerous sites on the South Australian coast. Shepherd (1979) investigated the flora of the Cape Northumberland region in the south-east of South Australia, focusing on rhodophytes but also including a preliminary study of growth and erosion processes in *E. radiata*. A few recent studies have investigated the photophysiology (Cheshire *et al.* 1996, Westphalen and Cheshire 1997) and composition (Collings 1996, Collings and Cheshire 1998) of this flora at the community level.

The proximity of the bulk of Australia's human population to the coastal regions has resulted in degradation of coastal ecosystems, largely through impacts on water quality. Waste water discharge, agricultural run-off and sand dredging all result in increased turbidity (Shepherd *et al.* 1989) and thus have an impact on coastal water quality and, consequently, the subtidal light environment. Marine macroalgae occurring on rocky reefs situated near population centres will experience changes in their light environment over and above "natural" fluctuations. Given their ecological role, the response of macroalgae to these changes has consequences for the entire system. It is therefore vital to understand how these algae respond to "unnatural" changes in their light environment in order to be able to predict the effects of these influences.

Here, I will present an overview of the ecophysiology of *E. radiata* in South Australia. The photosynthetic response of *E. radiata* to changing light regimes will also be examined.

Background

Ecklonia radiata (C. Agardh) J. Agardh

The genus *Ecklonia* consists of nine species, three of which occur in the southern hemisphere (*E. radiata*, *E. brevipes* and *E. maxima*). *E. radiata* was thought to be the only Australian representative, although in Western Australia one population of vegetatively reproducing *Ecklonia* has recently been assigned to *E. brevipes* (Huisman 2000). *E. radiata* is distributed in Australia from Geraldton in Western Australia along the southern Australian and Tasmanian coastlines to Caloundra in Queensland (Womersley 1987) and also occurs in New Zealand and South Africa. *E. radiata* occurs along the depth profile from the upper sublittoral to a depth of around 44 m (Womersley 1987).

E. radiata has a diplohaplontic life cycle, with a large macroscopic sporophyte that produces zoospores which develop into dioecious, microscopic gametophytes (Womersley 1987). The gametophytes produce oogamous gametes which, following fusion, develop into the sporophyte generation. Reproduction on the sporophyte takes place in sori, which develop on the surface of the primary and secondary laterals (Womersley 1987). Three morphological stages in the sporophyte generation were defined by Kirkman (1981) (Figure 1.1). Stage One plants have an entire, oblong shaped blade; Stage Two plants have small protuberances on the blade just above the stipe and also have simple entire secondary blades; Stage Three individuals have compound lateral blades (Kirkman 1981). Growth occurs mainly at the proximal end of the thallus in the meristematic region above the stipe, while erosion of older tissue takes place at the distal end.

Life history processes in *E. radiata* were comprehensively studied by Novaczek (1984b, 1984c, 1984a), who conducted culture and field studies on a long-stiped *E. radiata* population in Goat Island Bay, north-east New Zealand. Her work extended from previous culture studies on *Ecklonia* (see e.g. Papenfuss 1942, Jennings 1967) to investigate the factors controlling growth and reproduction in both the gametophyte and sporophyte phases, focusing particularly on the influence of light and temperature.

**Stage One
(new recruit)** **Stage Two
(juvenile)** **Stage Three
(adult)**
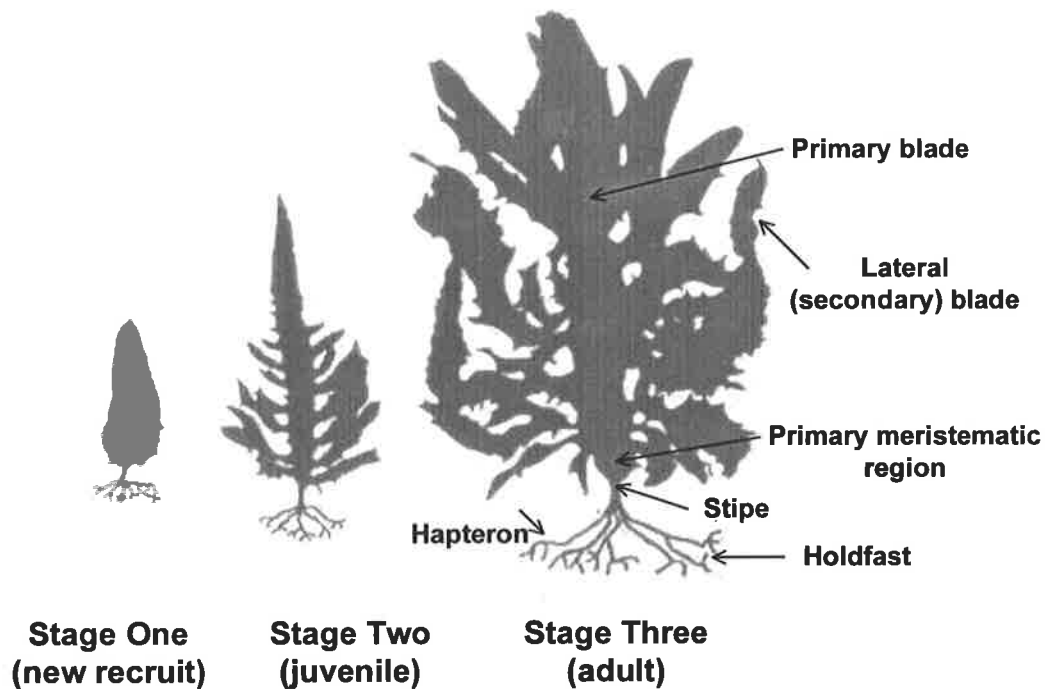
Figure 1.1 The three morphological stages of *Ecklonia radiata* as defined by Kirkman (1981). Stage one plants are up to 15 cm in length, stage two 15-70 cm and stage three 20-90 cm. Throughout this thesis stage two individuals are refered to as "juveniles" and stage three individuals as "adults" (from Kirkman 1981).

Novaczek (1980) suggested that in contrast to many Laminarialean populations in the northern hemisphere the growth strategy of *E. radiata* was controlled more by light than nutrient availability, with phenological events occurring later at greater depths (Novaczek 1984b). The peak in growth rates occurred in spring or summer and was lowest in autumn or winter. The timing of peaks in growth rates (frond and stipe elongation) and also of reproductive events (sorus production, zoospore release, sporophyte recruitment) were about three months later at the 15 m site in comparison to the7 m site (Novaczek 1984a).

This annual pattern of growth is similar to that found in short stiped *E. radiata* in Western Australia (WA) (Kirkman 1984, Hatcher *et al.* 1987, Kirkman 1989) and in New South Wales (NSW) (Larkum 1986), with a delay in maximum productivity at increased depth also found by Kirkman (1989). Rates of production in the WA studies (Kirkman 1984, Kirkman 1989) and NSW studies (Larkum 1986) were around 3-3.5 kgdwt m^{-2} y^{-1}, from shallow populations with densities of 20-25 plants m^{-2}.

Production rates were lowest in autumn (2-4.4 gdwt m^{-2} d^{-1}) and highest in spring or summer (13-20 gdwt m^{-2} d^{-1}) (Kirkman 1984, Larkum 1986). The rate of production of *E. radiata* at

Goat Island Bay was similar at around 3 kgdwt m^{-2} y^{-1} (Novaczek 1984a). *E. radiata* growing at densities of 5 plants m^{-2} at depth of 14 m off southern Tasmania displayed lower annual production rates of around 0.3 kgdwt m^{-2} y^{-1} and this population was considered to be light-limited for much of the year (Sanderson 1990). The dominant factor affecting seasonal patterns of production in the above studies is the light regime, although temperature was implicated in controlling both latitudinal limits of distribution (Novaczek 1984c, Hatcher *et al.* 1987) and growth rates at water temperatures greater than 18-20 °C (Kirkman 1984, Hatcher *et al.* 1987).

Nitrate availability may also limit growth at certain times of the year (Kirkman 1984). In addition, coastal upwellings, combined with other biotic and abiotic factors, were thought to be involved in causing the large between-site differences in growth rates and survivorship of *E. radiata* at Abrolhos reef in Western Australia (Hatcher *et al.* 1987). Production levels also decreased with increasing depth (Novaczek 1984a, Kirkman 1989), due primarily to a decrease in irradiance (Kirkman 1989). Ultraviolet radiation damage has also been implicated in reducing summer growth rates and in determining the upper depth limit for growth in *E. radiata* (Wood 1987).

West Island: Macroalgal community and Study site

West Island (35°36'25"S; 138°35'27"E) is a granite outcrop located in the north-western area of Encounter Bay, and is situated approximately 800 m offshore (Figure 1.2). The island is a Conservation Park and the subtidal region extending to 100 m from the island's shore has been an aquatic reserve since 1971 (Robinson *et al.* 1996). The southern region of the island is exposed to the prevailing south-westerly swell which originates in the Southern Ocean, and this portion of the island, as well as the eastern edge, is characterised by steep cliffs that descend from a height of ~40 m above sea level to a depth of up to 29 m below sea level (Shepherd and Womersley 1970). The more protected north-western region, where the West Island research station is located, slopes more gently from the summit and extends into the subtidal to a depth of around 5 m. Towards the northern edge of the island the subtidal region extends deeper into the sublittoral, to a depth of around 25 m. The island supports large breeding colonies of several seabird species including Fairy Penguins, Crested, Fairy and Caspian Terns, and Silver Gulls, as well as large numbers of both White's and Cunningham's Skinks. A colony of the New Zealand Fur Seal is also found near Penguin Rock on the northern edge of the island.
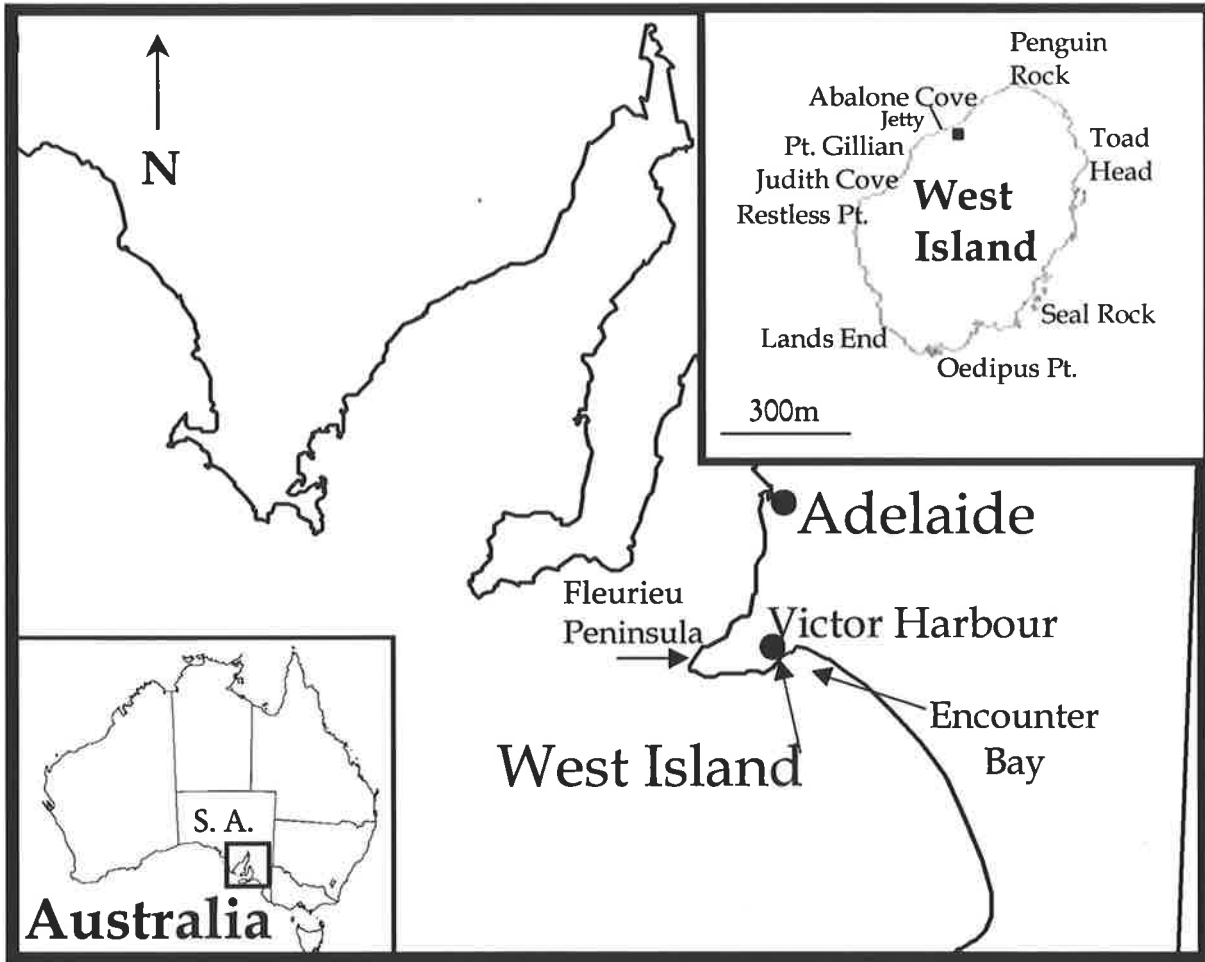
Figure 1.2 Location of West Island. The majority of the work in this thesis was conducted in the subtidal region between Point Gillian and Penguin Rock (see inset).

The subtidal region is characterised by large granite blocks, which form numerous crevices and caverns, and smaller granite boulders (Shepherd and Womersley 1970). A rich macroalgal flora is found on this substratum, and the various types of macroalgal communities and associations were described by Shepherd and Womersley (1970). The macroalgal community in the study area (see Plate 1.1) was dominated by *E. radiata* but was also comprised of other large stipate canopy-forming species, such as the Fucaleans *Cystophora*, *Scytothalia* and *Seirococcus*, with an understorey of species from genera such as *Corallina*, *Dictyota*, *Caulerpa*, *Codium*, *Phacelocarpus*, *Osmundaria* and *Plocamium*. The selected study sites were dominated by *E. radiata* forests, with predominantly encrusting coralline understoreys (Plate 1.2).

Plate 1.1 Example of the macroalgal community at West Island. The canopy is composed of large stipate species such as *E. radiata* (centre) and *Cystophora*, and the understorey is comprised of a diverse range of species, in particular rhodophytes (bottom).

Plate 1.2 The 3 m study site at West Island.

Aims

This thesis aims is to build on previous work on *E. radiata* in Australasian waters by utilising recent technological advances to further the understanding of the ecological role of this species. The first objective is to quantify the amount of carbon assimilated by sporophytes of *E. radiata* and to estimate the subsequent carbon contribution made by this alga. This work will provide an understanding of how *E. radiata* alters light harvesting and photokinetics in response to seasonal changes in the underwater environment. The second objective is to investigate the acclimation response of *E. radiata* sporophytes to short term changes in the light regime.

The specific aims are:

1. To measure photokinetics and light harvesting pigments in *E. radiata* in order to understand the photosynthetic response over seasons and depths (Chapter 2).

2. To quantify *in situ* the net primary production of *E. radiata*, over seasons and depths, and compare to rates of biomass accumulation (Chapters 3 & 4).

3. To conduct a series of *in situ* transplant experiments to determine the nature of *E. radiata*'s acclimation response (Chapter 5).

4. To provide a synthesis of the findings and to incorporate these into a schema of the annual carbon flow through an *E. radiata* forest (Chapter 6).

Chapter 2 : Seasonal and Depth Related Patterns in the Photosynthetic Apparatus

Macroalgae must contend with the highly variable physical environment in which they live. This chapter describes the pattern of change in the photosynthetic physiology of *E. radiata* across the depth profile and across seasons.

Introduction

Light has a profound influence on rates of photosynthesis, as it is energy from photons that drives the photosynthetic reactions. Photosynthesis is also limited by other environmental factors including temperature and the availability of nutrients and inorganic carbon. Light-limited photosynthesis is dependant upon the rate of photon absorption by the antennae pigments (light harvesting complexes; LHCI and LHCII) associated with photosystems I and II (PSI & PSII) (Figure 2.1) and the quantity of energy then transferred to the reaction centres of the photosystems, in addition to the subsequent efficiency of utilising the absorbed energy for photochemistry and ultimately fixing carbon dioxide (Kirk 1994, Falkowski and Raven 1997) (Figure 2.2). Therefore, understanding the photosynthesis-irradiance response is fundamental to an understanding of macroalgal primary production.

The underwater light field is variable on all temporal scales. The amount of light a particular chloroplast receives varies on a scale of milli-seconds, due to light flecks caused by surface waves or water motion, on a diel cycle through to a scale of months due to seasonal changes in solar angles. Irradiance levels also vary along the depth profile due to attenuation in the water column, which also results in changes in the spectral quality (Kirk 1994).

Algae (and higher plants) have evolved the ability to change their photosynthetic apparatus in response to variation in the light environment. This ability is essential because in order to survive and remain competitive macroalgae must be able to harvest and utilise enough light energy to remain productive in winter, whilst conversely not transfer damaging amounts of photons to their reaction centres in summer. This same challenge is experienced throughout the period of each day. The mechanisms algae employ include altering the functional absorption cross-section of photosystem II (σ_{PSII}), the number of reaction centres (RCs), the numbers of the components of the electron transport chain and elements of carbon metabolism (Falkowski and Raven 1997).

State transitions are rapid responses that enable algae to moderate the effective absorption cross-section of PSII on a scale of seconds. They occur in response to an uneven distribution of energy between PSI and PSII and are brought about by the coupling or decoupling of the
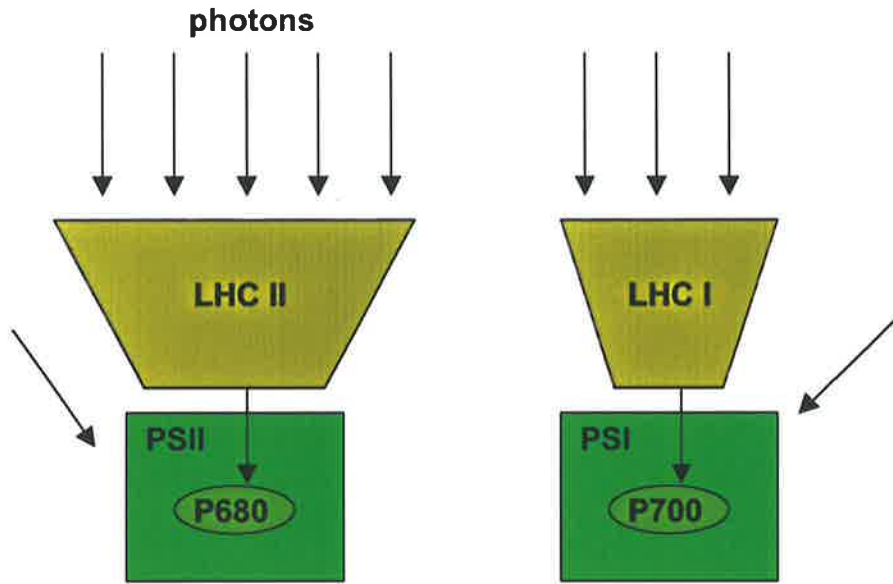
Figure 2.1 Representation of photon absorption and the primary photosynthetic events ("photochemistry"). Excitation energy originating from photons absorbed by the antennae pigments (e.g. chlorophyll *a* & *c* and fucoxanthin) in the light harvesting complexes II & I (LHCII & LHCI) is transferred to the reaction centre chlorophylls (P680 chlorophyll *a* & P700 chlorophyll *a*) of photosystems II & I (PSII & PSI). Once in the excited state the reaction centre chlorophylls donate an electron (initially to a modified chlorophyll *a* molecule called phaeophytin) and thus become photo-oxidated.

antennae of LHC II with the reaction centre of PSII (Falkowski and Raven 1997, Larkum and Howe 1997). This response is thought to be controlled by the redox state of the plastoquinone pool in the electron transport chain. When the plastoquinone pool is in a highly reduced state (e.g. when photon absorption is high) the LHC II is phosphorylated, which results in its decoupling, thereby reducing the effective absorption cross-section of PSII (Horton and Hague 1988, Falkowski and Raven 1997). The rapid nature of state transitions means that they can respond to changes in irradiance brought about, for example, by clouds moving across the sky or by movement of the canopy (Falkowski and Raven 1997). However, state transitions are ineffective in countering changes of a larger magnitude, such as those experienced throughout the course of a clear summer's day.
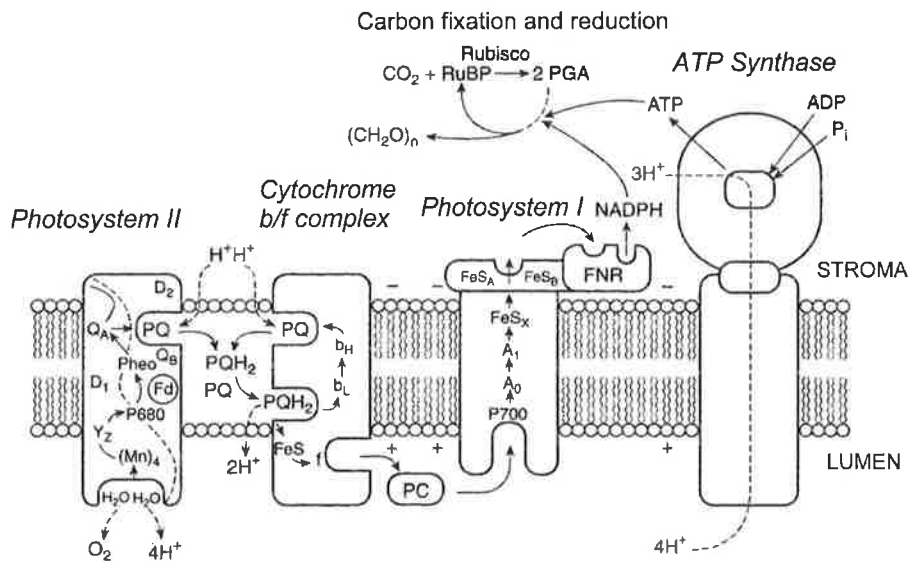
Figure 2.2 Photosynthetic electron transport (indicated by the solid arrows) across the thylakoid membrane in a chloroplast. PSII, PSI and the cytochrome complex cooperate in transporting electrons from H_2O across the membrane to NADP. This process involves a number oxidation-reduction reactions between various electron transporters, which include a tyrosine amino acid (Yz), mobile plastoquinones (PQ), and fixed plastoquinones (Q_A & Q_B). The process is initiated when the reaction center chlorophylls (P680 & P700) become photo-oxidated following transfer of the excitation energy from a photon by their light harvesting complexes. In the oxidated state the RC's can receive an electron from tyrosine, which is the primary acceptor of electrons following the oxidation of water. The sequential transfer of electrons, which ultimately results in the reduction of NADP to NADPH, causes a proton gradient to build up across the membrane. ATP synthase transports the protons back into the stroma and converts adenosine diphosphate (ADP) and inorganic phosphate (Pi) to adenosine triphosphate and water ("photosynthetic phosphorylation"). Energy in ATP and NADPH is then used for CO_2 reduction and carbohydrate formation in the Calvin-Benson cycle. (From Falkowski and Raven (1997); Figure 1.3).

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The level of irradiance experienced during the middle of the day can, potentially, be very damaging to an alga. If the amount of photons absorbed is in excess of the amount that can be utilised by photochemistry, chlorophyll triplet states can be formed, and these react with oxygen to form damaging singlet oxygen (Larkum and Howe 1997). Even at low irradiance a particular photosystem may, by chance, absorb potentially damaging quantities of photons. In order to protect the photosynthetic apparatus some absorbed energy is dissipated as heat, thermal dissipation, which effectively reduces the absorption cross-section of PSII by quenching at the antenna system (Falkowski and Raven 1997). Non-photochemical energy dissipation is correlated with the formation in the antennae system of PSII of an oxygenated carotenoid, zeaxanthin, (Demmig-Adams and Adams 1992). Zeaxanthin is one of the three interchangeable xanthophyll pigments that form the xanthophyll cycle, the other two being violaxanthin and antheraxanthin (Larkum and Howe 1997). In high irradiance situations violaxanthin, through a series of de-epoxidations, is converted to zeaxanthin, via antheraxanthin. This conversion can occur in around 30 minutes and acts to protect PSII from an overload of excitation energy, as might be experienced around midday. The epoxidation state of the xanthophyll cycle is thought to be regulated by acidification of the thylakoid lumen (Demmig-Adams and Adams 1992).

Over the course of the year the light environment changes considerably and algae have evolved the ability to photoacclimate in order to deal with these long term changes in irradiance. Photoacclimation generally involves some change in pigment concentration or relative proportions. A common acclimation response to lowering irradiance is to increase the concentration of chlorophylls (Ramus *et al.* 1976b, Wheeler *et al.* 1984, Henley and Ramus 1989a, Iglesias Prieto and Trench 1994, Gómez *et al.* 1997, Stengel and Dring 1998). This response has the effect of either increasing the effective absorption cross-section of PSII and/or increasing the number of photosynthetic units (RC's), thus increasing the capacity for capture of energy available photochemistry. However, the degree to which chlorophyll content can increase is limited, as at a certain concentration of pigments, the effect of self shading means any further increase in pigment levels will not lead to an increase in light absorption (the "package effect") (Kirk 1994). Similarly, pigment concentration will decline below the light level required for saturation of chlorophyll synthesis (Markager 1993) which places limits on the level of pigments at deep depths.

Another pigment change commonly noted is the increase of levels of non-light transferring carotenoids (e.g. β-carotene) in high irradiance situations, which decreases the effective

absorption cross-section of PSII (Falkowski and Raven 1997). Pigmentation changes are also thought to be controlled by the redox state of the plastoquinone pool (Falkowski and Raven 1997).

The photosynthesis-irradiance response has been extensively investigated in macroalgae, with several studies focusing on Laminarialean algae such as *Laminaria* (Hatcher *et al.* 1977, Drew 1983, Dunton and Jodwalis 1988, Gerard 1988, Dunton 1990, Sakanishi *et al.* 1990, Davison *et al.* 1991, Sakanishi *et al.* 1991), *Macrocystis* (Willenbrink *et al.* 1979, Arnold and Manley 1985, Gerard 1986), *Phyllariopsis* (Flores Moya *et al.* 1995), *Ecklonia* and *Eisenia* (Maegawa *et al.* 1987, Maegawa *et al.* 1988, Sakanishi *et al.* 1988, Yokohama and Maegawa 1988, Sakanishi *et al.* 1989, Haroun *et al.* 1992, Serisawa *et al.* 2001), and *Nereocystis* (Wheeler *et al.* 1984). The photosynthetic response of several species has been found to change in response to factors such as seasonal changes in light and water temperature (King and Schramm 1976b, Drew 1983, Sakanishi *et al.* 1989, Sakanishi *et al.* 1990, Davison *et al.* 1991, Cheshire *et al.* 1996), nutrient availability (Campbell *et al.* 1999), depth profile (Gerard 1986, Markager and Sand-Jensen 1992), thallus region (Dunton and Jodwalis 1988, Sakanishi *et al.* 1989) and reproductive status (Aruga *et al.* 1990). Collectively, these changes enable the seaweed to maintain an optimal photosynthetic rate in a highly variable environment.

Methodological differences used in the above experiments cloud conclusions that can be drawn from such studies. These methodologies ignore the lack of natural irradiance, variation and spectral quality (Drew 1983, Gerard 1984, Dunton and Jodwalis 1988, Kubler and Raven 1996), and of natural temperature and nutrient variations, the responses of algae to wounding (Hatcher 1977, Littler 1979, Arnold and Manley 1985, Sakanishi *et al.* 1988), "bottle effects" (e.g. changes in pH, nutrient depletion) (Littler 1979, Littler and Arnold 1985), and the variation in the photosynthetic light response throughout the thallus (Arnold and Manley 1985, Sakanishi *et al.* 1989). The importance of measuring individuals under natural conditions, especially when conclusions are applied to algae in their natural environment, has resulted in more and more studies of photosynthesis based on *in situ* measurements using entire organisms (Hatcher 1977, Dunton and Jodwalis 1988, Chisholm *et al.* 1990, Dunton and Tomasko 1994, Häder and Schäfer 1994, Cheshire *et al.* 1997, Westphalen and Cheshire 1997, Major 2000).

The carbon radioisotope method, based on the incorporation of the radioactive ^{14}C into algal cells (Steemann-Nielsen 1952) is widely used to measure rates of algal photosynthesis *in situ*, particularly that of phytoplankton. This method requires that the sample must be incubated

within a known volume of seawater, in bottles or bags, which can be suspended such that the sample experiences a natural light climate, but the incubations can only be of a limited duration due to build up of oxygen and the depletion of nutrients, and the results must then be extrapolated for the entire day. A similar problem is encountered when using the "light/dark" bottle approach to measuring algal photosynthesis (Littler and Arnold 1985).

Long term *in situ* measurements have been considered more difficult to perform than laboratory based measurements (Littler and Arnold 1985) or short term ^{14}C incubations. The development of automated photo-respirometers, such as that produced by Cheshire Systems™, has meant that whole algae can now be incubated over a 24 hour time period while experiencing natural irradiance and temperature fluctuations. Photo-respirometers depend on a series of short term incubations (e.g. 12 minutes duration) of whole algae contained within chambers placed on the seafloor. The oxygen concentration within the chambers (one of which is typically empty and acts as a control) is measured at short intervals (20 seconds) throughout the 24 hour period and is later converted into an oxygen production/consumption rate. At the end of each incubation period the seawater is refreshed by flushing of the chamber with ambient water so that that variations in seawater temperature and nutrient concentration throughout the 24 hour period are incorporated into the study. Stirring to constantly move water across an oxygen electrode also provides some movement of water in the chamber during each incubation. The respiration rate measured at night (i.e. the rate of oxygen consumption) is assumed to be the same during the day. This method also assumes that oxygen consumption via the Mehler reaction and by photorespiration is minimal (Hatcher *et al.* 1977, Falkowski and Raven 1997).

Studies that measure plant and algal photosynthesis, by oxygen evolution methods, generally assume that the production of one mole of oxygen is equal to the assimilation of one mole of carbon dioxide, i.e. that the photosynthetic quotient (PQ) is 1.0. This assumption is valid if the primary photosynthetic product is simple carbohydrate and if the nitrogen source is ammonium (Falkowski and Raven 1997). However, if the product formed by photosynthesis is more reduced than simple carbohydrate, such as in the case of mannitol or proteins and lipids, then the PQ will actually be higher than 1.0 (Axelsson 1988), and the process of nitrate reduction (to form ammonium) will also act to increase the photosynthetic quotient. Conversely, the process of photorespiration can result in PQs of less than unity. The actual range of PQs measured by Hatcher *et al.* (1977) using *Laminaria longicruris* was between 0.67 and 1.5.

In comparison with the volume of work conducted in the northern hemisphere on species of *Laminaria* remarkably little has been conducted on *Ecklonia*. The few studies conducted have focused on *Ecklonia cava* on the Japanese Pacific coast (Maegawa *et al.* 1987, Maegawa *et al.* 1988, Sakanishi *et al.* 1988, Sakanishi *et al.* 1989, Haroun *et al.* 1992). Whilst the response of *Ecklonia radiata* photosynthesis to fluctuating irradiance has been investigated in the laboratory by Dromgoole (1987, 1988) no investigation has yet been published on the seasonal photosynthesis of *E. radiata*. This thesis aims to investigate seasonal patterns of photosynthesis and growth in *E. radiata* by documenting the *in situ* photosynthesis-irradiance response and pigment composition with respect to changes in the light environment over seasons and depths. The

Methodology

Photo-respirometry

Methods

The photo-respirometer consists of five 11.5 litre UV-transparent Perspex chambers, which are sealed with an alga inside, and a water pump, and two sealed cylinders containing batteries and data loggers. Each chamber has an oxygen electrode and stirrer and a pump inlet connected to the main flushing system with a valve on the top to allow flushing water to exit (Plate 2.1) (Cheshire *et al.* 1996).

Following a 12 minutes incubation the pump flushed each chamber with ambient seawater for 3 minutes. A total of 96 incubations were run over the deployment period of 24 hours. During this period the oxygen concentration in each chamber was recorded every 20 seconds, as were ambient photon irradiance[1] and temperature readings.

Seven series of deployments were made at a depth of 3 m in Abalone Cove over a period from October 1998 to July 2000. During this time individuals were collected from depths of 3, 5, 10 and 12 m². Due to the size constraints of the chambers only juvenile algae were used in order to avoid the problems associated with self shading. Approximately eight algae from each depth were deployed during every series (the number of randomly selected replicates

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[1] Li-Cor quantum sensor, LI-185A; calibrated to ± 5% U.S. National Institute of Standards and Technology (NIST) specifications

varied due to logistical constraints). Epiphytes attached to the holdfast were removed prior to incubation. One chamber remained empty during several deployments in order to assess background levels of oxygen production/consumption, which remained insignificant. Immediately after each deployment the wet weight of each sample was recorded. Dry weights were later recorded after drying for 48 hours at 80 °C.
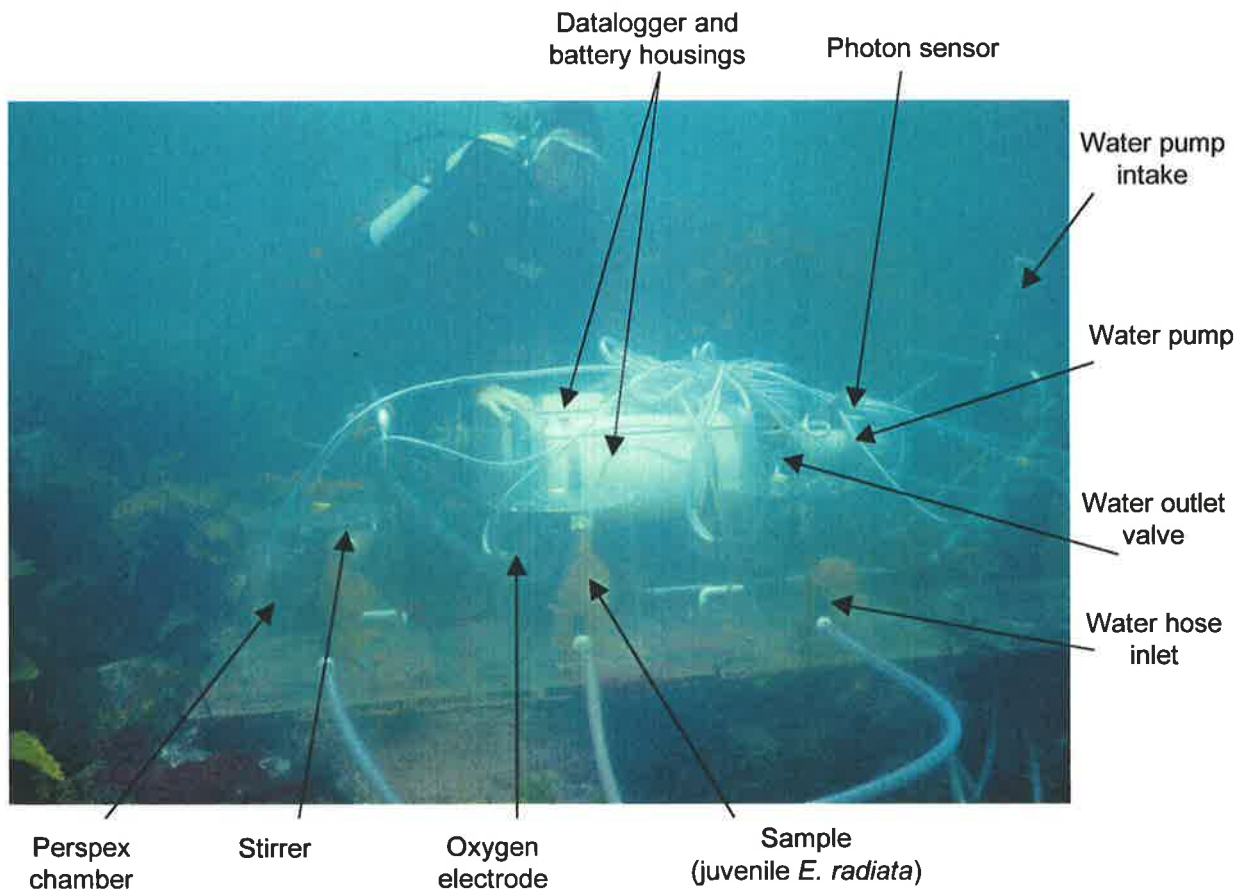
Plate 2.1 The photorespirometer used in this study, pictured here at the 3 m study site in Abalone Cove. All the main components are labelled except the temperature sensor, which is hidden from view (see text for details).

Photokinetic parameters were obtained using the software package PhotoPhys (Cheshire 1998). The rate of oxygen exchange during each 12 minute incubation was calculated using the slope of the line relating oxygen concentration to time. The average photon flux and temperature were also calculated for this period. The rates of oxygen exchange were corrected for the volume displaced by the alga. Photosynthesis vs. irradiance (PI) curves were then

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[2] Individuals from 5 m were used only for the first four series, and those from 12 m used only for the last four series.

created for each sample by plotting the oxygen exchange rate for each 12 minute incubation period against the mean photon flux for that period. A series of photokinetic parameters were then evaluated by fitting an exponential model to each curve (see Figure 2.3):

$$P_I = Pm_{gross} * (1 - e^{-I/Ik}) + Rd$$

where:

P_I = the production at any photon flux (I)

Pm_{gross} = the maximum gross photosynthesis

Ik = the sub-saturating photon irradiance

Rd = the dark respiration rate (oxygen consumption at $I=0$; negative value)

Additional parameters calculated were:

Pm_{net} = maximum net photosynthesis; defined as $Pm_{gross} - Rd$

Ic = the compensation photon irradiance

$I_{0.95}$ = the photon irradiance at which gross photosynthesis is 95% of Pm_{gross}; which is effectively a measure of saturating irradiance and is used because the model is asymptotic thus saturation is never attained)

α = a measure of photosynthetic efficiency; defined as Pm_{gross}/Ik
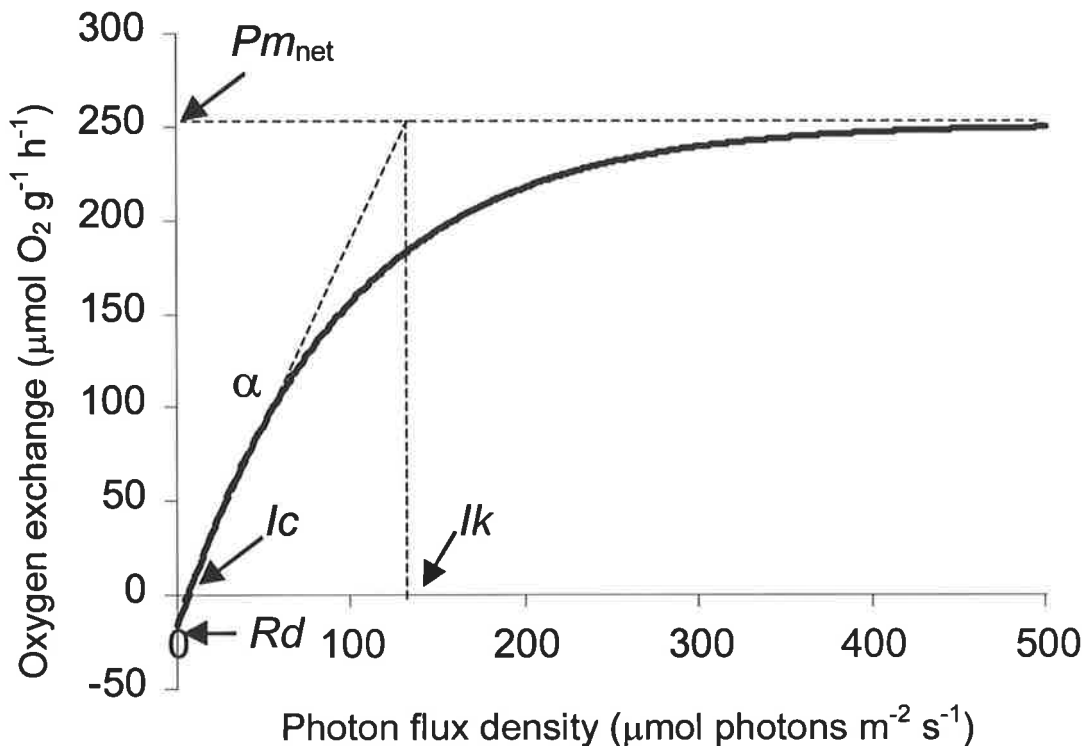
Figure 2.3 Typical photosynthesis-irradiance (or PI) curve displaying photokinetic parameters (see text for definitions).

In order to minimise the influence of photoinhibition on the results only morning data was used for the PI curves and subsequent calculation of the photokinetic parameters. As the estimation of Pm and Ik becomes arbitrary when $Ik > \frac{2}{3} I_{max}$, data was discarded when this occurred. Datasets were only used when r^2 values (the goodness of fit between the model (P_I) and observed oxygen exchange rates) were >0.90.

Additional photon irradiance measurements were taken over several days each month using a series of sensors at different depths. An average attenuation coefficient (k) for each month was calculated using the formula:

$$k = \frac{-\ln(I_{d2}/I_{d1})}{d_2 - d_1}$$

where I_{d1} and I_{d2} represent simultaneous light measurements at different depths, where d_1 is the shallower depth and d_2 is the deeper depth. This assumes that k remains constant across the depth gradient (Shepherd and Womersley 1970).

Analysis

The following null hypotheses were tested:

1. Within samples from a particular depth no difference in photokinetic parameters existed between months.

2. Within samples from a particular sampling period no difference existed in the photokinetic parameters from each depth.

Both these hypotheses were tested using a mulivariate analysis of variance (MANOVA) with Pm_{gross}, Ik and Rd as the response variables. Differences among depths/seasons were evaluated further by examining the 95% confidence intervals, as no *post hoc* test exists. In addition, the effect of depth of collection and time of year on all parameters was tested using a series of one-way analysis of variance (ANOVA) tests. All analysis were conducted using JMP (SAS Institute 1995).

Light Harvesting Pigments

Methods

Tissue discs were collected *in situ* at depths of 3 m and 10 m from a distal and a basal secondary blade from three adults, and from the distal region and the basal region of three

juveniles at each depth. The discs were cut using a 1.8 cm diameter hole-punch and rinsed in deionised water before being frozen in liquid nitrogen. Discs were then stored in a −80 °C freezer until extractions were conducted. Chlorophyll *a*, chlorophyll *c* and fucoxanthin were extracted using dimethyl sulphoxide (DMSO) and methanol (Duncan and Harrison 1982). Concentrations were determined using the equations developed by Seely *et al.* (1972).

Analysis

The null hypothesis that no difference in pigment content existed among adults and juveniles, among depths or between months was tested using a series of three way ANOVAs (time of year, depth collected and thallus position as the factors).

Results

Environmental Variables

Light and water temperature at a depth of 3 m varied considerably throughout the year (Table 2.1). Average maximum photon flux density in December was 705 μmol photons m^{-2} s^{-1} compared with only 280 μmol photons m^{-2} s^{-1} in May, and water temperature ranged from a minimum of 14.2 °C during June and a maximum of 20.7 °C in February.

Photokinetics

Seasonal patterns

Photokinetic parameters altered significantly at any one depth throughout the months (Table 2.2a; Figure 2.4; Appendix A). These changes were characterised at all depths by higher rates of gross and net maximum photosynthesis (Pm_{gross} and Pm_{net}) and lower sub-saturating photon irradiance values (Ik) during the low-light months (May and June) (Figure 2.5a and 2.5c; Table 2.3). Pm_{net} ranged from 94 to 361 $\mu molO_2.g^{-1}dwt.h^{-1}$ and Ik from 80 to 152 μmol photons m^{-2} s^{-1}. Gross photosynthetic capacity (Pm_{gross}) ranged from 108 to 377 $\mu molO_2$ $g^{-1}dwt$ h^{-1} and was significantly higher in winter at all depths except 3 m where the February and September rates were also large (Figure 2.5a; Table 2.3). During autumn and winter the efficiency of photosynthesis when light is limiting (α) was significantly higher (Figure 2.5e) and the photon fluence rate required for photosynthetic compensation (Ic) was significantly lower (Figure 2.5d; Table 2.3). Overall, Ic ranged between 3 and 21 μmol photons m^{-2} s^{-1}, and α varied between 1.04 and 4.33 $\mu molO_2.g^{-1}dwt$ h^{-1} / μmol photons m^{-2} s^{-1}.

Table 2.1 Light (photon flux density; μmol photons m^{-2} s^{-1}) and temperature (°C) readings from photorespirometer deployments at 3 m in Abalone Cove, West Island. Values represent the mean (± s.d.) from each deployment period. Maximum light values for 5, 7, 10 and 12 m were calculated with the attenuation coefficient (k) using the equation $I = I_{3m} \times e^{-k(d-3)}$ (where d is the deeper depth and I is irradiance at the deeper depth).

	Season	Deployment Period	I_{max} 3 m	k	I_{max} 5 m	I_{max} 7m	I_{max} 10 m	I_{max} 12 m	Daylength (hours)	Min Temp	Max Temp
October	Spring	9/10/1998- 23/10/1998	663.14 (41.68)	0.191	532.50	-	174.55	-	13.4 (0.2)	15.2 (0.3)	15.8 (0.3)
February	Summer	20/2/1999- 3/3/1999	673.55 (107.35)	0.283	402.21	-	92.65	-	13.2 (0.1)	19.3 (0.9)	20.7 (0.3)
May	Winter	10/5/1999- 9/6/1999	279.77 (95.42)	0.371	183.11	-	34.26	-	10.4 (0.2)	15.5 (0.3)	15.9 (0.4)
September	Spring	7/9/1999- 22/9/1999	468.77 (103.92)	0.2	383.26	210.34	115.60	77.49	12.1 (0.3)	14.4 (0.1)	14.7 (0.3)
December	Summer	30/11/1999- 14/12/1999	705.13 (102.45)	0.211	-	-	160.43	105.10	15.1 (0.2)	18.5 (0.5)	19.3 (0.6)
March	Autumn	8/3/2000- 21/3/2000	536.52 (124.63)	0.239	-	-	101.02	62.69	12.7 (0.1)	19.0 (0.2)	19.7 (0.4)
June	Winter	24/6/2000- 1/7/2000	350.26 (97.06)	0.266	-	-	54.30	31.88	10.0 (0.0)	14.2 (0.1)	14.6 (0.1)
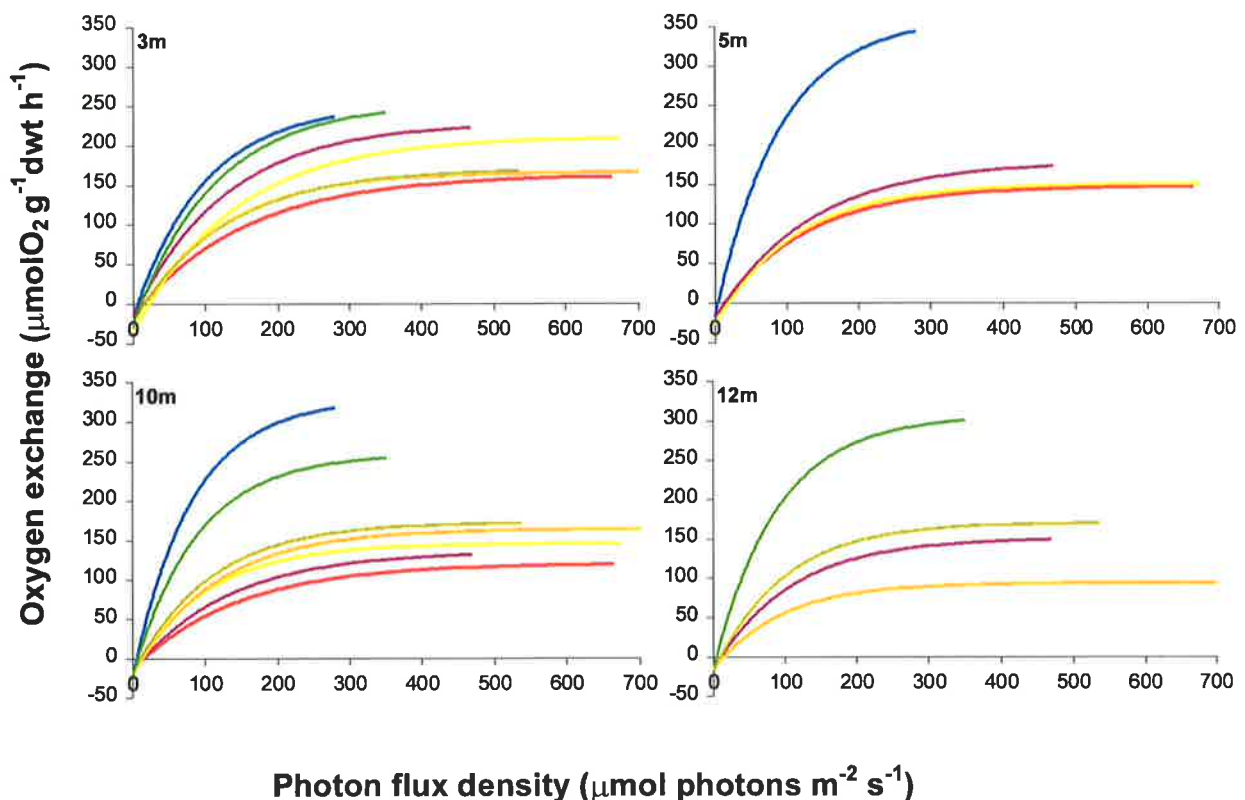
Figure 2.4 Photosynthesis vs. Irradiance (PI) curves for *Ecklonia radiata* created using an exponential model based on the average Pm_{gross}, Ik and Rd values from each depth for each month (--- = October; --- = December; --- = February; --- = March; --- = May; --- = June; --- = September). Data are shown for the range of irradiance values over which the algae were measured, i.e. up to the average maximum irradiance at the measurement depth (3 m) (see Table 2.1).

At all depths the amount of time that the irradiance exceeded Ic, Ik and $I_{0.95}$ varied significantly throughout the year (Table 2.3). In all cases these values were lower during winter (Table 2.4). The number of hours each day that the photon fluence rate exceeded Ic ranged from 14.4 hours at 3 m and 11.5 hours at 12 m in December, to 9.1 hours at 3 m and 6.7 hours at 12 m in June (Table 2.4). This means compensation irradiance was reached during 91-95% of the day at 3 m. Assuming the same day-length, plants at 12 m compensated for 66-76% of the day throughout the year. Algae at 3 m were able to compensate in winter (June) for ~63% of the number of hours that they are able to photosynthetically compensate for in summer (December). This is despite the fact that in winter the day is almost 3 hours shorter, and the I_{max} is only 39% of that in summer at 3 m.

Table 2.2 Summary of one-way MANOVA results for photokinetic parameters (Pm_{gross}, Ik and Rd) (*** $p \leq 0.001$, ** $p \leq 0.01$, * $0.01 < p \leq 0.05$, ns = not significant). a) Comparisons between months within each depth (compare along rows; b) Comparisons between depths for each month (compare down columns). Similarities between months/depths are defined by an overlap of the 95% CI and are indicated by the same letter.

a)

Depth (m)	Feb	Mar	May	Jun	Sep	Oct	Dec	p
3	a	a,b	c	c,d	c	b	a,b,d	***
5	a	-	b	-	a	a	-	***
10	a	a	b	not tested	a	a	a	***
12	-	b	-	c	a,b	-	a	***

b)

Depth (m)	Feb	Mar	May	Jun	Sep	Oct	Dec
3	a	a	a	a	a	a	a
5	a	-	b	-	a,b	a	-
10	a	a	a,b	not tested	b	a	a
12	-	a	-	b	b	-	b
p	ns	ns	**	**	**	ns	*

(a) Pm_{gross} (μmolO$_2$ g^{-1}dwt h^{-1})   (b) Rd (μmolO$_2$ g^{-1}dwt h^{-1})
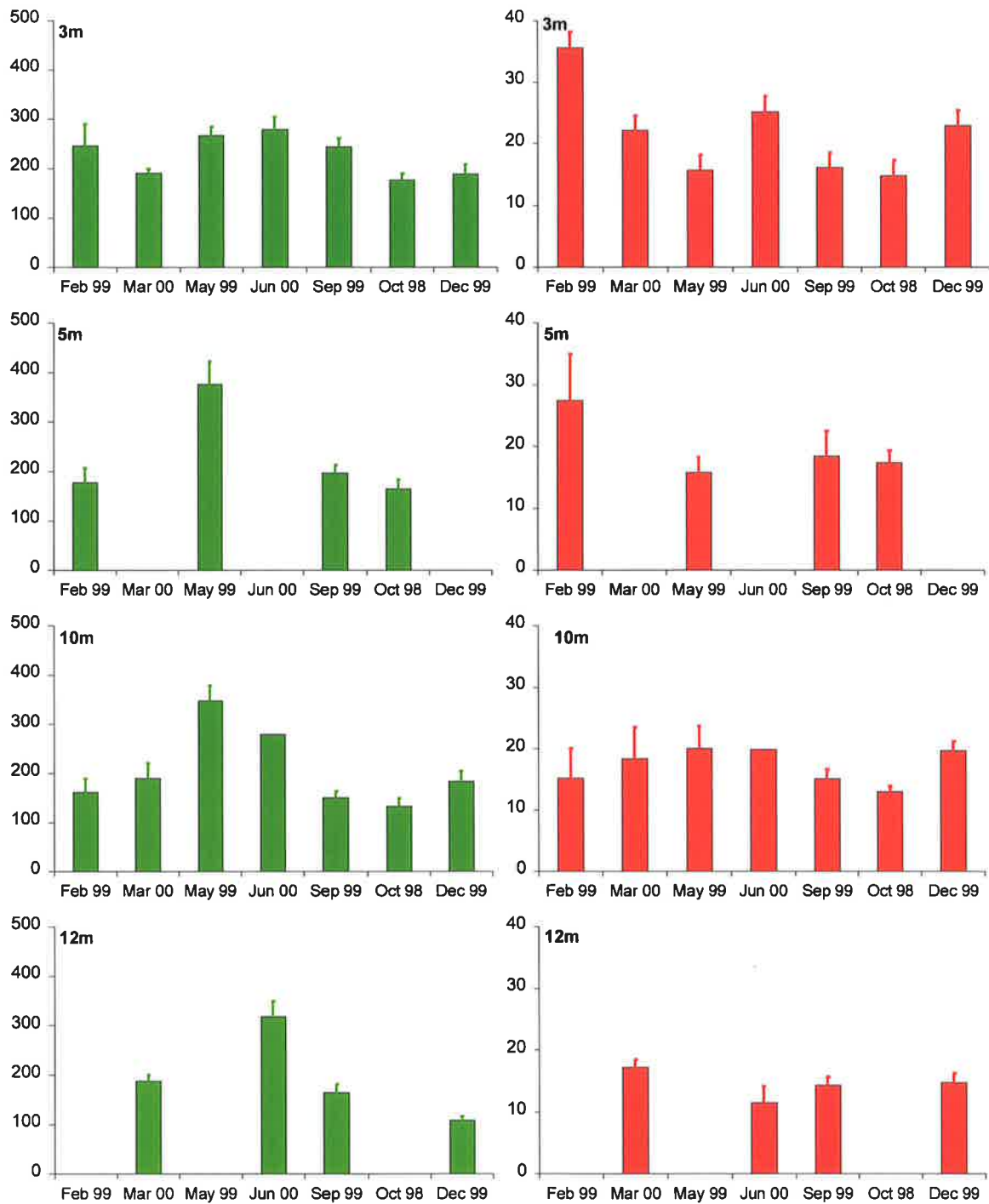
Figure 2.5 Photokinetic parameters ($\pm$ s.e.) from 3, 5, 10 and 12 m at different times of year. A0 average gross maximum photosynthetic rate (--- Pm_{gross}; μmolO$_2$ g^{-1}dwt h^{-1}), b) dark respiration rate (-- Rd; μmolO$_2$ g^{-1}dwt h^{-1}), c) sub-saturating photon irradiance (— Ic; μmol photons m^{-2} s^{-1}), d) photon irradiance required for photosynthetic compensation (--- Ik; μmol photons m^{-2} s^{-1}), and e) efficiency of photon use at low irradiance (--- α, μmolO$_2$ dwt h^{-1}/μmol photons m^{-2} s^{-1}). See Appendix A for sample sizes.

(c) *Ic* (μmol photons m^{-2} s^{-1})   (d) *Ik* (μmol photons m^{-2} s^{-1})
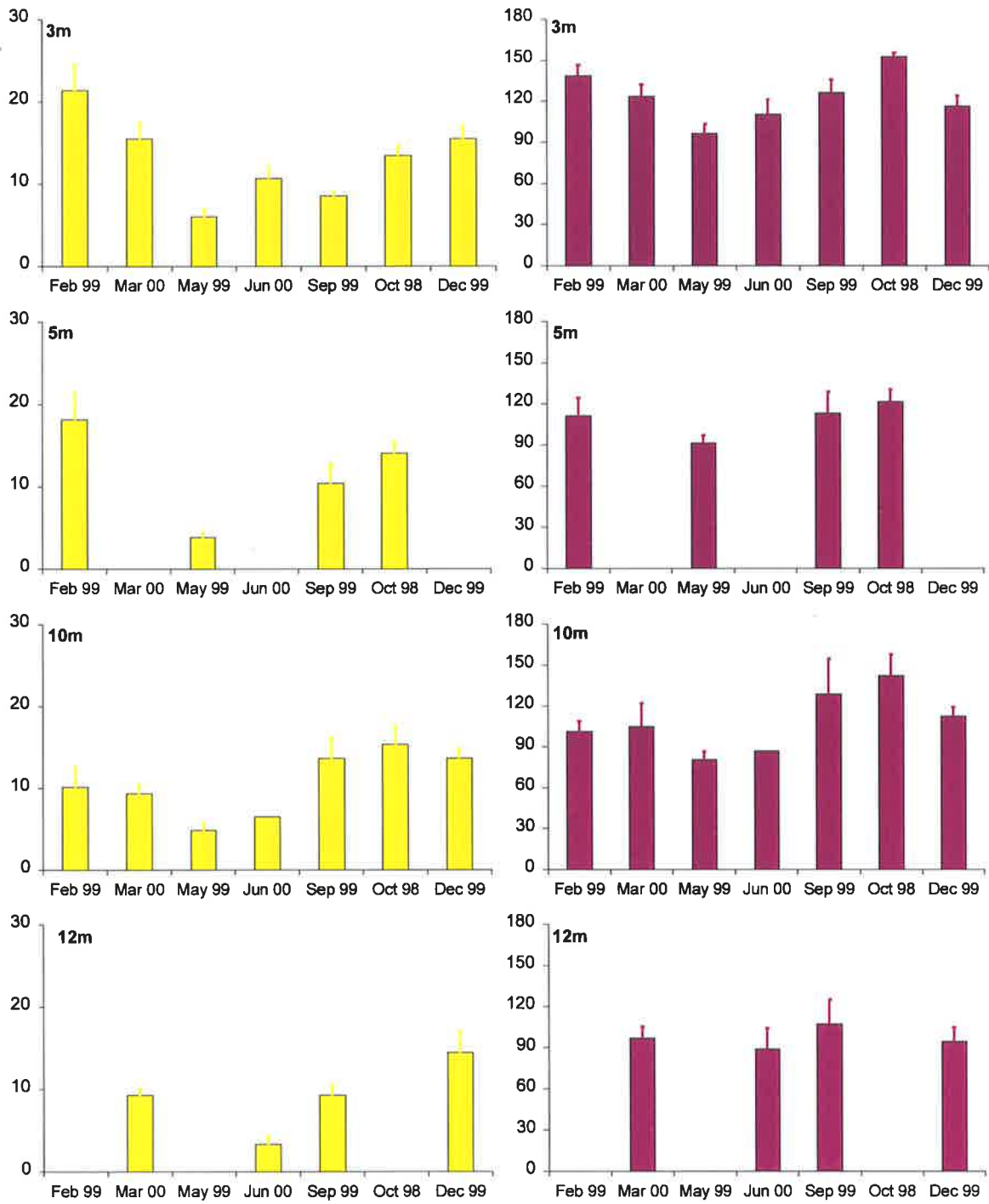
Figure 2.5 continued.

(e) α ($\mu molO_2$ $g^{-1}dwt$ $h^{-1}/\mu mol$ photons m^{-2} s^{-1})
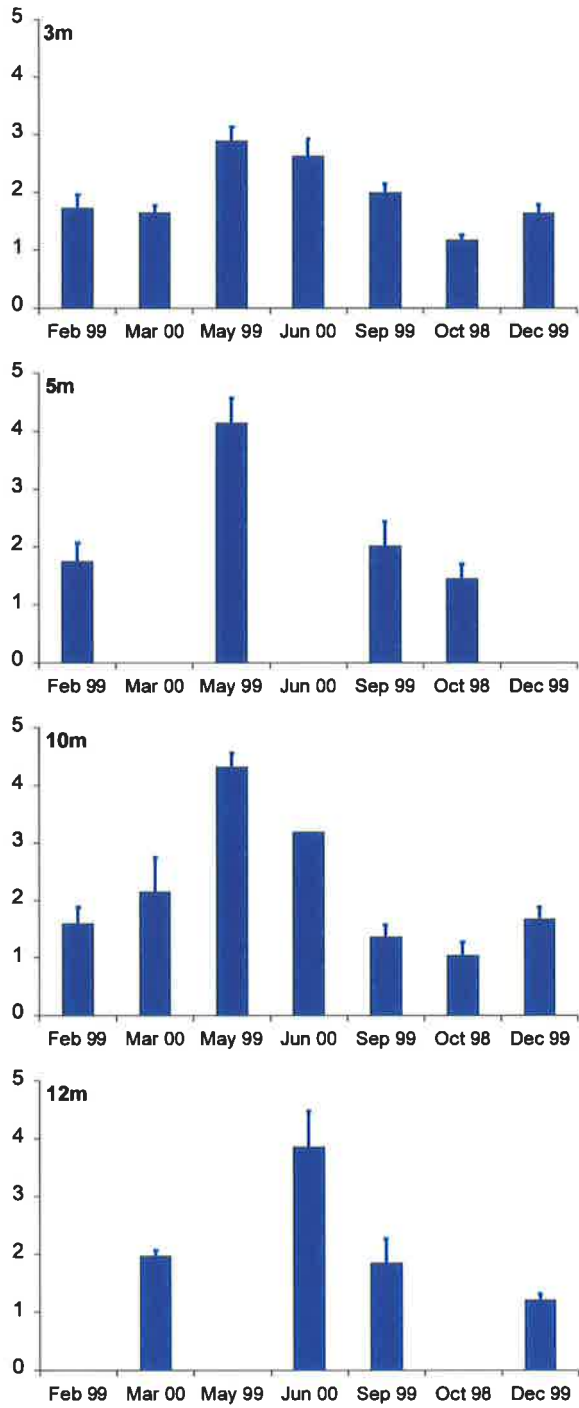
Figure 2.5 continued.

Table 2.3 Summary of ANOVA results and the *post hoc* Tukey-Kramer HSD comparisons (α = 0.05) for photokinetic parameters across seasons. The final column represents the ANOVA significance probability (*** $p \leq 0.001$ ** $p \leq 0.01$ * $p \leq 0.05$ ns = not significant).

a)	3 m depth							
	Feb	**Mar**	**May**	**Jun**	**Sep**	**Oct**	**Dec**	***p***
Pm_{gross}	a,b	a	b	a,b	a,b	a,b	a,b	**
Pm_{net}	a,b,c	a	b	b,c	a,b,c	a,c	a,c	**
Rd	b	a,b	a	a,b	a	a	a,b	***
Ik	a	a,b	b	a,b	a,b	a	a,b	***
Ic	b	b,d	a	a,c,d	a,c	a,b	b,c	***
α	a,b	a	c	b,c	a,b	a	a	***
I > *Ic*	b	b,c	d	e	c	b	a	***
I > *Ik*	a,b	b,c	d,e	e	c,d	b,c	a	***
I > $I_{0.95}$	a,b	a	b,c	c	a,b,c	a,b,c	a	***

b)	5 m depth							
	Feb	**Mar**	**May**	**Jun**	**Sep**	**Oct**	**Dec**	***p***
Pm_{gross}	a		b		a	a		***
Pm_{net}	a		b		a	a		***
Rd	a		a		a	a		ns
Ik	a	not measured	a	not measured	a	a	not measured	ns
Ic	a		b		a,b	a		***
α	a		b		a	a		***
I > *Ic*	a		c		b	a		***
I > *Ik*	a		b		b	a		***
I > $I_{0.95}$	a		a		a	b		***

Table 2.3 continued.

c)	10 m depth							
	Feb	Mar	May	Jun	Sep	Oct	Dec	p
Pm_{gross}	a	a	b	not tested	a	a	a	***
Pm_{net}	a	a	b		a	a	a	***
Rd	a	a	a		a	a	a	ns
Ik	a,b	a,b	b		a,b	a	a,b	*
Ic	a,b	a,b	b		a	a	a	***
α	a	a	b		a	a	a	***
$I > Ic$	a,b	b	b		b	a	a	***
$I > Ik$	a,b,c	a,b,c	c		b,c	a	a,b	**
$I > I_{0.95}$	not tested							

d)	12 m depth							
	Feb	Mar	May	June	Sep	Oct	Dec	p
Pm_{gross}	not measured	b	not measured	c	a,b	not measured	a	***
Pm_{net}		b		c	a,b		a	***
Rd		a		a	a		a	ns
Ik		a		a	a		a	ns
Ic		a,b		b	a,b		a	**
α		a		b	a		a	***
$I > Ic$								***
$I > Ik$								ns
$I > I_{0.95}$	not tested							

Photon irradiance exceeded Ic, Ik and $I_{0.95}$ for a significantly lower number of hours at deeper sites throughout the year (Table 2.5). However, this decline was not in proportion with the decrease in I_{max} between depths. For example in June the I_{max} at 12 m is only 9% of that at 3 m, but algae at 12 m are still able to attain photosynthetic compensation for 73% of the number of hours that algae at 3 m are able to compensate.

Photon irradiance exceeded the sub-saturating irradiance (Ik) at 3 m for 5.6-11.6 hours per day all year, whereas at 10 and 12 m irradiance did not exceed Ik in winter. Similarly saturating photon irradiance ($I_{0.95}$) was obtained for at least some period of the day (between 1.5 – 5.9 hours) all year only at 3 m, in contrast to 10 and 12 m where $I_{0.95}$ was not reached at any time of the year.

Table 2.4 Number of hours every day that *Ecklonia radiata* (at depths of 3, 5, 10 and 12 m) receives a photon irradiance in excess of the compensation photon irradiance (Ic), sub-saturating photon irradiance (Ik), and the photon irradiance required for gross photosynthesis to reach 95% of maximum gross photosynthesis ($I_{0.95}$).

Month	Depth (m)	I > Ic	% Day I > Ic	I > Ik	% Day I > Ik	I > I_{0.95}	% Day I > I_{0.95}
Feb	3	12.0 (0.8)	91	10.0 (0.6)	75	5.5 (1.7)	41
	5	12.0 (0.6)	91	8.5 (1.1)	64	3.0 (2.4)	22
	10	10.9 (0.6)	83	0.5 (1.0)	3	0	0
Mar	3	11.9 (0.4)	93	8.9 (1.7)	69	3.9 (3.0)	31
	10	9.9 (0.4)	79	1.5 (2.2)	12	0	0
	12	8.9 (1.2)	70	0	0	0	0
May	3	10.0 (0.3)	95	6.0 (1.5)	57	1.5 (1.4)	14
	5	10.0 (0.3)	96	4.8 (1.4)	46	0.2 (0.7)	2
	10	8.8 (0.9)	83	0	0	0	0
Jun	3	9.1 (0.5)	91	5.6 (1.5)	56	2.4 (2.2)	24
	10	8.5	85	0	0	0	0
	12	6.7 (1.1)	66	0	0	0	0
Sep	3	11.3 (0.4)	94	7.3 (1.4)	60	2.7 (2.0)	22
	5	10.8 (0.9)	89	5.2 (2.2)	42	0.6 (1.0)	5
	10	9.3 (1.1)	77	0.6 (1.1)	5	0	0
	12	7.9 (0.9)	66	0.2 (0.5)	1	0	0
Oct	3	12.3 (0.4)	93	9.0 (0.7)	68	3.0 (2.0)	22
	5	12.5 (0.1)	93	9.1 (0.8)	68	3.7 (2.0)	28
	10	11.4 (0.5)	85	3.2 (2.7)	24	0	0
Dec	3	14.4 (0.3)	94	11.6 (0.7)	76	5.9 (3.1)	39
	10	12.3 (1.4)	82	3.6 (2.1)	24	0	0
	12	11.5 (1.5)	76	0	0	0	0

Differences in photokinetics across the depth profile

Differences in photokinetic parameters between depths were significant during several months (March, May, June, September) (Figure 2.6; Table 2.2b; Table 2.5). During months with higher I_{max} values (see Table 2.1) Pm_{gross} and Ik tended to decrease with depth, and in low light months Pm_{gross} and Ik tended to increase with depth (Figure 2.6). Rd declined with depth except during May. The irradiance required for photosynthetic compensation (Ic) also tended to decrease with depth, significantly during March (autumn) and June (winter) (Tables 2.5b and 2.5d). Differences in photosynthetic efficiency at low light (α) were apparent between depths only during those months with low I_{max} values in deeper water (Figure 2.5e). During these months α tended to increase with depth, although this was only statistically significant during May (Table 2.5c).
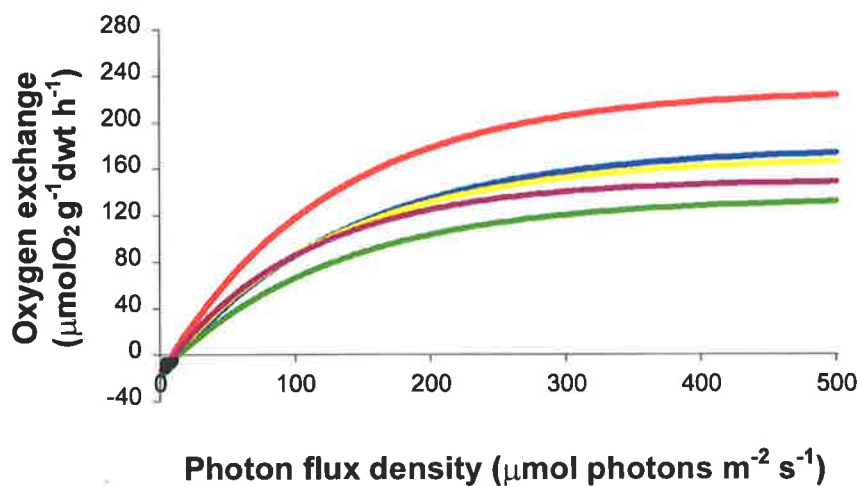
Figure 2.6 Average photosynthesis-irradiance (PI) curves for *Ecklonia radiata* using data collected *in situ*. Eight individuals were collected at 5 depths (--- = 3 m; --- = 5 m; --- = 7 m; --- = 10 m; --- = 12 m) during September 1999 (spring), and measured at 3 m. A significant difference in the primary photokinetic parameters (Pm_{gross}, Rd and Ik) was detected between depths (MANOVA, p < 0.01).

Table 2.5 Summary of ANOVA results and the *post hoc* Tukey-Kramer HSD comparisons (α = 0.05) comparisons for photokinetic parameters across depths. The final column represents the ANOVA significance probability (*** $p \leq 0.001$ ** $p \leq 0.01$ * $p \leq 0.05$ ns = not significant).

a)

a)	February 1999				
	3 m	5 m	10 m	12 m	*p*
Pm_{gross}	a	a	a	not measured	ns
Pm_{net}	a	a	a		ns
Rd	a	a	a		ns
Ik	a	a	a		ns
Ic	a	a	a		ns
α	a	a	a		ns
I > Ic	a	a	b		**
I > Ik	a	a	b		***
I > $I_{0.95}$	a	b	b		***

b)

b)	March 2000				
	3 m	5 m	10 m	12 m	*p*
Pm_{gross}	a	not measured	a	a	ns
Pm_{net}	a		a	a	ns
Rd	a		a	a	ns
Ik	a		a	a	ns
Ic	a		b	b	**
α	a		a	a	ns
I > Ic	a		b	b	***
I > Ik	a		b	b	***
I > $I_{0.95}$	a		b	b	***

Table 2.5 continued.

c)

c)	May 1999				
	3 m	**5 m**	**10 m**	**12 m**	*p*
Pm_{gross}	a	b	b	not measured	*
Pm_{net}	a	b	b		*
Rd	a	a	a		ns
Ik	a	a	a		ns
Ic	a	a	a		ns
α	a	b	c		**
$I > Ic$	a	a	b		***
$I > Ik$	a	a	b		***
$I > I_{0.95}$	a	b	b		***

d)

d)	June 2000				
	3 m	**5 m**	**10 m**	**12 m**	*p*
Pm_{gross}	a	-	not tested	a	ns
Pm_{net}	a	-		a	ns
Rd	a	-		b	**
Ik	a	-		a	ns
Ic	a	-		b	**
α	a	-		a	ns
$I > Ic$	a	-		b	**
$I > Ik$	a	-		b	***
$I > I_{0.95}$	a	-		a	ns

Table 2.5 continued.

e)	September 1999					
	3 m	5 m	7m	10 m	12 m	*p*
Pm_{gross}	a	a,b	a,b	b	b	***
Pm_{net}	a	a,b	a,b	b	b	***
Rd	a	a	a	a	a	ns
Ik	a	a	a	a	a	ns
Ic	a	a	a	a	a	ns
α	a	a	a	a	a	ns
I > Ic	a	a	-	b	b	***
I > Ik	a	b	-	c	c	***
I > $I_{0.95}$	a	b	-	b	b	***

f)	October 1998				
	3 m	5 m	10 m	12 m	*p*
Pm_{gross}	a	a	a		ns
Pm_{net}	a	a	a		ns
Rd	a	a	a		ns
Ik	a	a	a		ns
Ic	a	a	a	not measured	ns
α	a	a	a		ns
I > Ic	a	a	b		***
I > Ik	a	a	b		***
I > $I_{0.95}$	a	a	b		***

g)	December 1999				
	3 m	5 m	10 m	12 m	*p*
Pm_{gross}	a		a	b	**
Pm_{net}	a		a	b	**
Rd	a		a,b	a	**
Ik	a		a	a	ns
Ic	a	not measured	a	a	ns
α	a		a	a	ns
I > Ic	a		b	b	***
I > Ik	a		b	b	***
I > $I_{0.95}$	a		b	b	***

Light Harvesting Pigments

Time of year had a significant effect on all pigments in juveniles and on chlorophyll *a* levels in adults (Table 2.6). Thallus region and time of year had a significant interactive effect on the chlorophyll *a* content in adults. Chlorophyll *a* in the basal region remained almost constant throughout the year, whereas in the distal region it varied (Figure 2.7). Chlorophyll *a* content did not, however, vary in a distinct seasonal pattern, although the higher values did tend to occur in months with lower I_{max} values (i.e. the two winter months, and September). There was no effect of depth on any pigment levels in adults. In contrast, depth had a significant effect on both chlorophyll *a* and chlorophyll *c* in juveniles, with higher amounts in algae at 3 m relative to those at 10 m (Figure 2.7). Fucoxanthin to chlorophyll *a* ratios were higher than the chlorophyll *c* to chlorophyll *a* ratios (Figure 2.8; Figure 2.9) and neither ratio varied significantly across time, depth or thallus region in the adults (Table 2.7). However, both ratios varied with time of year and thallus region in the juveniles (Table 2.7).

Physiological Parameters and Environmental Variables

There were several significant correlations between photokinetic parameters and several significant correlations with irradiance, seawater temperature, day-length and pigment concentrations (Table 2.8). These included positive relationships between Pm_{gross} and both α and chlorophyll *a* concentration, and negative relationships between both Pm_{gross} and α and irradiance. Chlorophyll *a* concentration also correlated positively with α and negatively with both irradiance and Ik. The relationship between α and Ic was also negative.

Table 2.6 Summary of ANOVAs used to determine the significance of depth of collection, time of year and thallus position on photosynthetic pigments concentration in adult and juvenile *Ecklonia radiata* (*** $p \leq 0.001$ ** $p \leq 0.01$ * $p \leq 0.05$ ns = not significant).

Source of Variation	Adults			Juveniles		
	Chl *a*	Chl *c*	Fux	Chl *a*	Chl *c*	Fux
Time of year	*	ns	ns	***	*	***
Depth of collection	ns	ns	ns	**	***	ns
Time of year * Depth of collection	ns	ns	ns	***	*	***
Thallus region	ns	ns	ns	ns	ns	ns
Time of year * Thallus region	**	ns	ns	ns	ns	ns
Depth of collection * Thallus region	ns	ns	ns	***	**	ns
Time of year * Depth of collection * Thallus region	ns	ns	ns	**	ns	*

Table 2.7 Summary of ANOVAs used to determine the significance of depth of collection, time of year and thallus position on pigment stoichiometry in adult and juvenile *Ecklonia radiata* (*** $p \leq 0.001$ ** $p \leq 0.01$ * $p \leq 0.05$ ns = not significant).

Source of Variation	Adults		Juveniles	
	Chl *c*:Chl *a*	Fux:Chl*a*	Chl *c*:Chl *a*	Fux:Chl *a*
Time of year	ns	ns	***	*
Depth of collection	ns	ns	ns	ns
Time of year * Depth of collection	ns	ns	ns	ns
Thallus region	ns	ns	*	***
Time of year * Thallus region	ns	ns	ns	ns
Depth of collection * Thallus region	ns	ns	ns	ns
Time of year * Depth of collection * Thallus region	ns	ns	ns	ns
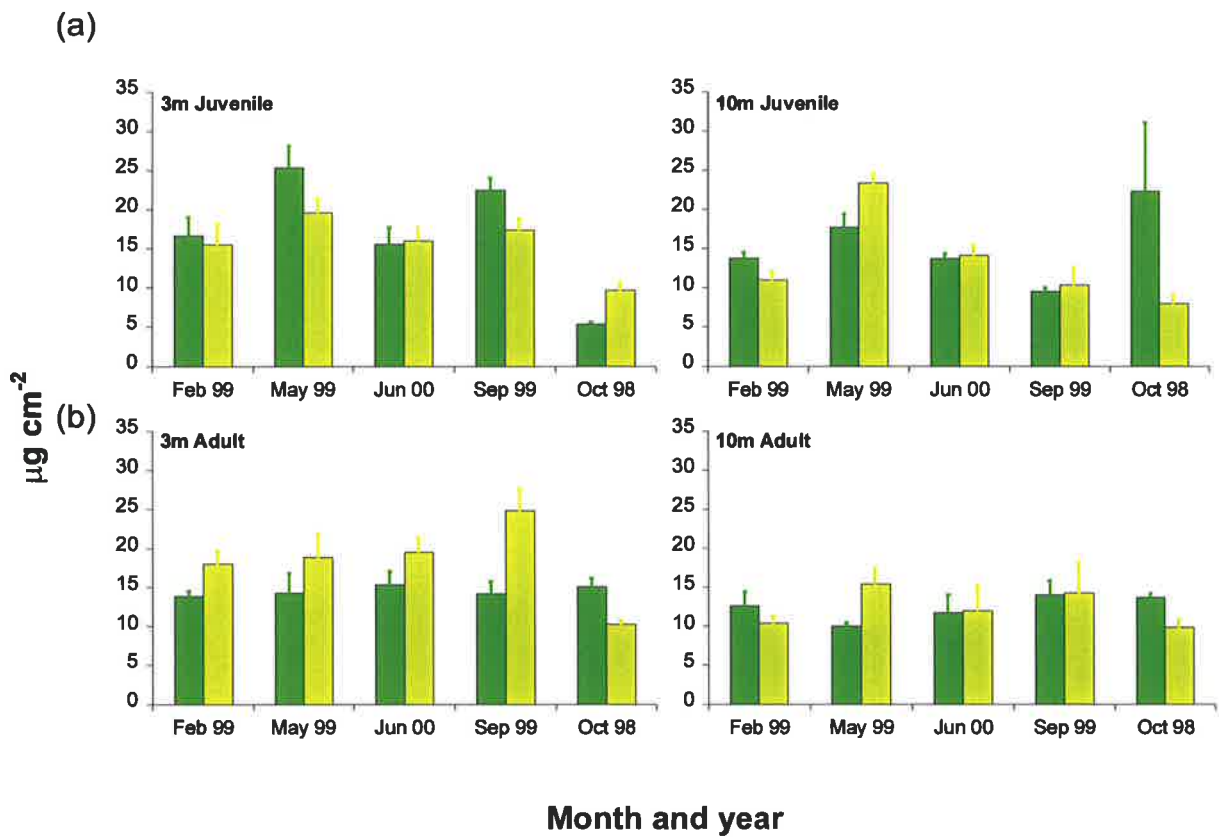
Figure 2.7 Chlorophyll *a* concentration in the basal (---) and distal (—) region of (a) juvenile and (b) adult *Ecklonia radiata* at different times of the year (mean ± s.e.; n=3).
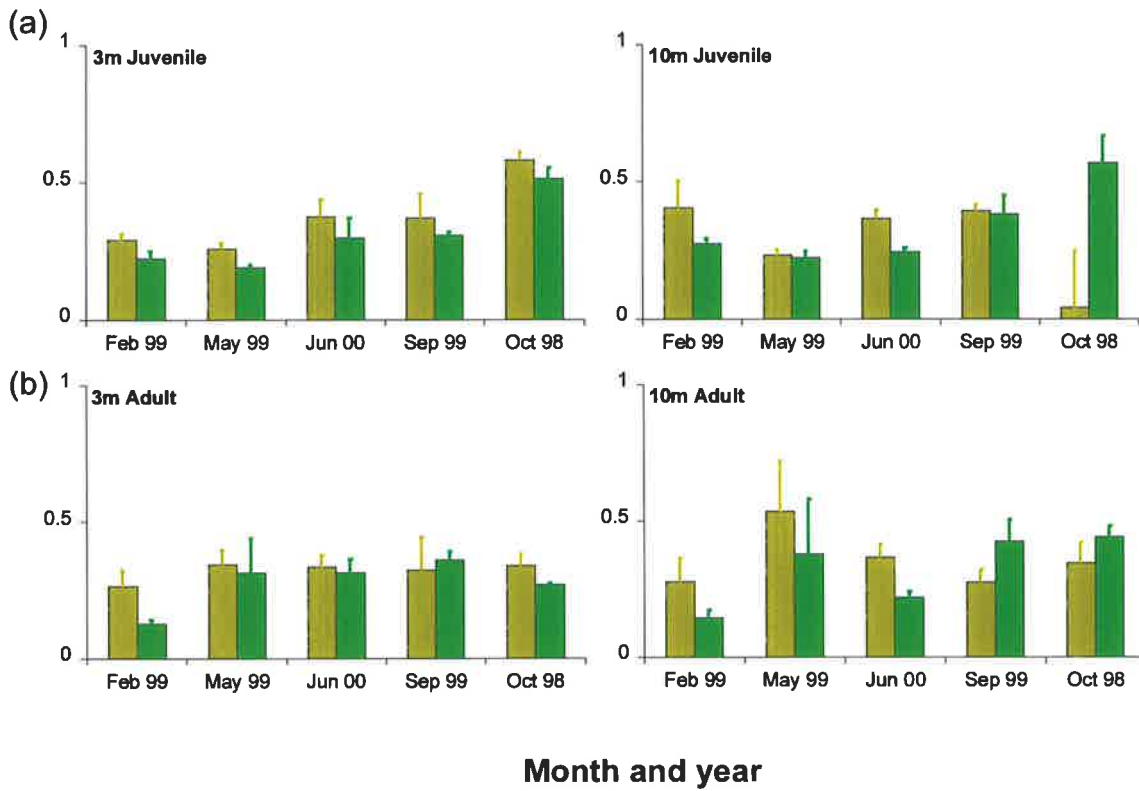
Figure 2.8 Chlorophyll *ca* ratios (mean ± s.e.) in the basal (···) and distal (---) region of (a) juvenile and (b) adult *Ecklonia radiata* at different times of the year (n=3).
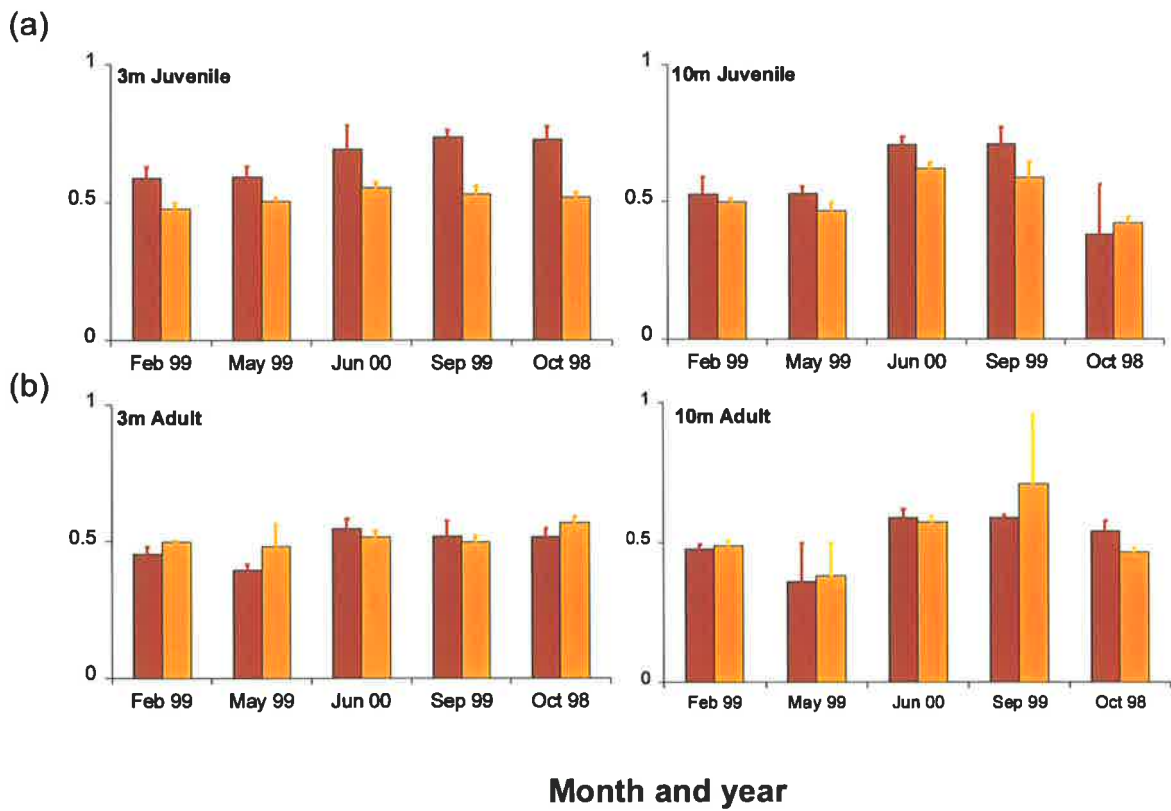
Figure 2.9 Fucoxanthin:chlorophyll *a* ratios (mean ± s.e.) in the basal (---) and distal (---) region of (a) juvenile and (b) adult *Ecklonia radiata* at different times of the year (n=3).

Table 2.8 Synthesis of the linear regression analyses; multiple R values; *** $p \leq 0.001$ ** $p \leq 0.01$ * $p \leq 0.05$ ns = not significant.

	Pm_{gross}	Ik	Ic	Rd^a	α	Day-length	Min Temp	Max Temp	I$_{max}$	Chl a	Chl c	Fux	Chl c:a	Fux:Chla
Pm_{gross}		-0.50*	-0.65***	ns	0.94***	-0.77***	ns	ns	-0.76***	0.85***	ns	0.69**	-0.73*	ns
Ik			0.69***	ns	-0.73***	0.44*	ns	ns	0.51*	-0.67**	ns	ns	0.73*	ns
Ic				0.57**	-0.78***	0.74***	0.51*	0.54**	0.78***	-0.61*	-0.59*	ns	ns	ns
Rd					ns	ns	0.44*	0.48*	ns	ns	ns	ns	ns	ns
α						-0.78***	ns	ns	-0.83***	0.84***	ns	0.61*	-0.70*	ns
Daylength							0.63**	0.63**	0.88***	-0.73**	-0.73**	-0.73**	ns	ns
MinTemp								0.99***	0.53**	ns	-0.69**	ns	ns	ns
Max Temp									0.51*	ns	-0.73**	ns	ns	ns
I$_{max}$										-0.76**	-0.52*	ns	ns	ns
Chl a											ns	0.73**	-0.77**	ns
Chl c												0.59*	ns	ns
Fux													ns	ns
Chl c:a														ns
Fux:Chl a														

^{a} Expressed as a positive number

Discussion

This work has addressed basic questions about seasonal changes in the photosynthetic physiology of *Ecklonia radiata*. Measurement of photosynthetic parameters *in situ* revealed that *E. radiata* displays distinct seasonal and depth related patterns in its photosynthesis-irradiance response. This alteration of photokinetic parameters enables the alga to remain productive and competitive throughout widely different light environments, varying across both seasons and depths.

Gross photosynthetic capacity (Pm_{gross}) varied consistently across all depths within the range 123 to 392 $\mu molO_2$ $g^{-1}dwt$ h^{-1}, with the highest values occurring in winter. Net rates of light-saturated photosynthesis (Pm_{net}) varied within the range 108 and 377 $\mu molO_2 g^{-1}dwt$ h^{-1}, which agrees closely with the values reported for many other Laminarialean algae (Table 2.9), including those reported by Sakanishi *et al.* (1989) for *Ecklonia cava*. Values were generally higher than those of Cheshire *et al.* (1997) who used similar methods to this study, but dealt with small, phaeophycean dominated, boulder communities (some including young *E. radiata*) at a depth of 4.5 m at West Island. The seasonal variation in Pm_{net} demonstrated for *E. radiata* in the current study is in contrast to the boulder macroalgal community (Cheshire *et al.* 1997) and *E. cava* (Sakanishi *et al.* 1989) neither of which varied significantly between summer and winter. Seasonal variation in sub-saturating photon irradiance (*Ik*) was similar in the current study to that found by Cheshire *et al.* (1997), with both displaying lower values for winter in comparison to summer. However, as the values obtained for summer in the current study were similar to the winter values of Cheshire *et al.* (1997) the actual range of values in this study were lower. There was also a clear seasonal variation in photosynthetic efficiencies at low light (α) in both studies, although the range and magnitude of values was larger in the current study. These results show that *E. radiata* consistently has a higher efficiency of photon use, requires a lower irradiance to reach photosynthetic saturation and has a higher photosynthetic capacity in comparison to that of the surrounding macroalgal community.

Seasonal changes in the photosynthesis-irradiance response of *E. radiata* allowed it to maintain an optimal photosynthetic performance across a range of environmental conditions. In winter, when irradiance is lowered, photosynthetic efficiency at sub-saturating levels increases, and the irradiance required for saturation of photosynthesis decreases. During this same period the maximum potential rate of photosynthesis increases, and respiratory requirements

Table 2.9 Rates of photosynthesis for members of the Laminariales

Study	Model	Pmax	Rd	Ic	Ik	α
King and Schramm 1976b [b] (*Laminaria digitata*)	Net photosynthesis at saturating light intensity; artificial light; tissue discs; 5-15 °C	47-125	7-39	-	-	-
Hatcher et al. 1977 [a] (*Laminaria longicruris*)	Net photosynthesis during 5 hour midday incubation; *in situ* (10 m depth); whole plants; 1.2-16 °C	70	-	-	-	-
Littler and Arnold 1982[b] "Thick Leathery" functional form group	Net photosynthesis using light/dark bottles; natural light; 13-21 °C	63				
Wheeler et al. 1984 (*Nereocystis luetkeana*)	Net photosynthesis at highest measuring intensities; artificial light; tissue discs; 6-18 °C	50-540			22-64	
Arnold and Manley 1985 [b] (*Macrocystis pyrifera*)	Net photosynthesis using light/dark bottles; artificial light; whole blades; 17-20 °C	255	56.6	-	-	
Gerard 1986 (*Macrocystis pyrifera*)	Net photosynthesis during 1-2 hour incubation; whole blades; *in situ* (0-9 m depth)	226-286	-	-	280-295	0.80-2.1
Dunton and Jodwalis 1988 [b] (*Laminaria solidungula*)	Net photosynthesis during 1.3-2 hour incubations; whole plants; *in situ* (6-7 m)	42-110	-	-	38-46	1.0-3.0
Sakanishi et al. 1989 (*Ecklonia cava*)	Light-saturated photosynthetic rate ; artificial light; tissue discs; 13-24 °C	220	10-44	-	-	-
Sakanishi et al. 1990 [a] (*Laminaria longissima*)	Light-saturated photosynthetic rate ; artificial light; tissue discs; 0-15 °C	197-350	3-18	1-8	66-133	-
Cheshire et al. 1994 (Phaeophycean dominated boulder communities)	Non-linear exponential; *in situ* (4 m); whole plants; 15-19 °C	160- 178	9; 27	8.0; 33.9	149; 214	1.2; 0.9
Campbell et al. 1999 (*Undaria pinnatifida*)	Hyperbolic; artificial light; tissue discs; 15 °C	994-2383	200-250	13-17	96-142	10-17
Current study (*Ecklonia radiata* 3 m)	Non-linear exponential; *in situ*; whole plants; 14-20 °C	177-278	15-36	6-21	97-152	1.17-2.90
Current study (*Ecklonia radiata* 10 m)	"	132-348	13-20	5-15	81-142	1.04-4.33

[a] using conversion factor of 0.005 gdw cm-2 based on Henley and Dunton 1995)

[b] converted assuming a PQ of 1

are lower. A reverse of these responses occurs in summer, when irradiance is high, which may serve to protect the algae from photodamage caused by the absorption of too many photons. These changes are the result of processes which are involved in the photoacclimation and thermalacclimation of the photosynthetic apparatus.

The pattern of variation in those photokinetic parameters that reflect light harvesting ability and utilisation (the photoacclimation response) can be understood in terms of changes in biophysical parameters (Falkowski and Raven 1997). The processes on which photoacclimation is dependant involve altering the number of reaction centres (RC's), the functional absorption cross-section of PSII (σ_{PSII}) and the rate of photosynthetic electron transport (turnover rate) (Falkowski and Raven 1997). *E. radiata*'s efficiency of photon use at low irradiance (α) clearly increased during winter and the overall correlation with irradiance was significantly negative. This response is characteristic of photoacclimation to low irradiance (Falkowski and LaRoche 1991). Low irradiance conditions typically induce an increase in either the number of reaction centres, or the functional absorption cross-section of the reaction centres (σ_{PSII}), or a combination of both. These changes lead to the higher ability to capture and utilise available photons as is displayed by *E. radiata* in winter (i.e. higher α). In addition, the size of the absorption cross-section directly influences the irradiance at which photosynthesis becomes sub-saturated (*Ik*). During the current study *E. radiata* did reach sub-saturation at lower irradiance during winter when the maximum irradiance were lower and this positive relationship between *Ik* and irradiance was found to be significant.

Chlorophyll *a* concentrations were significantly affected by time of year in both the adults and the juveniles, tending to be higher in winter, which is consistent with an increase in the number of reaction centres in response to lowered irradiance (Falkowski *et al.* 1981). The negative correlation between irradiance and chlorophyll *a* content was also significant. The exception to this pattern is the basal thallus region of the adults, which due to self shading by the canopy, experiences a light environment that is more variable but has lower irradiance all year (Appendix B).

Several mechanisms can lead to alterations in the size of the functional absorption cross-section which, as mentioned above, also impacts on the ability to capture photons. In response to lowered irradiance algae commonly increase the amount of light harvesting (antennae) pigments which are associated with each reaction centre (Ramus *et al.* 1976a, Ramus *et al.* 1976b, Ramus *et al.* 1977, Falkowski and Owens 1980, Falkowski *et al.* 1981,

Henley and Ramus 1989a, Sukenik *et al.* 1990, Falkowski and LaRoche 1991, Iglesias Prieto and Trench 1994). Increasing the concentration of light harvesting pigments increases the amount of photons that can potentially be absorbed by each LHC, i.e. increases σ_{PSII}. Previous studies have also reported an increase in the amount, or proportion, of photoprotective pigments (e.g. carotenoids, xanthophylls) in high irradiance (Henley and Ramus 1989a, Demers *et al.* 1991, Henley and Dunton 1995, Uhrmacher *et al.* 1995, Logan *et al.* 1996, Stengel and Dring 1998). Increases in photoprotective pigments maintains photon absorption by the LHC in high light whilst not increasing energy transfer to the reaction centres, thus decreasing the effective absorption cross-section of PSII (Demmig-Adams 1990, Falkowski and LaRoche 1991).

An alteration in the proportion of antennae pigments (chlorophyll *c* and fucoxanthin) in comparison to chlorophyll *a* indicates changes in σ_{PSII} (Wheeler 1980b, Falkowski and LaRoche 1991). In this study, the pigment stoichiometry of juvenile *E. radiata* did in fact change significantly throughout the year, implying *E. radiata* does have some capacity for altering σ_{PSII} either through the production of new tissue or by restructuring the existing pigment suite. However, chlorophyll *c* to chlorophyll *a* ratios were generally lowest in winter, which is inconsistent with the above photoacclimation theory (Falkowski and LaRoche 1991), whereas changes in fucoxanthin to chlorophyll *a* ratios did not follow any seasonal pattern. In addition, pigment stoichiometry did not change in adults over season, depth or thallus region. The chlorophyll *c* to chlorophyll *a* ratios are more consistent with the suggestion of Campbell *et al.* (1999) that in low irradiance situations chlorophyll *a* may be manufactured in preference to other pigments.

The acclimation response of *E. radiata* involves alterations in the number of reaction centres, and indicates that changes in the size of the functional absorption cross-section of PSII may be less important.

Pigment stoichiometry and chlorophyll *a* concentrations were similar to those reported for *Ecklonia* species and other kelps (Wheeler 1980b, Drew 1983, Gerard 1986, Sakanishi *et al.* 1989, Machalek *et al.* 1996). Possibly an increase in photoprotective pigments could account for the higher *Ik* levels measured during summer, however xanthophyll concentration was not measured in this study. A photoprotective role has been attributed to fucoxanthin in other species due to increases in fucoxanthin to chlorophyll *a* after exposure to high irradiance (Ramus *et al.* 1977, Stengel and Dring 1998). However, as no disproportional increase was

observed in response to higher irradiance in this study its main role in *E. radiata* appears to be light harvesting,. Unlike chlorophyll *a* and *c* which were negatively correlated with irradiance, no relationship was detected between fucoxanthin concentration and maximum irradiance.

Ecklonia radiata displayed a clear seasonal variation at all depths in the rate of light-saturated photosynthesis, with rates being highest in winter when irradiance and water temperatures are low. This relationship is highlighted by the highly significant negative correlation between irradiance and Pm_{gross}.

The maximum potential rate of photosynthesis is directly related to the number of functional photosynthetic units (Falkowski and Raven 1997). An increase in the number of reaction centres during winter, is therefore consistent with an increase in chlorophyll *a* concentration, would enable a higher potential rate of photosynthesis. This theory is supported by the highly significant positive relationships found between Pm_{gross} and chlorophyll *a* content (Figure 2.10; Enríquez *et al.* (1996). Furthermore, Gerard (1988) noted a close correlation between higher rates and chlorophyll content in her study of *Laminaria saccharina*, leading to the conclusion that increased numbers of photosynthetic units were in part responsible for the higher *Pm* values.
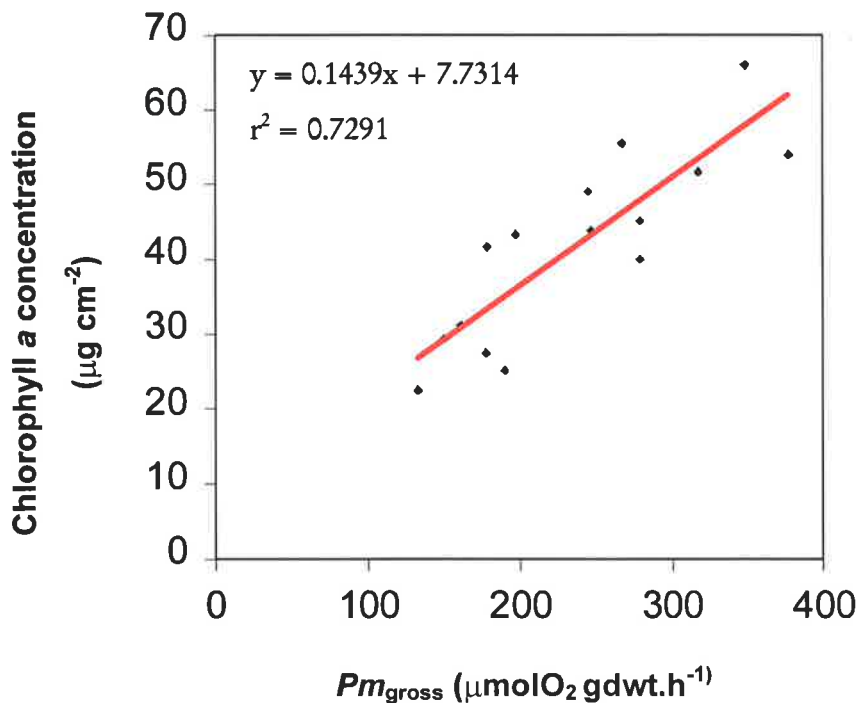
Figure 2.10 The correlation between chlorophyll *a* content and Pm_{gross}. The data plotted are the values from all depths from all months in which pigment analyses were conducted (October 1998, Feburary, May and September 1999, June 2000). The relationship is highly significant (linear regression; $p < 0.001$).

Another potential factor contributing to the changes in photosynthetic potential is the level of nutrients, in particular nitrogen, in the water column. Nitrogen limitation can lead to a decrease in photosynthetic rates due to the effects on the photochemistry of PSII and carbon metabolism (Turpin 1991, Falkowski and Raven 1997). No data exists for nitrogen levels in the study region, however it is reasonable to assume that levels would increase during winter, enhancing photosynthetic capacity (Chapman *et al.* 1978, Smith *et al.* 1983, Wheeler and Weidner 1983, Stengel and Dring 1998). The Mediterranean-type climate of the region means that rainfall is seasonal, occurring generally in winter (Appendix C). An increase in the input of nutrients to the water column at this time would occur by winter rainfall washing off considerable quantities of guano from the West Island land mass, in addition to inputs to the general coastal area by flowing rivers with rural catchment areas. A correlation between nitrate content concentration in the water and photosynthetic capacity has been reported previously for *Macrocystis integrifolia* (Smith *et al.* 1983) and *L. saccharina* (Chapman *et al.* 1978). Additionally, Stengel and Dring (1998) demonstrated that chlorophyll *a* concentration in the fucoid *Ascophyllum nodosum* increases under nitrogen enrichment and Wheeler *et al.* (1984) found a significant correlation between chlorophyll *a* concentration and internal nitrogen levels in the kelp *Nereocystis luetkeana*. The peak of chlorophyll *a* concentration in juveniles in this study did indeed occur in winter.

The higher photosynthetic capacity in this study also coincided with lower water temperatures. The photosynthetic metabolism of several kelp species has been shown to be regulated by temperature (Davison *et al.* 1991 Davison and Davison 1987 Davison *et al.* 1991 Machalek *et al.* 1996 Davison 1987, Sakanishi *et al.* 1989, Sakanishi *et al.* 1990). Photosynthetic rates at light saturation are dependant on the rate of the enzyme-catalysed Calvin cycle reactions, which are affected by temperature. Davison and Davison (1987) found an inverse relationship in *L. saccharina* between growth temperature and both the standard (20 °C) activity of the Calvin cycle enzymes RuBisCO and GADPH (NADPH-dependant) as well as with photosynthetic capacity measured at 15 °C. However, this relationship did not hold when photosynthetic capacity was measured at growth temperature (Davison and Davison 1987), where it remained relatively constant over 0 °C to 20 °C. They postulated that the variation in activity of the Calvin cycle enzymes compensates for the effect of low temperatures on photosynthetic capacity, allowing it to remain relatively uniform over the experimental temperature range.

The inverse relationship between growth temperature and photosynthetic rates in *L. saccharina* was later confirmed (Davison 1987, Machalek *et al.* 1996), and Sakanishi *et al.* (1989) found a similar effect in their investigation of *Ecklonia cava*. They revealed that when tissue discs were measured at a constant 20 °C photosynthetic rates were lower during spring and summer in comparison with autumn and winter, however when discs were measured at *in situ* temperatures (13-24 °C) there was little difference in photosynthetic capacity throughout the year (Sakanishi *et al.* 1989). Sakanishi *et al.* (1990) also report higher photosynthetic rates in winter for *Laminaria longissima*, when measured at a constant 10 °C. However, in contrast to *E. cava* they found that *L. longissima* had a much lower photosynthetic capacity in winter in comparison to summer when measured at *in situ* water temperatures, which varied over a much wider range (-1-15 °C). By comparison, in this study photosynthetic capacity actually increased in winter. It is conceivable that if changes in the activity of Calvin cycle enzymes occurs at a similar magnitude in *E. radiata* as other kelps, then this may actually overcompensate for temperature effects, as the temperature ranges at the study site are not extreme (14-20 °C). However, the higher photosynthetic rates were not found in all months with low temperatures (i.e. winter and spring)- they only occurred in those months which recorded low irradiance as well (i.e. only winter).

An interactive effect of irradiance and temperature on the photosynthetic capacity of *E. radiata* is in contrast with the work of Machalek *et al.* (1996). They found photosynthetic rates increased in *L. saccharina* when the algae was grown at low temperatures, regardless of growth irradiance (i.e. high or low), when compared to algae grown at high temperatures (Machalek *et al.* 1996). This issue is further complicated by the fact that higher nitrogen levels are likely to coincide with the lowest temperatures (see above). Wheeler and Weidner (1983) found a positive correlation in *L. saccharina* between inorganic nitrogen concentration in the water and the activity of Calvin cycle enzymes. Clearly further work is needed to determine the exact nature of the effect of thermal- and photoacclimation processes, and of nutrient levels on seasonal photosynthetic rates in *E. radiata*.

Dark respiration showed no significant annual variability, with the exception of algae at 3 m. This lack of seasonally related variation has been reported for other Laminariales *E. cava* (Sakanishi *et al.* 1989, Haroun *et al.* 1992) and *Phyllariopsis purpurascens* (Flores Moya *et al.* 1995). Despite the uniformity in respiratory requirements throughout the year, the irradiance required to balance photosynthesis and respiration (*Ic*) changed significantly at all depths, reducing in winter in concurrence with the surrounding community (Cheshire *et al.* 1996). In

contrast with Cheshire *et al.* (1996) however, the mechanism for the reduction appears to be not only lowered dark respiration rates, but an increased photosynthetic efficiency, indicated by the higher α and reduced *Ik* values in winter as discussed above (these were significantly negatively correlated). This is in accordance with Machalek *et al.* (1996) who found that variation in *Ic* in *L. saccharina* was due to changes in photosynthetic efficiency not respiratory requirements.

This study has provided evidence that *E. radiata* exists in different acclimation states along the depth profile. In winter, individuals at deeper depths are characterised by higher photosynthetic efficiencies (α), lower sub-saturating irradiance (*Ik*), and the irradiance required for photosynthetic compensation (*Ic*) tended to decrease with depth throughout the year, all of which are characteristics of algae acclimated to lower irradiance (Falkowski and LaRoche 1991). The changes associated with decreasing depths are in agreement with the seasonal acclimation, and with patterns observed in other algae (Gómez *et al.* 1997). The characteristics of the deeper *E. radiata* are similar to the those of *E. radiata* observed in winter, in that they are consistent with an increase in the number of RC's and/or the size of the functional absorption cross-section of PSII.

During times of high irradiance (i.e. summer) the rate of light-saturated photosynthesis decreased with depth. This is likely to be an artefact of the study design as all measurements were done at shallow depths, due to logistical constraints, which meant that the irradiance experienced, even during the morning, was often higher than deeper plants experienced at their natural depth. For example, the I_{max} value for 10 m was regularly reached by ~ 9 am at 3 m throughout the year. The ability of these deeper depth acclimated individuals to cope with supra-saturating irradiance would be restricted by lower levels of photoprotective pigments (e.g. xanthophylls) and the larger functional absorption cross-section and/or increased numbers of RC's which characterise their acclimation state (Henley *et al.* 1991a). Photodamage could result in a lower apparent *Pm* due to a reduction in the population of functional photosystems. Additionally, the assumption was made that deeper plants measured at 3 m are behaving as they would at their growth depth. This ignores the possible impact that differences in spectral quality of irradiance between depths (Kirk 1994) and the decrease in irradiance variability with depth (Dromgoole 1987, Dromgoole 1988, Wing and Patterson 1993, Kuebler and Raven 1996) may have on photosynthetic responses in *E. radiata*.

During months with low levels of irradiance the rate of light-saturated photosynthesis increases with depth. This finding is consistent with the above discussion of changes in Pm values across the seasons. It is also in agreement with photoacclimation theory, which predicts that relative numbers of reaction centres and/or the functional absorption cross-section of the reaction centres (σ_{PSII}) will increase in response to low light levels in addition to an increase in the processing ability of the Calvin cycle (Falkowski and Raven 1997).

This investigation has quantified the seasonal response in the photosynthetic apparatus of juvenile *E. radiata*. Several issues must be acknowledged before extrapolating these results into a model of production by a mature *E. radiata* population. Numerous studies have reported differences in the photosynthesis-irradiance response of mature versus juvenile algae of the same species. Wheeler *et al.* (1984) reports higher Pm values for discs of older tissue in comparison to that of discs from younger tissue in *Nereocystis luetkeana*, whereas Stengel and Dring (1998) report the opposite for the fucoid *Ascophyllum nodosum*. Ramus and Rosenberg (1980) report higher Pm values for mature *Dictyota dichotoma* (Dictyotales). Campbell *et al.* (1999) found a significant interaction between thallus age and season in their study of *Undaria pinnatifida* on both Pm and Ik whereas Sakanishi *et al.* (1989) found that young and old bladelets from *E. cava* had similar seasonal responses but that photosynthetic rate on a dry weight basis decreased with age, a pattern they attributed to an increase in dry weight per area with age. Similarly, Enríquez *et al.* (1995) reported that Pm and α negatively correlate with thickness of tissue.

The impact of reproduction on net photosynthetic rates was not included in this study of juveniles. However, Aruga *et al.* (1990) noted that the sorus portion of *E. cava* thalli had lower Pm values and higher respiration rates than the non-sorus portion. Also, the effect of self-shading was minimised in this study because of the use of juvenile *E. radiata*. However the availability of light in lower thallus regions of mature plants will almost certainly be periodically reduced due to shading by the canopy. Additionally, respiration rates may be expected to differ all year between adults and juveniles due to differences in the structural versus photosynthetic component of the thallus.

In combination, these differences between adults and juvenile may lead to an overestimation of adult productivity when extrapolated from juvenile data. However, preliminary data comparing the efficiency of PSII in adults and juveniles indicated that juvenile *E. radiata* may be more susceptible to photoinhibition (Figure 2.11). This may mean that the Pm values for
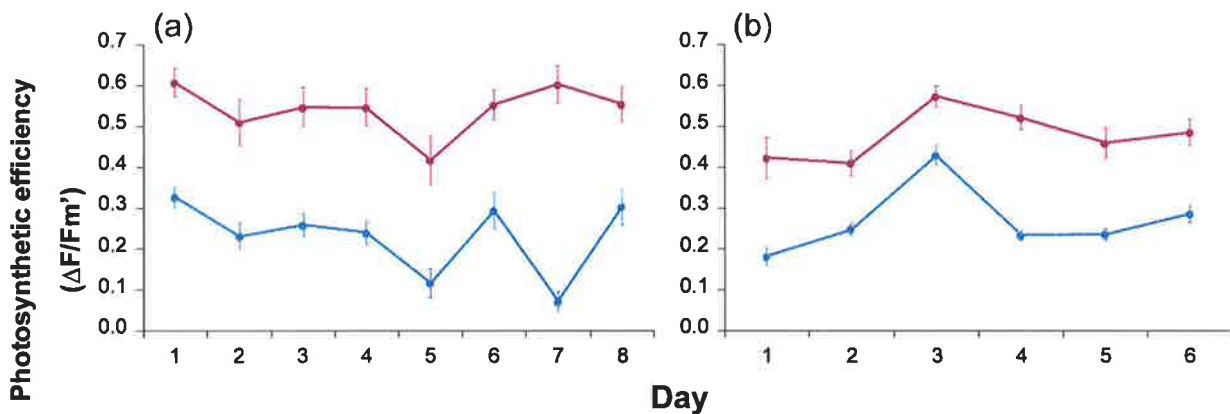
Figure 2.11 PSII efficiency (effective quantum yield; $\Delta F/Fm'$) of adult (---) and juvenile (—) *E. radiata* measured at high light (midday) over several days during December 1999 (a) and March 2000 (b). The midday depression in juveniles is consistently larger than that seen in adults. Both adults and juveniles showed complete recovery of photosynthetic efficiency by early evening. All measurements were conducted using a diving-PAM fluorometer (see Chapter 5 for details) at a depth of 3 m.

adult *E. radiata* may actually be higher than that measured in juveniles. A study of the *in situ* photosynthesis-irradiance response of adult *E. radiata* is needed to determine the generality of the juvenile PI response. This study will otherwise make the assumption that the rate of photosynthesis per gram thallus weight is comparable in both juvenile and adult *E. radiata*.

In conclusion, *E. radiata* possesses an ability to alter its photosynthetic apparatus in response to seasonal changes in its environment, producing an optimal photosynthetic performance over the course of the year. This ability to acclimate resulted in *E. radiata* at a depth of 3 m being able to photosynthetically compensate for at least 90% of the day all year. In winter, despite a maximum irradiance of only a third of the summer level, the algae are exposed to an irradiance above *Ik* for at least half of the day. The photoadaptive strategy of *E. radiata* therefore has important ecological benefits.

Chapter 3 : Primary Productivity of *Ecklonia radiata*

The photosynthetic apparatus of *Ecklonia radiata* shows distinct changes in response to seasonal variation in the underwater environment (Chapter 2). This chapter outlines how the ability to acclimate to a changing irradiance environment enables *E. radiata* to maintain rates of daily carbon assimilation at a high level throughout the year.

Introduction

A significant proportion of the organic carbon produced in the nearshore region of the world's oceans derives from macroalgal photosynthesis (Kirk 1994). Kelp has long been recognised as being capable of extremely high rates of primary production (Mann 1972, Mann 1973) and have been the subject of considerable research into algal productivity. The work by Parke (1948) provided a basis for studies on the primary production of the Laminariales. Subsequently a substantial body of work has been produced in the northern hemisphere (e.g. John 1971, Buggeln 1974, Chapman and Craigie 1977, Kain 1977, Chapman and Craigie 1978, Gerard and Mann 1979, Kain 1979, Lüning 1979, Chapman and Lindley 1980, Dieckmann 1980, Fortes and Lüning 1980, Calvin and Ellis 1981, Gagné *et al.* 1982, Dean and Jacobsen 1984, Wheeler and Druehl 1986, Gendron 1989, Dunton 1990, Flores Moya *et al.* 1993), while in the southern hemisphere Novaczeck (1984a, 1984b), Larkum (1986) and Kirkman and co-workers (Kirkman 1981, Mann and Kirkman 1981, Kirkman 1984, Hatcher *et al.* 1987, Kirkman 1989) investigated kelp productivity in Australasia.

A large body of the above research estimated growth rates in terms of biomass accumulation rates, blade elongation or frond area increments as a *de facto* measure for primary productivity. These techniques have proved a useful tool to elucidate growth strategies in kelp, particularly in relation to nutrient availability and seasonal changes in light and temperature (Buggeln 1974, Chapman and Craigie 1977, Buggeln 1978, Chapman and Craigie 1978, Chapman *et al.* 1978, Lüning 1979, Chapman and Lindley 1980, Fortes and Lüning 1980, Calvin and Ellis 1981, Gagné *et al.* 1982, Dean and Jacobsen 1984, Wheeler and Druehl 1986, Gendron 1989, Dunton 1990, Castric-Fey *et al.* 1999). However, neither the amount of carbon lost to processes such as exudation, blade erosion and herbivory nor the amount incorporated into storage carbohydrates is accounted for by these methods (Larkum 1986, Murthy *et al.* 1986), and as such they are not a true measure of gross primary production. Furthermore, studies utilising more accurate measures of carbon assimilation rates, such as those measuring oxygen evolution, have often based estimates of daily and annual net productivity on data collected during short term incubations, often performed under artificial conditions and/or utilising

only small portions of thallus (Drew 1983, Flores Moya *et al.* 1995, Gómez *et al.* 1997). Diurnal variations in photosynthetic rate due to both endogenous and environmental factors (Ganzon Fortes 1997) have been observed in all three classes of macroalgae (Ramus and Rosenberg 1980, Coutinho and Zingmark 1987, Gao 1990, Huppertz *et al.* 1990, Henley *et al.* 1991a, Hanelt 1992, Henley *et al.* 1992, Hanelt *et al.* 1993, Henley 1993, Franklin *et al.* 1996, Figueroa *et al.* 1997, Ganzon Fortes 1997, Schofield *et al.* 1998). Thus, basing production estimates on measurements conducted at only one period of the day may result in inaccurate estimates (Ramus and Rosenberg 1980, Ganzon Fortes 1997). Very few studies have reported rates of macroalgal primary productivity that are based on *in situ* measurements of photosynthesis and irradiance over 24 hour periods (Cheshire *et al.* 1996, Westphalen and Cheshire 1997). Furthermore, only a few investigations of macroalgal productivity have included a temporal component (Hatcher *et al.* 1977, Flores Moya *et al.* 1995, Cheshire *et al.* 1996).

Photosynthetic activity of many macroalgal species often shows an afternoon depression in photosynthetic oxygen production. This is often the result of "photoinhibition", and complicates the estimation of daily productivity. Photoinhibition is the reversible decrease in photosynthetic efficiency that occurs in response to the absorption of excess light energy by PSII. Photoinhibition is now recognised as involving two major components. The first type, "dynamic photoinhibition" (Osmond and Grace 1995), protects the photosynthetic apparatus from excess energy absorption. It involves nonphotochemical (thermal) dissipation, generally via the xanthophyll cycle, although cyclic electron transport may also be involved (Demmig-Adams and Adams 1992, Long *et al.* 1994). The xanthophyll cycle exists in higher plants and some algal groups, including the Phaeophyceae (Uhrmacher *et al.* 1995, Franklin *et al.* 1996, Hanelt *et al.* 1997b, Schofield *et al.* 1998, Harker *et al.* 1999), and consists of the light-dependant conversion of three oxygenated carotenoids (violaxanthin, antheroxanthin and zeaxanthin). Under conditions of excess energy absorption violaxanthin is converted by sequential de-expoxidations to zeaxanthin through the intermediate antheroxanthin (Demmig-Adams and Adams 1992). The relationship between thermal dissipation and zeaxanthin content has often been found to be linear in higher plants under a variety of conditions (Demmig-Adams 1990, Demmig-Adams *et al.* 1990, Demmig-Adams and Adams 1992). The xanthophyll cycle protects the plant or alga from photodamage by decreasing the functional absorption cross-section of PSII and facilitating the dissipation of excess energy as harmless thermal radiation. Recovery of photochemical efficiency occurs quickly, usually within minutes, when the irradiance become non-saturating. The pH gradient across the thylakoid

membrane declines and this situation triggers the sequential expoxidation of the xanthophyll pool resulting in accumulation of the non-quenching violaxanthin (Osmond and Grace 1995).

The second type of photoinhibition, "chronic photoinhibition" (Osmond and Grace 1995), involves the inactivation of PSII after absorption of excess amounts of photons, and generally involves damage to the D1 polypeptide of PSII reaction centres by singlet oxygen species (Kyle 1987, Prásil et al. 1992). When the repair (turnover) of the D1 protein fails to keep up with the rate of damage, photosynthetic efficiency declines (Falkowski and Raven 1997). Inactivation of PSII is dependant on the dose of photons absorbed not the rate of photon absorption (Prásil et al. 1992). In higher plants one PSII unit is inactivated for every 10^6 to 10^7 photons absorbed (Anderson et al. 1997). Inactivation of PSII will thus occur in low light conditions but is more rapid under saturating light conditions. Inactivated PSII enhance the non-photochemical dissipation of energy, thereby protecting the remaining functional PSII (Öquist et al. 1992, Long et al. 1994, Anderson et al. 1997, Krause 1998). The accumulation of non-functional PSII occurs when turnover of the D1 protein is prevented. Although the mechanism preventing D1 degradation, and the insertion of newly synthesised D1, is not understood, this represents an important photoprotective device, particularly for "shade plants" with a small xanthophyll pigment pool (Anderson et al. 1997). The decline in photochemical efficiency associated with high light induced damage to PSII is reversed slowly (over hours) (Osmond and Grace 1995). If efficiency is not "recovered" before irradiance drops to below saturation then carbon assimilation rates will be affected (Henley 1993, Long et al. 1994). Long et al. (1994) calculated that a hypothetical tree canopy in England would see a reduction in potential carbon assimilation rates of 9% due to photoinhibition, and Ögren and Rosenqvist (1992) found a significant reduction in afternoon carbon dioxide uptake in photoinhibited Salix (willow).

The extent to which carbon assimilation rates will be affected by photoinhibition is dependant on the capability of the plant or alga to engage photoprotective processes and on an ability to repair damaged PSII. Plants that are acclimated to high irradiance conditions have a larger pool of xanthophyll pigments than those acclimated to "shade" conditions (Demmig-Adams and Adams 1992). Similar findings in macroalgae suggest that shallower species and individuals have a greater capacity for thermal dissipation of excess energy than those growing in deeper water (Henley et al. 1991b, Franklin et al. 1992, Hanelt 1992, Franklin et al. 1996, Hanelt et al. 1997a, Sagert et al. 1997, Hanelt 1998, Rodrigues et al. 2000). In addition, it seems that the capacity for D1 synthesis is also dependant on light history, as the turnover rate is

increased in "sun" plants (Öquist *et al.* 1992, Long *et al.* 1994, Anderson *et al.* 1997). Productivity rates of algae acclimated to a particular measurement depth (i.e. 3 m) are therefore less likely to be significantly lowered due to photoinhibition when compared to rates of algae which are acclimated to a lower irradiance, which have reduced photoprotective and repair capacities (i.e. 10 and 12 m algae).

The repair and avoidance mechanisms themselves have a carbon and energy cost, i.e. xanthophyll pigments have a production and maintenance cost (Raven 1994). However, the benefits, in terms of carbon acquisition, of avoiding damage or of quickly repairing damage theoretically outweigh this expense (Raven 1989). In addition, there is no evidence that growth rates or photosynthetic yields are lowered due to the presence of these repair and avoidance mechanisms (Raven 1994).

Many aspects of photoinhibition and associated recovery processes have been studied in macroalgae in recent years (e.g. Kain and Jones 1987, Herbert 1990, Huppertz *et al.* 1990, Franklin *et al.* 1992, Hanelt 1992, Hanelt *et al.* 1992, Hanelt *et al.* 1993, Hanelt *et al.* 1995, Herrmann *et al.* 1995, Uhrmacher *et al.* 1995, Bruhn and Gerard 1996, Franklin *et al.* 1996, Häder *et al.* 1996, Figueroa *et al.* 1997, Hanelt *et al.* 1997a, Hanelt *et al.* 1997b, Sagert *et al.* 1997, Häder *et al.* 1998, Hanelt 1998, Schofield *et al.* 1998, Harker *et al.* 1999, Rodrigues *et al.* 2000). Photoinhibited individuals have generally been found to have lowered photosynthetic efficiencies and at higher irradiance photosynthetic capacity is also reduced (Hanelt *et al.* 1992, Henley 1993, Hanelt *et al.* 1995, Bruhn and Gerard 1996, Häder *et al.* 1996, Hanelt *et al.* 1997a), which is associated with either an increase in thermal dissipation of excess energy or with damage to the photosynthetic apparatus. Variation in photoprotective potential is related to the irradiance environment through both acclimation (Henley *et al.* 1991a, Franklin *et al.* 1996, Häder *et al.* 1996, Hanelt 1998) and adaptation (Herbert 1990, Hanelt *et al.* 1997a, Hanelt 1998). Recovery of photosynthetic activity begins when irradiance decreases and is generally complete by early evening, unless photodamage has occurred (Huppertz *et al.* 1990, Hanelt *et al.* 1997a, Hanelt *et al.* 1997b, Schofield *et al.* 1998). Despite the number of studies on this topic, none have directly sought to determine the impact of photoinhibition on the carbon assimilation rates of macroalgae *in situ*. Photoinhibition on a daily basis may affect carbon assimilation rates if a complete recovery from photodamage does not occur each day (Henley 1993, Bruhn and Gerard 1996).

The aim of this work is firstly, to quantify across the depth profile the seasonal productivity of the kelp *E. radiata* in terms of oxygen evolution rates measured *in situ*; and secondly, to

determine the extent to which a midday depression in photosynthetic efficiency affects carbon assimilation rates in *E. radiata*.

Methodology

Net 24 Hour Productivity

Methods

Productivity estimates were based on the photokinetic parameters derived from morning photosynthesis and irradiance (PI) data, as described in Chapter 2. Rates of net 24 hour productivity were obtained by integrating the PI curve for each sample over the average light field measured at (or calculated for) the depth and time period (month) in which each individual was collected. This method was chosen in order to compare photosynthetic rates of algae at the depth of collection even though rates were measured under different light fields (i.e. on different days) (Cheshire *et al.* 1996, Tun *et al.* 1997). The light field was based on the average maximum irradiance for each depth at each time period and the average photoperiod for each month, measured at 3 m (Table 2.1). Total 24 hour respiration was calculated assuming that respiration rates in the light are the same as those measured in the dark (Cheshire *et al.* 1996), and gross 24 hour productivity was calculated as the sum of net 24 hour productivity and total 24 hour respiration.

Analysis

The following null hypotheses were tested:

1. There is no difference in rates of productivity or respiration within depths.

2. Within samples from a particular depth there is no seasonal difference in productivity rates.

Differences among depths and months were tested using one-way ANOVAs (two ways were not possible due to uneven sampling design i.e. 5 m and 12 m were not sampled at all times). When variances were heterogeneous a Welch ANOVA (Welch 1951) was used. Differences among means were isolated using Tukey-Kramer HSD (honestly significant difference) test.

Photoinhibition

Methods

In order to assess the impact of photoinhibition on *in situ* productivity rates, a comparison was made between the rates of daily gross productivity that were calculated using PI data collected up to I_{max} (generally solar noon) and the rates based on all the PI data collected throughout the entire day. Both data sets included all data collected during darkness. This method makes the assumption that no reduction in oxygen evolution due to photoinhibition occurs before I_{max}. As photodamage is more likely to occur at times of high irradiance this assumption is valid (Anderson *et al.* 1997), although individuals collected from 10 m and 12 m would be more likely to experience photoinihibtion during the morning. The impact of photoinhibition on oxygen production (carbon assimilation rates) will only become apparent when irradiance declines from supersaturating (i.e. after I_{max}), when electron transport replaces RuBisCO as the rate limiting feature (Long *et al.* 1994, Ögren 1994).

Analysis

The difference between rates of gross 24 hour productivity was calculated using morning PI data only and using PI data from the whole day (ΔGross 24 hour) for each individual. For each depth during each month the hypothesis that the population mean did not differ from zero was tested using a two-tailed paired sample Student's t-test. The effect of season and depth of collection on ΔGross 24 hour was tested using 3 m and 10 m data by a two-way ANOVAs (time period and data type as the factors).

Results

Effect of Depth

A significant effect of depth on both net 24 hour and gross 24 hour productivity was detected during all months (Table 3.1; Table 3.2; Figure 3.1). However, respiration rates remained constant over depth, except in June when the rate at 3 m was higher than at 10 m and 12 m and in December when the rate at 3 m was significantly higher than that at 12 m (Table 3.1; Table 3.2).
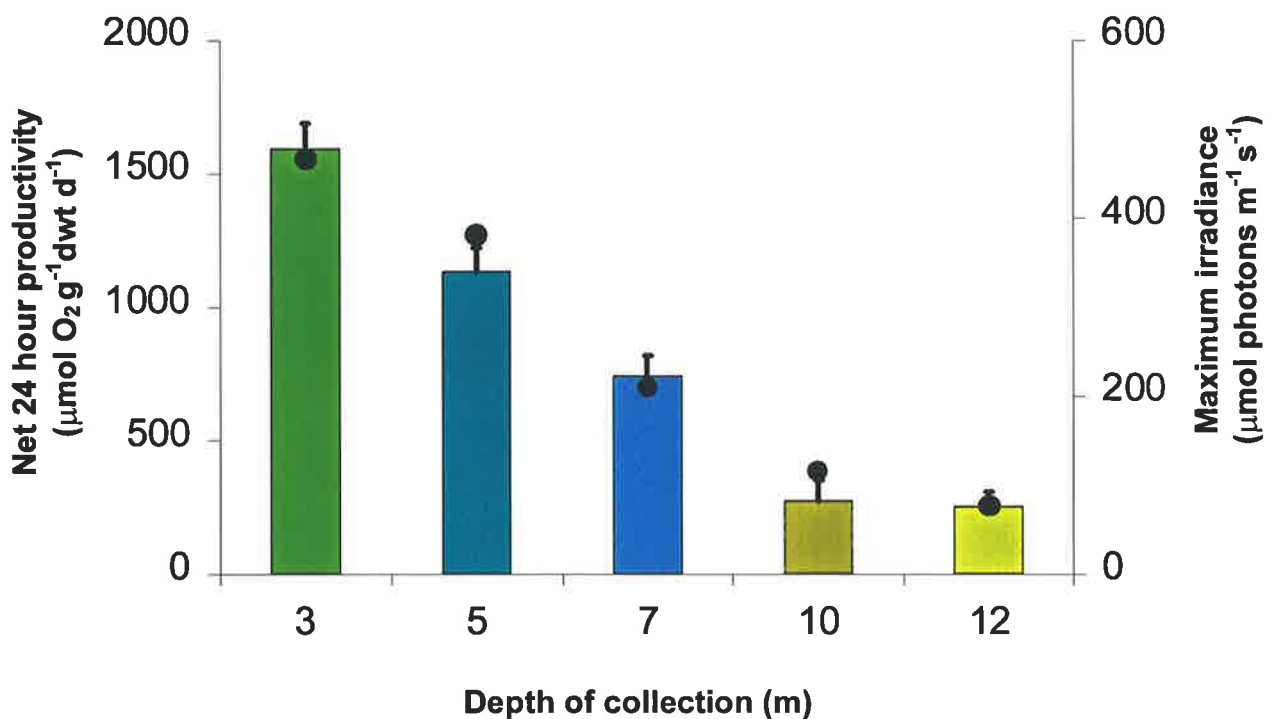
Figure 3.1 Rates of net daily productivity (mean ± s.e.) by *Ecklonia radiata* collected from five depths and measured at 3 m during September 1999. Average maximum irradiance (●) at 3 m represents the mean of eleven days observations, whilst the irradiance for the other depths were calculated based on the 3 m value and an attenuation coefficient (k) of 0.2 (see Table 2.1).

Table 3.1 Net 24 hour productivity, gross 24 hour productivity and 24 hour respiration rates (μmol O_2 g^{-1}dwt d^{-1}) of *Ecklonia radiata* at West Island, South Australia. Values are the means (*sd*) (n $\cong$ 8) calculated by integrating the PI curves over an average light field measured (or calculated) during each month (see text for details).

	Depth	February	March	May	June	September	October	December
Net Productivity	3	1482.15 (*542.64*)	1196.47 (*296.95*)	1379.49 (*370.95*)	1188.60 (*366.10*)	1591.53 (*313.17*)	1302.67 (*229.48*)	1621.23 (*475.27*)
	5	944.25 (*380.11*)	-	1694.13 (*517.99*)	-	1133.88 (*224.42*)	1173.42 (*455.59*)	-
	10	337.51 (*220.61*)	461.09 (*234.50*)	182.80 (*222.06*)	218.27	269.46 (*194.14*)	450.38 (*278.80*)	759.48 (*332.48*)
	12	-	201.41 (*91.53*)	-	253.90 (*194.35*)	251.32 (*136.85*)	-	279.14 (*145.68*)
Respiration	3	854.80 (*546.19*)	531.30 (*195.73*)	376.79 (*183.18*)	603.97 (*111.58*)	386.08 (*97.89*)	355.57 (*80.16*)	550.35 (*165.85*)
	5	657.99 (*484.47*)	-	378.66 (*180.31*)	-	443.30 (*235.81*)	418.20 (*123.08*)	-
	10	366.02 (*233.62*)	441.10 (*273.94*)	481.29 (*229.25*)	476.07	363.12 (*84.52*)	309.95 (*53.63*)	473.70 (*98.75*)
	12	-	412.19 (*90.36*)	-	274.83 (*130.95*)	343.56 (*73.30*)	-	354.59 (*101.86*)
Gross Productivity	3	2336.96 (*1023.70*)	1727.77 (*252.70*)	1756.27 (*411.98*)	1792.57 (*390.76*)	1977.61 (*340.34*)	1658.24 (*241.68*)	2171.58 (*574.80*)
	5	1602.24 (*700.96*)	-	2072.79 (*658.54*)	-	1577.17 (*324.66*)	1591.62 (*517.21*)	-
	10	703.53 (*240.60*)	902.19 (*483.08*)	664.09 (*97.04*)	694.34	632.58 (*158.93*)	760.33 (*310.02*)	1233.18 (*409.90*)
	12	-	613.60 (*64.22*)	-	528.74 (*153.74*)	594.88 (*192.69*)	-	633.74 (*111.35*)

Table 3.2 Summary of ANOVA results and the *post hoc* of Tukey-Kramer HSD ($\alpha = 0.05$) comparisons for gross 24 hour and net 24 hour productivity and 24 hour respiration rate. Similarities between depths are defined by the results of the *post hoc* tests and are indicated by the same letter The final column represents the ANOVA significance probability for comparisons made each month across depths. (*** $p \leq 0.001$, ** $p \leq 0.01$, * $0.01 < p \leq 0.05$, ns = not significant).

a)	February 1999				
	3 m	**5 m**	**10 m**	**12 m**	***p***
Gross 24Hr	a	a,b	b	not measured	**
Net 24Hr	a	a,b	b	not measured	**
Resp 24Hr	a	a	a		ns

b)	March 2000				
	3 m	**5 m**	**10 m**	**12 m**	***p***
Gross 24Hr	a	not measured	b	b	***
Net 24Hr	a	not measured	b	b	***
Resp 24Hr	a		a	a	ns

c)	May 1999				
	3 m	**5 m**	**10 m**	**12 m**	***p***
Gross 24Hr	a	a	b	-	***
Net 24Hr	a	a	b	-	***
Resp 24Hr	a	a	a	-	ns

d)	June 2000				
	3 m	**5 m**	**10 m**	**12 m**	***p***
Gross 24Hr	a	not measured	b	b	***
Net 24Hr	a	not measured	b	b	**
Resp 24Hr	a		b	a,b	**

continued over.

Table 3.2 continued.

e)	September 1999					
	3 m	**5 m**	**7m**	**10 m**	**12 m**	***p***
Gross 24Hr	a	a	b	c	c	***
Net 24Hr	a	b	c	d	d	***
Resp 24Hr	a	a	a	a	a	ns

f)	October 1998				
	3 m	**5 m**	**10 m**	**12 m**	***p***
Gross 24Hr	a	a	b	not measured	**
Net 24Hr	a	a	b		***
Resp 24Hr	a	a	a		ns

g)	December 1999				
	3 m	**5 m**	**10 m**	**12 m**	***p***
Gross 24Hr	a	not measured	b	c	***
Net 24Hr	a		b	c	***
Resp 24Hr	a		a,b	b	**

Seasonal Productivity

Rates of daily productivity were similar at each depth all year (Table 3.1; Figure 3.2) despite an up to five-fold drop in the maximum irradiance throughout the year in addition to changes in day-length (Table 2.1). Net 24 hour production generally remained constant over time at all depths, in fact there were no significant differences between rates throughout the year at both 3 m and at 12 m (Table 3.3). Net daily productivity rates averaged around 1300 $\mu molO_2 g^{-1}dwt$ d^{-1} at 3 m to 250 $\mu molO_2 g^{-1}dwt$ d^{-1} at 12 m. At 5 m and 10 m however, time of year did have a significant effect on productivity (Table 3.3). At 5 m the rate during May was higher than that during February. Conversely, at 10 m the rates during May and September were significantly lower than those measured during December. Gross 24 hour production also remained fairly constant, differing through time only at 10 m (Table 3.1; Table 3.3) where the December rate was higher than those during May and September. Respiration rates were also steady over time, altering only at 3 m where they were higher during February (Table 3.1; Table 3.3).
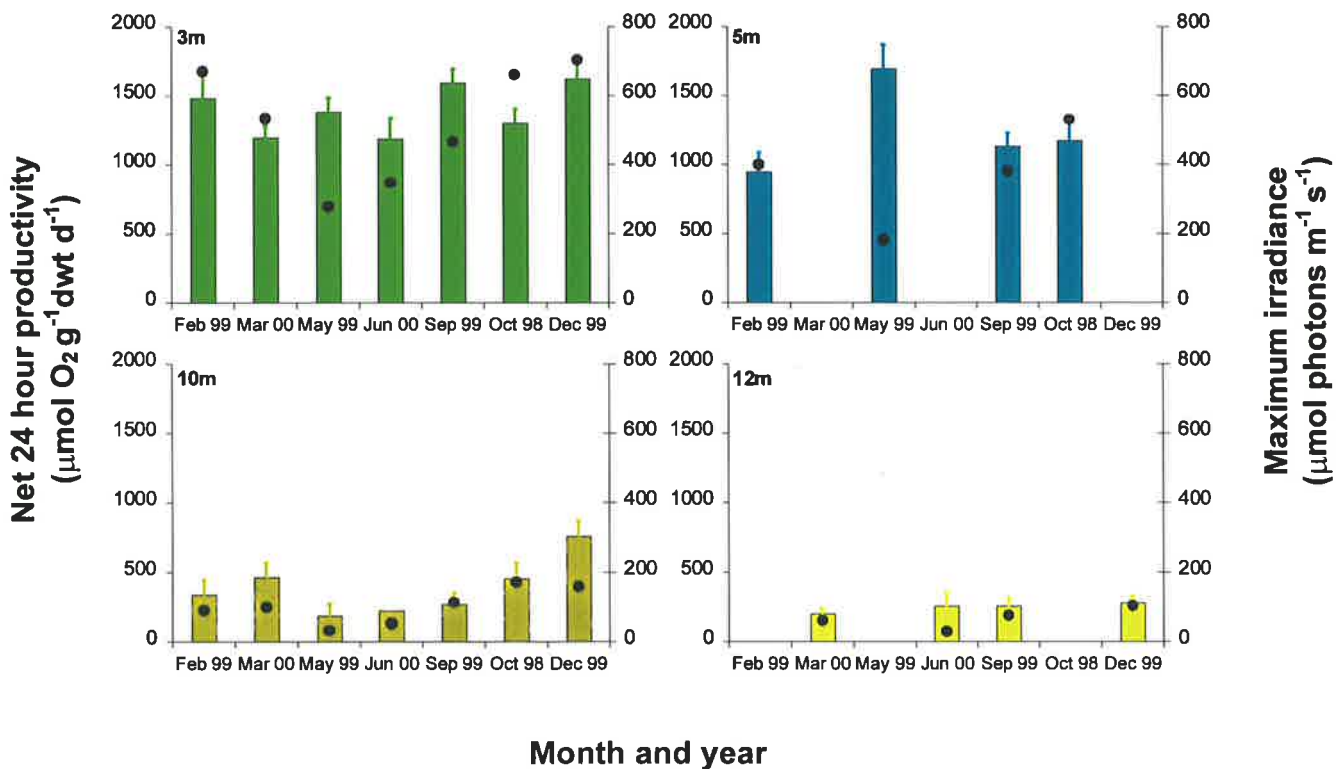
Figure 3.2 Seasonal change in mean (± s.e.) rate of net daily productivity by *Ecklonia radiata* at four depths at West Island, South Australia. Average maximum irradiance level (•) at each depth is also shown (based on data in Table 2.1). Note that the y-axis scales differ between depths but that the intervals remain constant.

Table 3.3 Summary of ANOVA results and the *post hoc* Tukey-Kramer HSD (α = 0.05) comparisons for gross 24 hour and net 24 hour productivity and 24 hour respiration rate. The final column represents the ANOVA significance probability for comparisons among months made for each depth (*** $p \leq 0.001$, ** $p \leq 0.01$, * $0.01 < p \leq 0.05$, ns = not significant).

a)	3 m							
	Feb	**Mar**	**May**	**June**	**Sep**	**Oct**	**Dec**	***p***
Gross 24Hr	a	a	a	a	a	a	a	ns
Net 24Hr	a	a	a	a	a	a	a	ns
Resp 24Hr	b	a,b	a	a,b	a	a	a,b	***

b)	5 m							
	Feb	**Mar**	**May**	**June**	**Sep**	**Oct**	**Dec**	***p***
Gross 24Hr	a	not measured	a	not measured	a	a	not measured	ns
Net 24Hr	a		b		a,b	a,b		**
Resp 24Hr	a		a		a	a		ns

c)	10 m							
	Feb	**Mar**	**May**	**June**	**Sep**	**Oct**	**Dec**	***p***
Gross 24Hr	a,b	a,b	b	a,b	b	a,b	a	**
Net 24Hr	a,b	a,b	b	a,b	b	a,b	a	**
Resp 24Hr	a	a	a	a	a	a	a	ns

d)	12 m							
	Feb	**Mar**	**May**	**June**	**Sep**	**Oct**	**Dec**	***p***
Gross 24Hr	not measured	a	not measured	a	a	not measured	a	ns
Net 24Hr		a		a	a		a	ns
Resp 24Hr		a		a	a		a	ns

Photoinhibition

In addition to the rates of gross 24 hour productivity calculated from "morning" PI data, rates were also calculated using the PI data collected from the "all day" data (Appendix A). These data sets produced differing results during most months (Figure 3.3), with rates of gross productivity higher when calculated using only "morning" PI data (i.e. the ΔGross 24 hour value was positive). These differences were significant during several months, particularly those with high irradiance (e.g. spring and summer).

ΔGross 24 hour was significantly higher at 10 m (Two-way ANOVA; $p < 0.05$) and varied significantly across months (Two-way ANOVA; $p < 0.001$), notably there was no detectable ΔGross 24 hour during May, the month with the lowest irradiance. The interaction between depth and month was highly significant (Two-way ANOVA; $p < 0.001$).
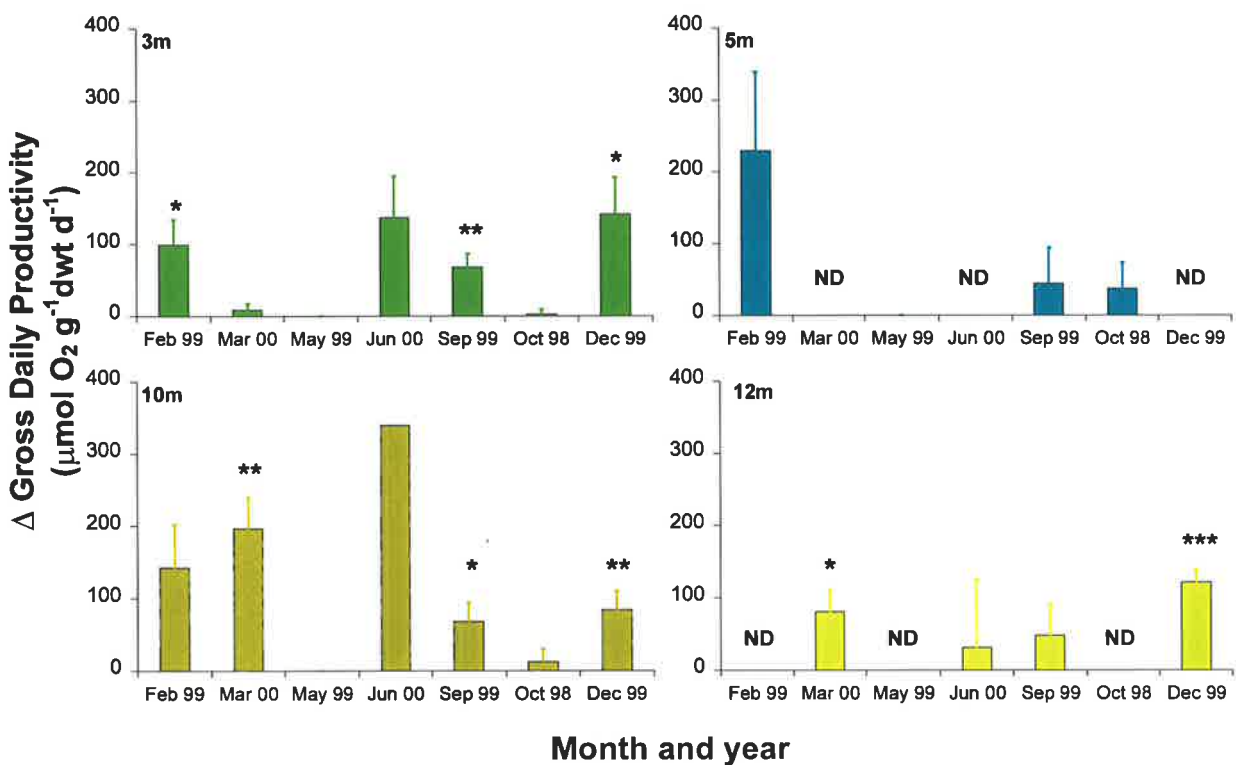
Figure 3.3 The difference between the rates of daily gross productivity when calculated using photokinetic parameters derived from only morning photosynthesis-irradiance (PI) data and from using the morning <u>and</u> afternoon PI data. The y-axis represents the "morning data" rate minus the "all day data" rate (mean ± se). "ND" indicates that no data was collected for that depth (5 or 12 m) during that particular month. Asterisks indicate the probability results of significant two tailed paired sample Student's t-tests (*** $p \leq 0.001$, ** $p \leq 0.01$, * $0.01 < p \leq 0.05$) that tested for a significant difference between each mean ΔGross 24 hour and a hypothesised population mean of zero.

Discussion

Ecklonia radiata maintains a high, relatively constant rate of net productivity all year which is a strong indication of the ecological importance of seasonal changes in photoacclimation state. These acclimatory changes are characterised by lower compensatory irradiance (Ic), higher potential maximum rates of photosynthesis (Pm_{gross}) and higher photosynthetic efficiency at low light (α) during winter when irradiance is lowest. The outcome of this alteration in acclimation state is that rates of productivity were not significantly lower in winter despite a significant reduction in the level of irradiance and shorter day-lengths.

The lack of seasonal variability in *E. radiata* productivity contrasts with significant drops in productivity during winter compared to summer and spring which have been reported elsewhere. Several of these studies were conducted at locations with more extreme seasonal differences in irradiance than those found in southern Australia (e.g. Nova Scotia, Hatcher *et al.* 1977; Scotland, Drew 1983; Antarctica, Drew and Hastings 1992), and a larger decline in rates in winter is to be anticipated. However, productivity rates in the phaeophycean dominated 4m boulder communities at West Island studied by Cheshire *et al.* (1996) also decline significantly in winter relative to summer (438 cf. 1002 $\mu molO_2$ $g^{-1}dwt$ d^{-1}). Both the current study and Cheshire *et al.* (1996) were conducted at the same location, with similar environmental conditions (Appendix D & Table 2.1) and thus the irradiance regime cannot explain this difference. The boulder community displayed similar seasonal changes in photokinetic parameters (Chapter 2) but did not include an alteration in maximum potential gross photosynthesis (Pm_{gross}). Additionally, the boulder community values for both Ic and α were lower during both winter and summer when compared with the current values for *E. radiata* at a depth of 3 m. This means that *E. radiata* is able to reach photosynthetic compensation and saturation for a much longer portion of the day. In summer, the boulder community experienced irradiance above that required for photosynthetic compensation for 54% of daylight hours but only 37% during winter. By contrast, *E. radiata* was able to compensate for over 90% of daylight hours all year round. Similarly, *E. radiata* experienced irradiance higher than the saturating irradiance ($I_{0.95}$) for ~40% of daylight hours in summer, as opposed to just 14% for the boulder community. In winter, the boulder community never attained irradiance at or above $I_{0.95}$ whereas *E. radiata* experienced levels above $I_{0.95}$ for 14-24% of daylight hours. This has profound consequences on rates of daily net productivity and is reflected in the differing abilities of *E. radiata* and the boulder community to maintain productivity rates at low light levels.

The summer rates of net and gross productivity and respiration of *E. radiata* compare well with those published for other brown algae in a variety of locations (see Table 3.4). An average net productivity rate of around 1300 μmolO$_2$ g^{-1}dwt d^{-1} was maintained at a depth of 3 m throughout the year. This rate equates to approximately 0.016 gC g^{-1}dwt d^{-1} (assuming a photosynthetic quotient (PQ) of 1.0). Equivalent rates at 5, 10 and 12 m were approximately 0.012, 0.005 and 0.003 gC g^{-1}dwt day^{-1} (assuming averages of 1000, 400 and 250 μmolO$_2$ g^{-1}dwt d^{-1} respectively). Assuming these rates are maintained all year, annual productivity ranges from 5.8 gC g^{-1}dwt year^{-1} (12.64 gdwt g^{-1}dwt y^{-1} assuming tissue contains 45% carbon Drew and Hastings 1992) to 1.1 gC g^{-1}dwt y^{-1} (2.44 gdwt g^{-1}dwt y^{-1}) across the depth profile. These rates are comparable with 3.15 gC g^{-1}dwt y^{-1} for the West Island boulder community at 4m (converted using an average of summer and winter productivities) and with 1.36 gC g^{-1}dwt y^{-1} for *Laminaria longicruris* at 10 m in Nova Scotia (Hatcher *et al.* 1977) (converted using 0.005 gdw cm^{-2} based on Henley and Dunton 1995). Similarly, Flores Moya *et al.* (1995) calculated that *Phyllariopsis purpurascens* (Phyllariaceae, Phaeophyta) at 30m in the Straits of Gibraltar averaged 1.7gC g^{-1}dwt over its production cycle of around 7 months.

A large proportion of the net amount of annually assimilated carbon is eventually released into the surrounding waters and made available to secondary producers (Chapter 4). The contribution of carbon made by *E. radiata* on an annual basis is high. A portion of this assimilate must be used for maintenance processes and seasonal reproduction. Members of the Laminariales do not produce reproductive laterals. Rather, existing fronds develop a region of reproductive sori; this does not represent such a large allocation of resources as that which occurs in members of the Fucales (other canopy dominants), many of which develop specialised reproductive structures (Womersley 1987). Most of the assimilated carbon is therefore released as dissolved or particulate matter or eroded from the necrotic distal region of the algae and may be an important food source for grazing animals and filter feeders. Tissue is turned over annually up to 12 times (i.e. 12 gdwt g^{-1}dwt y^{-1} at 3 m) represents a very large contribution of particulate carbon into *E. radiata* dominated systems. However, a significant portion of assimilated carbon is probably released in the form of exudates which is an important food source for heterotrophic organisms (Williams and Yentsch 1976, Brylinsky 1977). Brown algae have long been recognised for releasing large amounts of dissolved organic carbon, with estimates ranging from only 1.1-3.8% of net

Table 3.4 Comparison with published daily oxygen production/consumption rates ($\mu molO_2$ g^{-1}dwt d^{-1}) for phaeophycean algae. Rates are those reported for summer and are based on daily irradiance measured *in situ*.

Study	Species	Depth	Lat/Long	Net 24Hr	Gross 24Hr	Resp 24Hr
Current study	*Ecklonia radiata*	3 m	35°36'S 138°35'E	1621	2171	550
Current study	*Ecklonia radiata*	10 m	35°36'S 138°35'E	400-759	1233	474
Hatcher *et al.* 1977[a]	*Laminaria longicruris*	10 m	44°30'N 64°50'W	1300	1650	350
Drew 1983[b]	*Laminaria digitata*	0-1 m	56°34'N 2°46'W	2050	-	-
Drew 1983[b]	*Laminaria saccharina*	0-1 m	56°34'N 2°46'W	1560	-	-
Drew 1983[b]	*Laminaria hyperborea*	0-1 m	56°34'N 2°46'W	110	-	-
Drew and Hastings 1992	*Himantothallus grandifolius*	6 m	45°35'S 60°45'W	730	-	-
Gomez *et al.* 1997[c]	*Himantothallus grandifolius*	10 m	62°S 58°30'W	2598	-	-
Flores-Moya *et al.* 1995[b]	*Phyllariopsis purpurascens*	30 m	36°26'N 05°04'W	1698	-	-
Cheshire *et al.* 1996	Phaeophycean community	4 m	35°36'S 138°35'E	1002	1656	654

[c] using conversion factor of 0.005 gdw cm-2 based on (Henley and Dunton 1995)
[b] based on laboratory photosynthesis measurements
[c] converted from carbon units assuming a PQ of 1.0

Table 3.5 Comparative drop in net productivity and irradiance as a % of 3 m levels

Month	Depth (m)	Net 24Hr as % of 3 m Net 24Hr	PAR as % of 3 m PAR
Feburary	5	63	60
	10	23	13
March	10	39	19
	12	16	12
May	5	122	65
	10	13	12
June	10	18	16
	12	21	9
September	5	71	82
	10	17	25
	12	16	17
October	5	90	80
	10	35	26
December	10	47	23
	12	17	15

carbon assimilation (Brylinsky 1977) to as high as 35-40% of net primary production (Khailov and Burlakova 1969, Sieburth 1969, Hatcher *et al.* 1977).

Unlike seasonal trends in productivity there is a significant difference in rates of productivity across the depth profile. The drop in rates of both net and gross productivity was similar to the decline in light levels (Table 3.5), however net productivity did not reduce to the same extent as the irradiance. This finding is consistent with the acclimation in *E. radiata* to changes in irradiance across the depth profile (Chapter 2), and although this ability is reduced compared with the level of acclimation displayed across seasons, this result shows it is still clearly of ecological significance.

This work has shown that during certain times of the year rates of daily productivity in *E. radiata* are also affected by photoinhibition. The primary productivity of certain higher plants and algae has been shown to be reduced due to the effects of photoinhibition on photosynthetic processes (Ögren and Rosenqvist 1992, Long *et al.* 1994). The classic afternoon depression in net oxygen evolution rates was observed for *E. radiata* on days of high maximum irradiance in PI curves at all depths. Throughout the year photosynthetic efficiency at low light (α) was reduced when calculated using data which included the

photoinhibition affected afternoon period (Appendix A). Photosynthetic efficiency at this time is reduced by thermal dissipation via the xanthophyll cycle and by the accumulation of damaged reaction centres which also act as quenchers. With the exception of winter, photosynthetic capacity (Pm) was also reduced when compared to the parameters calculated using only morning data, which is an indication that *E. radiata* is susceptible to photoinhibition at all depths (Hanelt *et al.* 1992, Hanelt *et al.* 1995, Bruhn and Gerard 1996, Hanelt *et al.* 1997a).

To have a significant effect on carbon assimilation rates photosynthetic efficiency must remain lowered when irradiance decline in the afternoon (Long *et al.* 1994). The results in this study indicate that this variously occurred in *E. radiata* during spring, autumn and summer. Rates of gross daily productivity were as much as 6.5, 14, 48, and 19% lower when calculated using the whole days PI data for 3, 5, 10 and 12 m respectively relative to morning rates. Importantly, this reduction was generally larger for individuals from the greater depths, i.e. overall plants from 10 m had significantly larger ΔGross 24 hour values in comparison to those from 3 m. This suggests differences in the extent of damage and/or the kinetics of recovery from photoinhibition. Algae in shallower water are acclimated to high irradiance conditions and as such are likely to have a significant pool of xanthophyll pigments and a good ability to repair damaged reaction centre proteins (Demmig-Adams and Adams 1992). When exposed to high midday irradiance these algae have a good capacity to protect themselves from photodamage and also to quickly repair any that does occur, so that by the time irradiance drop to sub-saturating levels, photosynthetic efficiency is recovered, resulting in no loss, or a reduced loss, in net carbon assimilation rates. By contrast, the shade acclimated deeper algae experienced "chronic" photoinhibition as their acclimation state does not provide them with a large pool of xanthophyll cycle pigments (Demmig-Adams and Adams 1992) or an ability to repair damaged reaction centre proteins sufficiently fast enough to keep up with the rate of photodamage (Öquist *et al.* 1992, Long *et al.* 1994, Anderson *et al.* 1997). In addition to the differences in photoprotective ability, these algae may experience photodamage more readily because their shade acclimated state may cause them to absorb a higher level of excess photons in comparison to algae acclimated to high irradiance conditions. Rates of recovery of photosynthetic efficiency in deeper algae were in fact slow enough to significantly lower productivity rates to a greater extent than that observed in 3 m algae. Presumably the reduction in carbon assimilation rates due to photodamage would be even greater without the resources diverted to damage repair and avoidance mechanisms (Raven 1989).

Several studies have shown that individuals or species that inhabit deeper waters tend to be more susceptible to "chronic" photoinhibition (Henley *et al.* 1991b, Franklin *et al.* 1992, Hanelt 1992, Franklin *et al.* 1996, Hanelt *et al.* 1997a, Sagert *et al.* 1997, Hanelt 1998, Rodrigues *et al.* 2000). For example, the degree of photoinhibition and level of recovery in the red alga *Chondrus crispis* was directly related to the depth of collection in experiments conducted under both artificial and natural irradiation (Sagert *et al.* 1997). Similarly in the green alga *Halimeda tuna* the extent and duration of photoinhibition, measured by oxygen production and chlorophyll fluorescence yield, was greater in individuals collected from a depth of 5 m compared to those collected from the surface (Häder *et al.* 1996).

The light environment experienced by the deeper algae differs not only in terms of the irradiance but also in its spectral quality, which may also explain reduced productivity. In particular, harmful ultraviolet radiation (UVR; 320-400nm) is more rapidly attenuated in the water column than photosynthetically active radiation (PAR; 400-700nm) (Kirk 1994); thus algae growing at 12 m will experience lower UVR levels than those reaching 3 m. In kelp beds off the Western Australian coast transmission of UVR at 10 m was less than 10% of that at the surface whereas it was around 30% at a depth of 3 m (Wood 1987). The damaging effects of UVR, particularly UV-B, on *E. radiata* were documented by Wood (1987), and included reduced growth, decreased photosynthetic pigmentation and tissue necrosis. Other studies suggest that the targets and effects of UVR on the photosynthetic apparatus of algae (and higher plants) are similar to those of high PAR, i.e. damage to D1, resulting in photoinhibition (Melis *et al.* 1992, Larkum and Wood 1993, Teramura and Sullivan 1994, Franklin and Forster 1997, Herrmann *et al.* 1997). Algae can produce specific UVR blocking substances (Post and Larkum 1993, Montecino and Pizarro 1995), the production of which is increased when algae are exposed to higher solar radiation (i.e. UVR and PAR levels) (Wood 1987). This means that deeper algae exposed to the irradiance environment at 3 m are unlikely to contain appropriate levels of UV blocking pigments to protect themselves from the levels of UVR radiation encountered in shallower water, in addition to the inadequate protection from high PAR. It is therefore quite likely that the increased level of photoinhibition in deeper algae identified in this study was in part due to damage from UVR in addition to the higher intensity of PAR experienced at a depth of 3 m.

In summary, the rate of daily net primary productivity of *E. radiata* remains high throughout the year. Changes in the properties of the photosynthetic apparatus means that lower light levels in winter are compensated for and the rate of daily productivity remains similar to that

achieved in summer, when irradiance is up to five times higher and day-length is over 3 hours longer. The effect of photoinhibtion in reducing potential carbon assimilation rates is significant, especially during months with high irradiance. When measured at a depth of 3 m algae acclimated to the irradiance environment of 10 m experienced a greater degree of chronic photoinhibtion compared to algae acclimated to the 3 m environment.

Chapter 4 : The Growth Strategy

Ecklonia radiata is capable of high rates of daily net productivity (Chapter 3). This chapter investigates what proportion of this assimilated carbon is incorporated as tissue. The pattern of growth (biomass accumulation) throughout the year and across the depth profile was investigated using the traditional "hole-punch" method and the information is presented in context with net productivity rates described in Chapter 3.

Introduction

In the previous chapter the rate of net primary productivity of *E. radiata* was shown to be relatively constant all year. This finding is clearly at odds with previous studies on the primary production of *E. radiata* (Kirkman 1984, Larkum 1986, Kirkman 1989), which demonstrated consistent seasonal patterns in the rate of tissue production. This discrepancy is based on methodological differences as earlier studies defined primary productivity as the net increase in <u>organic matter</u> (i.e. growth) (Kirkman, 1984 #36) whereas the current study accurately defined primary productivity as the net increase in <u>organic carbon</u> (which was derived from oxygen evolution rates).

While growth, or biomass accumulation, is dependant on photosynthetically derived carbon skeletons, other resources are also necessary. One factor of vital importance to the growth of all living organisms is the availability of nutrients, which varies throughout the year in many marine systems. For example nitrogen, which is necessary for the production of amino acids, proteins and other important compounds, has been found to limit the growth of many marine algae (Lobban and Harrison 1994). For this reason the seasonal pattern of growth will not always follow the pattern of seasonal primary productivity. In addition, assimilated carbon is lost to several other processes such as maintenance, defence, and reproduction. All these processes have competing demands for photosynthate that fluctuate throughout the year, and as a consequence the rate of growth (tissue production) will not always reflect the rate of carbon assimilation. For example, phlorotannins are produced in many temperate phaeophycean algae and act primarily as a chemical defence against herbivores. Steinberg (1995) found a decrease in growth rate associated with an increase in pholorotannin level in *E. radiata* during spring. Steinberg (1995) did, however, caution that these changes may be independent of each other as no pathway is yet known that links pholorotannin production and growth.

The pattern and rate of growth is further separated from the pattern and rate of carbon assimilation by the ability of many macroalgal species to store significant amounts of carbon as polysaccharides (i.e. laminaran and mannitol in brown algae). This carbon is translocated, along with recent photoassimilates, to meristematic regions to be used for growth, particularly when the rate of carbon assimilation is low (Hatcher *et al.* 1977, Chapman and Craigie 1978, Dunton and Schell 1986, Zimmerman and Kremer 1986, Dunton 1990).

Whilst measuring growth rates will not provide a true measure of productivity, it nevertheless provides important information. The growth strategy of a species impacts on its ability to persist as individuals and populations in a particular location, by influencing its competitive ability and thus its capacity to exist in a temporally variable environment (e.g. in terms of light and nutrients).

The production of a photosynthetically-capable biomass is vital for the maintenance of individuals and species, as this becomes the "production house" for future development. In addition, it is the carbon which is incorporated into biomass, as well as that which is exuded as secondary metabolites, which becomes available to consumer populations, and eventually to higher trophic levels. It is therefore necessary to understand the growth strategy of a species to fully understand the ecological significance of its primary production.

Past work on the productivity of *E. radiata* has involved adaptations of the "hole punch" method of Parke (1948), with which she measured the growth of *Laminaria saccharina* and established a clear seasonal variation in growth rate for this species. This method relies on the fact that the primary meristem of kelps, including *E. radiata*, is located at the junction of the stipe and blade, so that movement of a hole punched in the basal area of the blade over a certain time period gives a good measure of growth in terms of length increments (Parke 1948). Mann and Kirkman (1981) adapted this method to provide a measurement of total biomass accumulation by multiplying the increase in length by a measure of biomass per unit length taken from the "zone of maximal biomass" in each plant. As an estimate of gross daily production this method is flawed as it does not take into account respiratory costs or the exudation of dissolved organic materials (Mann and Kirkman 1981). In addition, Larkum (1986) observed that neither frond expansion in regions other than the primary meristem or remobilisation of stored reserves are accounted for with the hole punch method. Larkum (1986) argued, that as the tissue which is measured in the "zone of maximal biomass" varies in age from two to three months old, this parameter (unit frond weight) should be related to the increase in length measured two to three months previously.

The seasonal pattern of biomass accumulation (gdwt g^{-1}dwt d^{-1}) established by previous studies of *E. radiata* in Western Australia is defined by a reduction in rate during late summer (January-February) and in autumn (March-May) with a maximum in spring (Kirkman 1984, Kirkman 1989). Larkum (1986) in a study in New South Wales also found a maximum rate of biomass accumulation (gdwt plant^{-1} d^{-1}) during spring (September) and a minimum from mid-summer (January) through to the end of autumn (May). Kirkman (1984) suggested that increasing temperature was responsible for the late summer reduction in growth and that at other times light or nutrients may be limiting. Hatcher *et al.* (1987) also found that growth was negatively correlated with seawater temperatures above 20 °C. In addition, they established that *E. radiata* did not acclimate to the higher seawater temperatures found on the Abrolhos Reef, where plants were smaller and growth was slower than at the higher latitude Marmion Reef. They suggested that although seawater temperature may be implicated as a factor controlling the latitudinal limits of the species, other factors must be involved (Hatcher *et al.* 1987). Rates of biomass accumulation in *E. radiata* appear to follow primary frond elongation, that shows a similar seasonal pattern (Larkum 1986, Hatcher *et al.* 1987). The rates of annual production of biomass were in the region of 2.9-4.4 kg dwt m^{-2} y^{-1} for shallow water *E. radiata* and around 0.3-1.8 kg dwt m^{-2} y^{-1} for deeper water (10-15 m) *E. radiata* growing in Western Australia (Kirkman 1989), New South Wales (Larkum 1986), South Australia (Shepherd 1979), Tasmania (Sanderson 1990) and in New Zealand (Novaczek 1984a). Hayashida (1977) reports that an *Ecklonia cava* forest in Japan yielded about 2.8 kg dwt m^{-2} y^{-1}, which was estimated using a "harvest method".

A large quantity of work has also been conducted on the growth of northern hemisphere members of the order Laminariales. This work has focused on describing seasonal growth cycles of *Laminaria* and *Macrocystis* and correlating the seasonality of growth with factors such as nutrients, light availability and temperature (Buggeln 1974, Chapman and Craigie 1977, Buggeln 1978, Chapman and Craigie 1978, Chapman *et al.* 1978, Lüning 1979, Chapman and Lindley 1980, Fortes and Lüning 1980, Calvin and Ellis 1981, Gagné *et al.* 1982, Dean and Jacobsen 1984, Wheeler and Druehl 1986, Gendron 1989, Dunton 1990, Castric-Fey *et al.* 1999), as well as water motion (John 1971, Gerard and Mann 1979).

The aim of this study is to quantify the biomass accumulation rates of *E. radiata* throughout the year that will provide a basis for understanding the growth strategy of this species at West Island. This work will enable a comparison of the growth of *E. radiata* at West Island with other populations throughout Australasia. In addition, comparison of biomass accumulation

rates with the already established rates of carbon assimilation (Chapter 3) will enable, for the first time, the proportion of assimilated carbon allocated to growth to be calculated. The importance of factors such as nutrients, hydrodynamics and reproductive state on the growth strategy are acknowledged and discussed, but were not measured in this study.

Methodology

Methods

This work was conducted adjacent to sites used for algal collection in the photorespirometry work i.e. at depths of 3, 5, 10 and 12 m; at each depth two sites were selected. The methods employed are similar to those of Larkum (1986). At each site during each sampling period 15 Stage Three individuals (i.e. 30 per depth), representative of the population at each depth, were randomly selected and tagged with fluorescent survey tape and a 5 mm diameter hole punched 10 cm from the junction of the stipe and blade. The finding of Mann and Kirkman (1981) that lateral extension is confined to the proximal 10 cm of the blade in *E. radiata* is consistent with other studies (Shepherd 1979, Sanderson 1990), and is assumed to also apply for the West Island population. Tagged algae were harvested after a period of 25-30 days and the distance the hole moved (the primary blade extension), the thallus wet weight, and the weight of the blade strip 10-15 cm from the blade/stipe junction were recorded. The 10-15 cm strip for this population represents the "zone of maximum biomass" as the thallus is fully developed at this stage and has not yet become necrotic. Generally the blade tips in the 15-20 cm region and beyond were either necrotic or showed signs of erosion or herbivory, similar to that reported for the Fairlight Bay population of Larkum (1986). Occasionally the 15-20 cm strip was of a slightly higher weight and was used in calculations for those individuals. The blade strip was aired dried on the island then once in the lab was dried for 24 hours at 80 °C and the dry weight recorded. The WW:DW ratio of the strip was then used to calculate the dry weight of the entire thallus. The rate of biomass accumulation (BA) per plant (gdwt plant^{-1} d^{-1}) was estimated each season (t) by the equation,

$$BA = \frac{xw}{5d}$$

where x = the distance moved by the hole (cm), w = mean dry weight per 5 cm strip at $t+1$ (i.e. the next season) (g), and d = duration of experiment (days) (Larkum 1986). The assumption is made, based on the elongation rates from a pilot study and the

recommendations of Larkum (1986), that a period of 60-90 days is needed for newly initiated growth to mature, i.e. to reach the 10-15 cm region. The value of w used at each time period (t) was thus that which was measured in the subsequent time period ($t+1$). For the last time period of the study (winter), the w value used was that measured in spring, i.e. the first measurement time period, and data from 3 m and 10 m was used for missing data for 5 m and 12 m respectively. The rate of BA per plant was then divided by the dry weight of the entire thallus to derive an estimate of BA in units of weight (gdwt g^{-1}dwt d^{-1}), i.e. a measure of relative growth rate, referred to here as "relative biomass accumulation" rate, RBA.

Analysis

A series of two-way ANOVAs were used to test the null hypothesis that neither season or site had an influence on rates of BA, RBA and elongation or biomass per length unit and a series of one-way ANOVAs were used to test the null hypothesis that depth did not have an influence on rates of BA, RBA and elongation or biomass per unit length. Variance heterogeneity was checked using a Brown-Forsythe test, and all data were $\sqrt{x+3/8}$ transformed to improve homogeneity. *Post hoc* comparison of means was done using Tukey-Kramer HSD test, with the alpha value set at 0.05.

Results

Seasonal Pattern in Biomass Accumulation (BA)

A consistent seasonal pattern in the rate of biomass accumulation (BA) per plant was evident at all depths (Figure 4.1a). The most obvious feature of this pattern was a significant decline of the rate of BA per plant during autumn (Figure 4.1a; Table 4.1) and an increase in the BA rate during summer was also evident at 3 m and 10 m. The autumn decline was due to a significant decrease in the rate of elongation rather than a decrease in biomass per length unit (gdwt cm^{-1}), however the opposite was the case in summer (Figure 4.2; Table 4.1). Overall, a significant correlation was found between tissue density and BA ($r = 0.72$; $p < 0.01$), but not BA and elongation rate ($r = 0.57$; $p = 0.05$).
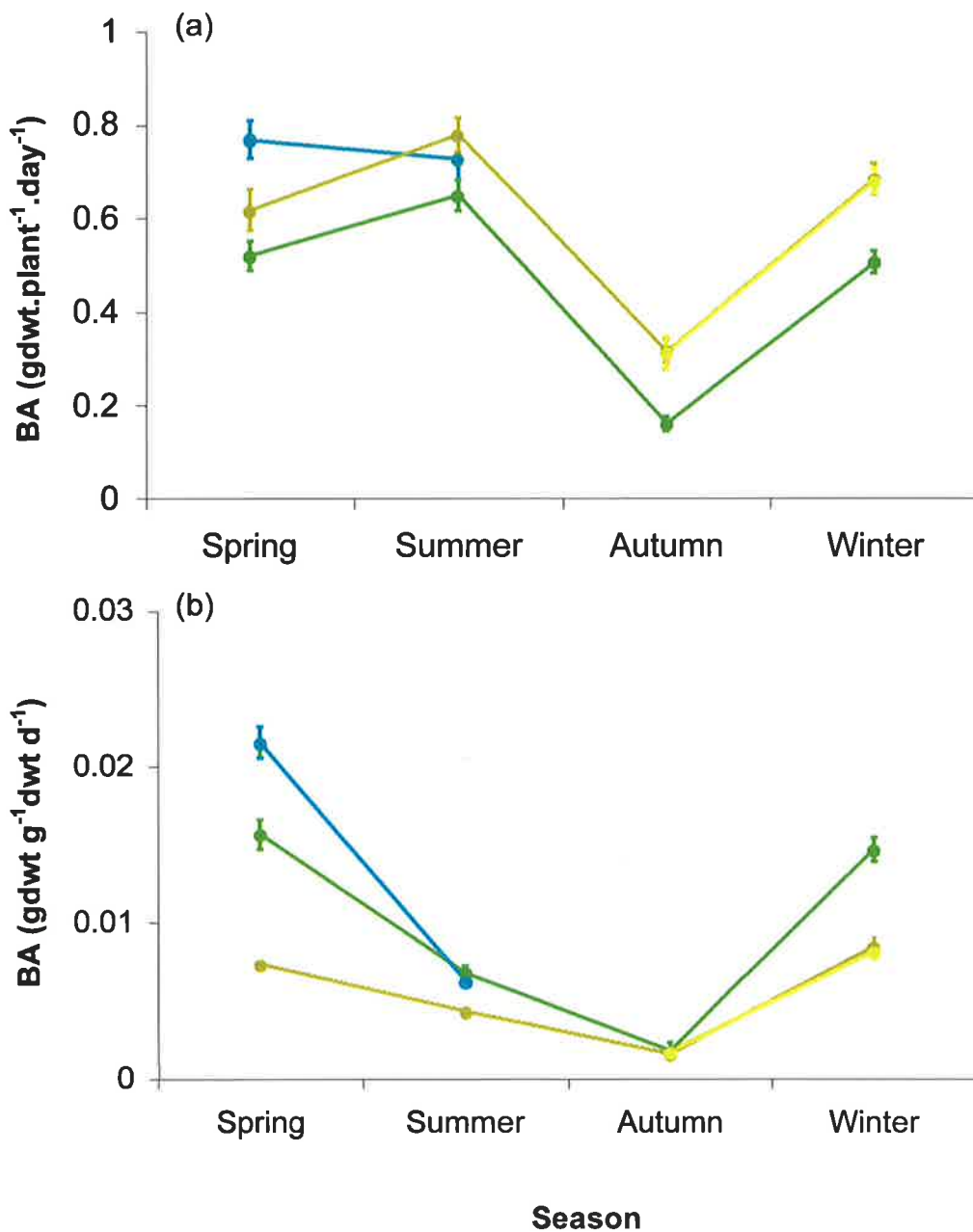
Figure 4.1 Growth rates (mean ± s.e.) by *Ecklonia radiata* at four depths off West Island, South Australia (--- = 3 m; --- = 5 m; --- = 10 m; --- = 12 m). (a) biomass accumulation (BA) rates were calculated by using the average biomass per strip from the next season as recommended by Larkum (1986). Biomass accumulation rates were divided by thallus weight to arrive at relative biomass accumulation (RBA) rates (b). Where standard errors are less than the size of the point they are not shown. See Table 4.1 for sample sizes.

Table 4.1 Summary of two-way ANOVA results and the *post hoc* Tukey-Kramer HSD (α = 0.05) comparisons for growth parameters (BA, biomass accumulation rates; RBA, relative biomass accumulation rate). The final column represents the ANOVA significance probability (*** $p \leq 0.001$, ** $p \leq 0.01$, * $0.01 < p \leq 0.05$, ns = not significant).

	3 m	10 m	Depth p
BA (gdwt.plant^{-1}.day^{-1})	a	b	***
RBA (gdwt.g^{-1}dwt.day^{-1})	a	b	***
Elongation rate (cm.day^{-1})	a	b	***
Biomass per length (gdwt.cm^{-1})	a	b	***

	Spring	Summer	Autumn	Winter	Season p
BA (gdwt.plant^{-1}.day^{-1})	a	b	c	a	***
RBA (gdwt.g^{-1}dwt.day^{-1})	a	b	c	a	***
Elongation rate (cm.day^{-1})	b	a,b	c	a	***
Biomass per length (gdwt.cm^{-1})	a	a	b	a	***

	Spring		Summer		Autumn		Winter		Depth x Season p
	3	10	3	10	3	10	3	10	p
BA (gdwt.plant^{-1}.day^{-1})	c	b,c	a,c	a	d	e	c	a,b	*
RBA (gdwt.g^{-1}dwt.day^{-1})	a	b	b	c	d	d	a	b	***
Elongation rate (cm.day^{-1})				not tested					ns
Biomass per length (gdwt.cm^{-1})									ns
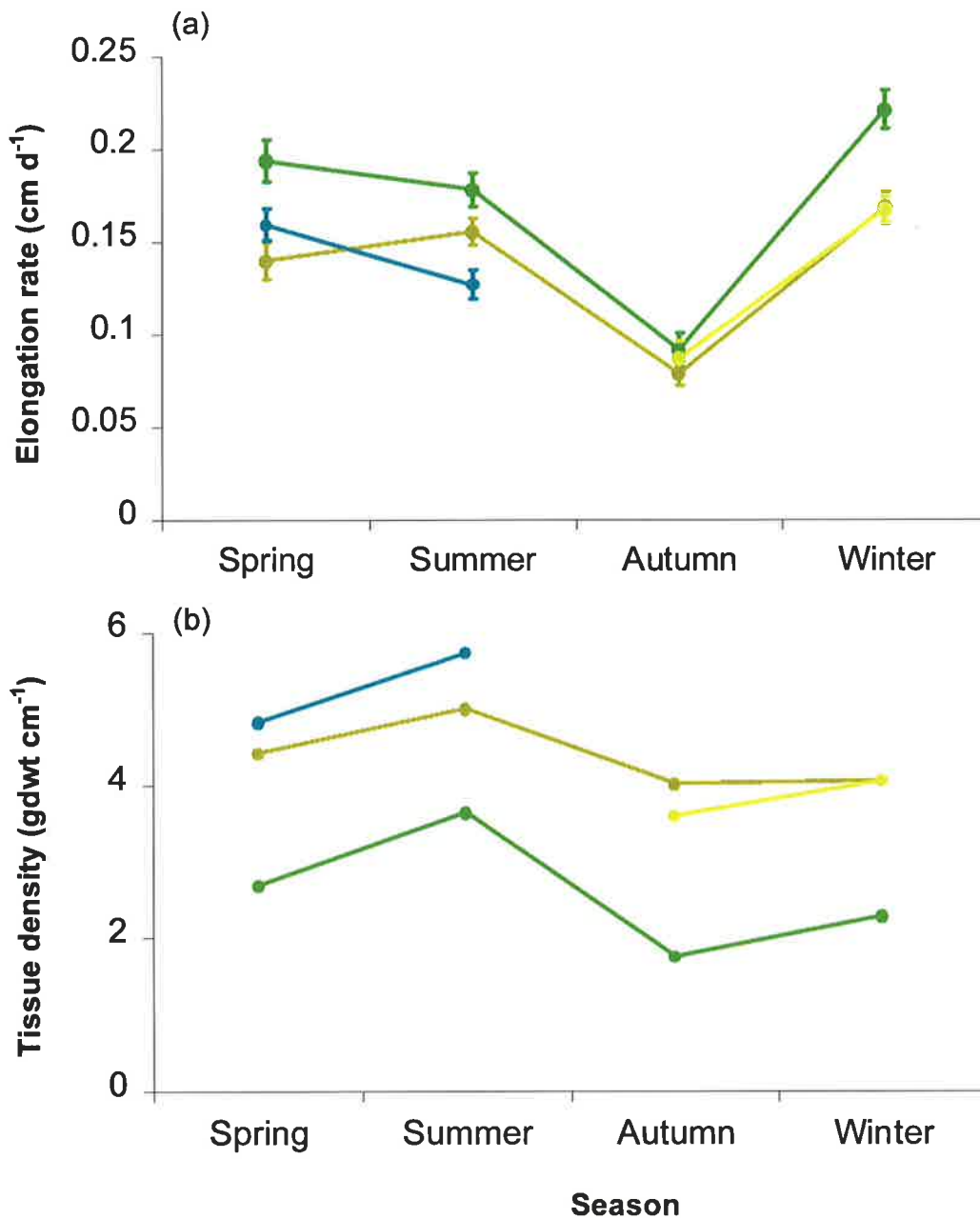
Figure 4.2 Elongation rates (a) and tissue density (b) of *E. radiata* throughout the year (mean ± se) (--- = 3 m; --- = 5 m; --- = 10 m; --- = 12 m). Error bars are not displayed when they are less than the size of the point. Tissue density values are plotted for t-1, i.e. the data plotted for spring was that which was measured in summer. The reasoning behind this is that tissue laid down in the meristematic region takes ~60-90 days to reach the region 10-15cm above the stipe. The tissue density measurements were taken from the 10-15 cm strip, and thus the density measured in summer actually represents the growth which was initiated in spring.

Relative Biomass Accumulation (RBA)

Rates of RBA throughout the year are significantly greater at 3 m and 5 m than at 10 m and 12 m except during autumn (Figure 4.1b; Table 4.1). A significant interaction was found between depth and season for both BA and RBA (Table 4.1). Individuals at 3 m and 5 m are much smaller than those at 10 m and 12 m (Table 4.2) and so the rate of RBA increases disproportionately. Similarly, thallus dry weight was highest during summer and autumn so the rate of RBA at these times is disproportionaly decreased. The correlation between RBA and elongation rate was significant ($r = 0.71$; $p < 0.01$).

Table 4.2 Thallus weight and wet weight: dry weight ratios and number of samples used for growth measurements (mean(se)).

	Season	Thallus dwt	ww:dw	n
3 m	spring	33.22 (2.76)	5.49 (0.16)	26
	summer	96.75 (5.80)	6.5 (0.22)	24
	autumn	90.49 (6.65)	5.58 (0.42)	22
	winter	34.56 (1.98)	7.53 (0.16)	29
5 m	spring	25.70 (3.38)	5.5 (0.27)	26
	summer	116.68 (13.01)	5.27 (0.18)	20
10 m	spring	84.73 (6.63)	5.64 (0.11)	30
	summer	183.29 (10.90)	5.19 (0.20)	19
	autumn	199.94 (18.52)	3.9 (0.31)	18
	winter	81.56 (6.47)	6.61 (0.13)	23
12 m	autumn	186.77 (15.92)	4.24 (0.13)	17
	winter	84.02 (4.70)	6.85 (0.16)	30

Growth Rates Across the Depth Profile

Depth was also found to have a significant effect on the rate of BA per plant throughout the year (Table 4.1). The rate of BA per plant was lowest at a depth of 3 m in all seasons, significantly so during summer, autumn and winter (Table 4.1). This is related to a consistently lower tissue density at 3 m in comparison to individuals at 10 m and 12 m (Figure 4.2b; Table 4.1). The elongation rate at 3 m was either higher (spring and winter) or similar (autumn) to that at the other depths. The rate of BA per plant and per gram dry weight was remarkably similar between 10 m and 12 m. The rate of elongation was slightly slower at 10 m but the tissue density was slightly higher.

Proportion of Net 24 Hour Productivity

The proportion of net 24 hour productivity allocated to biomass accumulation increased with depth and was highest during winter and spring (Figure 4.3).
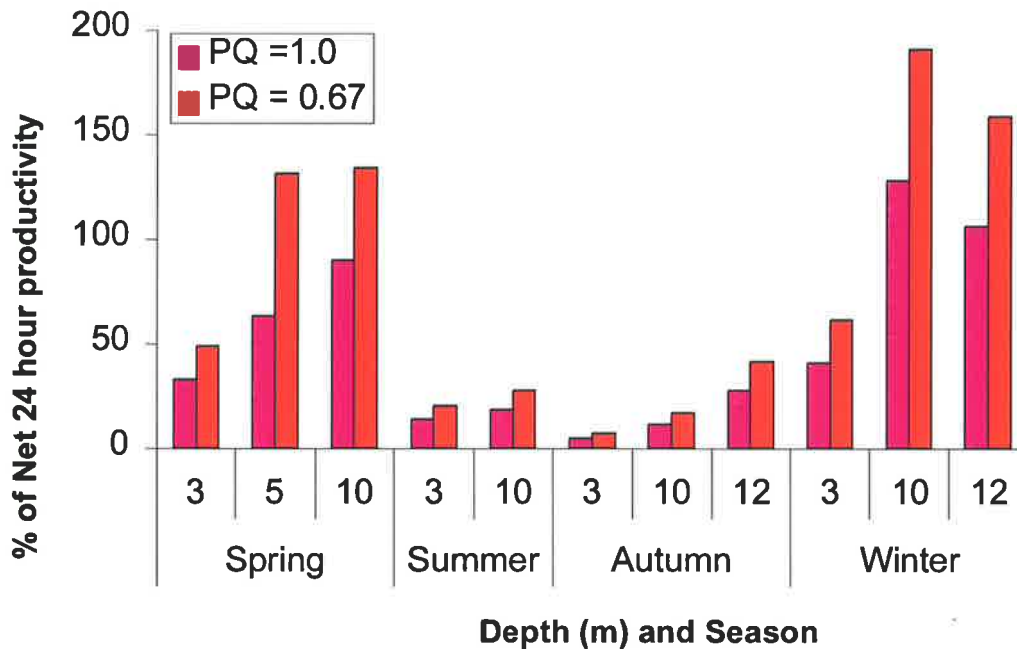
Figure 4.3 Mean rate of biomass accumulation as a percentage of mean net 24 hour productivity (see Table 3.1). Net 24 hour productivity rates were converted from oxygen units to gCHO $g^{-1}dwt$ d^{-1} using photosynthetic quotients (PQ; O_2:CO_2) of 1.0 and 0.67[3].

Discussion

Seasonal changes in biomass accumulation

A clear seasonal pattern in the biomass accumulation (BA) rates of *E. radiata* at West Island was found that was consistent across all depths. The pattern is defined by a significant reduction in elongation rates during autumn, halving the biomass accumulation per plant at this time. Similarly, the relative biomass accumulation (RBA) rates remained at their lowest during autumn, but were also reduced during summer. This pattern of growth in *E. radiata* at West Island is consistent with other Australasian populations (Kirkman 1984, Novaczek 1984a, Larkum 1986, Hatcher *et al.* 1987, Kirkman 1989, Steinberg 1995). Rates of growth (0.002-0.02 gdwt $g^{-1}dwt$ d^{-1}) and frond elongation (0.79-2.21 mm d^{-1}) were also similar to those

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[3] A photosynthetic qoutient of less than 1.0 would result if photorespiration was an important factor. Evidence suggests that photorespiration in kelps is minimal (Hatcher 1977), however, 0.67 is used here to calculate the lowest net 24 hour production in gCHO $g^{-1}dwt$ d^{-1} that could result from the measured production rates (μmol O_2 $g^{-1}dwt$ d^{-1}).

found in *E. radiata* at other locations and are broadly comparable to other kelps in a variety of locations (see Table 4.3). However, rates of elongation were generally lower than for the simple thallus of *Laminaria*, and were much lower than the maximum rate of 29 mm per day recorded for *Macrocystis pyrifera*.

Ecklonia radiata in Fairlight Bay (New South Wales) displayed the lowest rates of biomass accumulation during autumn (May & April), although rates were not much higher during summer (January), whilst a clear peak was recorded in spring (September) (Larkum 1986). In contrast to the current study, the lowest elongation rates were recorded by Larkum (1986) during summer, although extension rates during autumn were also low. The peak in growth did, however, coincide with the peak in elongation rates (i.e. in spring). Similarly, a spring peak and a late summer/autumn decline in relative biomass accumulation was observed in the shallow *E. radiata* populations of Marmion Reef, in Western Australia (Kirkman 1984, Kirkman 1989). At a deeper site (10 m) the peak in growth was delayed by two months, but the lowest rate at both depths was recorded in autumn (Kirkman 1989). The Goat Island Bay (New Zealand) populations studied by Novaczek (1984a) exhibited a similar pattern with a spring peak in elongation rates on a shallow reef (7 m) and a summer peak at the deep reef (15 m). The similarity of the annual growth strategy displayed by the West Island population to these other geographically widespread populations is important given the lack of temporal replication in the current study. Additionally, whilst the absolute rates varied between years, in Kirkman's (1984) study the phenology of growth (i.e. spring peak and autumn low) was consistent between years.

The seasonal pattern in relative biomass accumulation rates can be predicted by the seasonal change in elongation rates (r = 0.71; p < 0.01). However, this correlation was not as high as that found by Hatcher *et al.* (1987) (r = 0.90; p < 0.01) or that calculated from the data of Larkum (1986) by (Hatcher *et al.* 1987) (r = 0.91; p < 0.05). Hatcher's (1987) assertion that the use of elongation rates alone enables growth patterns of *E. radiata* to be studied non-destructively may thus not hold for this population. The seasonal pattern of biomass accumulation in this study is even less adequately described by elongation rates as the correlation was not significant.

The growth strategy of *E. radiata* at West Island is characterised by the maintenance of a relatively constant rate of growth across all seasons other than autumn, and this is reflected in alterations in both relative biomass accumulation rate and in thallus biomass. During spring and winter thallus dry weight (i.e. the amount of photosynthetic tissue) is low due to storm

Table 4.3 Range of biomasss accumulation and elongation rates reported in the literature for *E. radiata* and other members of the Laminariales.

Study	Species	Depth	Latitude & Longitude	gdwt g^{-1} dwt d^{-1}	gdwt plant^{-1} d^{-1}	gdwt cm^{-1}	mm d^{-1}
Current study	*Ecklonia radiata*	3 m	35°36'S 138°35'E	0.002-0.02	0.16-0.65	1.75-2.68	0.91-2.21
Current study	*Ecklonia radiata*	10 m	35°36'S 138°35'E	0.002-0.008	0.32-0.78	4.02-5.73	0.79-1.68
Kirkman 1984	*Ecklonia radiata*	2-7 m	31°48'S 115°42'E	0.002-0.009	-	-	-
Larkum 1986	*Ecklonia radiata*	1.5 m	33°48'S 151°16'E	-	0.20-0.61	1.6-4[a]	0.76-1.96
Hatcher *et al.* 1987	*Ecklonia radiata*	2-5 m	28°45'S 113°45'E	-	-	0.12-1.62[b]	0.4-2.25
Hatcher *et al.* 1987	*Ecklonia radiata*	5 m	31°48'S 115°42'E	-	-	1.54[b]	0.9-3.0
Kirkman 1989	*Ecklonia radiata*	5 m	31°48'S 115°42'E	0.003-0.01	-	-	-
Kirkman 1989	*Ecklonia radiata*	10 m	31°48'S 115°42'E	0.002-0.008	-	-	-
Sanderson 1990	*Ecklonia radiata*	14 m	43°50'S 147°50'E	-		4.6	2.19
Buggeln 1974	*Alaria esculenta*	tanks	47°33'N 52°40'W	-	-	-	0.071-0.51
Castric-Fey *et al.* 1999	*Undaria pinnatifida*	1 m	48°38'N 2°03'W	-	-	-	15
Van Tussenbroek 1989	*Macrocystis pyrifera*	4 m	51°30'S 58°00'W	-	0.07-0.42 (per frond)	-	5-29
Zimmerman and Kremer 1986	*Macrocystis pyrifera*	3-15 m	33°27'N 118°29'W	-	-	-	50-143
Parke 1948	*Laminaria saccharina*	1 m	56°14'N 5°39'W	-	-	-	2.6-17.4
Chapman and Craigie 1977	*Laminaria longicruris*	6 m	44°30'N 64°50'W	-	-	-	1.7-5.9
Gerard and Mann 1979	*Laminaria longicruris*	10 m	44°30'N 64°50'W	-	-	6.14	2-10
Chapman and Lindley 1980	*Laminaria solidungula*	8 m	69°21'N 81°42W	-	-	-	0.2-2
Dieckmann 1980	*Laminaria pallida*	8 m	33°59'S 18°21'E	-	-	-	0.5-12
Calvin and Ellis 1981	*Laminaria groenlandica*	3-7 m	58°22'N 134°42'W	-	-	-	0.1-7.8
Gendron 1989	*Laminaria longicruris*	4 m	47°05'N 65°38'W	-	-	-	4-22

[a] 10-15cm strip
[b] converted using a ww:dw ratio of 7.14

damage during this time. As the rate of relative biomass accumulation was higher at this time, the amount of tissue accumulated by each plant remains similar to that recorded during summer, when thallus size is large but relative growth is low. During autumn, when thallus biomass is still high, the rate of relative biomass accumulation is at its lowest, thus the tissue accumulated by each plant is particularly low. This reduction in relative growth during both summer and autumn is an important feature of the growth strategy, and contrasts with the near constant rate of net assimilation observed throughout the year (Figure 3.2; Chapter 3).

No previous study has been conducted in South Australian waters on the growth strategy of Laminarialean algae. Hotchkiss (1999), however, included a study of growth processes in an investigation of the life history strategies of three species of *Cystophora* (Fucales), conducted at Cape Jervis on the tip of the Fleurieu Peninsula (see Figure 1.2). The relative growth rates (mm mm^{-1} d^{-1}) of the three species studied were at a maximum in late summer and in autumn, the same period in which *E. radiata* displayed minimum rates. Seasonal patterns of biomass production in subtidal Fucalean algae are more closely linked to reproductive cycles, as a high level of resource allocation to reproductive biomass (~90% of total biomass) occurred in all *Cystophora* species, with a peak in the biomass of reproductive laterals in late winter and spring (Hotchkiss 1999). Elongation rates in these species were at a maximum prior to the development of reproductive tissue and at a minimum in winter and spring when effort was directed to reproduction.

The influence of the reproductive cycle on the pattern of growth in *E. radiata* (and many other kelps) is likely to be less dramatic, due to the lack of specialised reproductive laterals. It is possible, however, that the onset of the process of spore production may contribute to the low growth rates shown in autumn. The reproductive phenology of *E. radiata* has not been studied in South Australian waters, but the timing of events may be similar to the population studied by Novaczek (1984a), where maximum spore production occurred in autumn and winter and where reproductive tissue accounted for approximately 20% of total tissue production. Sorus production peaked following a decline in lamina expansion (Novaczek 1984a). Sanderson (1990) also found that in *E. radiata* growing in southern Tasmanian waters the area of the thallus occupied by sori increases to a maximum in winter. If this is also the case in South Australia, then an increase in the level of resource allocation to reproductive processes, e.g. sori development during autumn, may have an influence on the level of resources available for vegetative growth and therefore on the lowered growth rates witnessed

in autumn. This has been observed in other kelps, De Wreede (1984) found a decline in stipe elongation which coincided with the onset of reproduction in the kelp *Pterygophora califomica*.

The growth strategies of other kelp are more closely linked to environmental factors than to the reproductive cycle (Buggeln 1974, Chapman and Craigie 1977, Buggeln 1978, Chapman and Craigie 1978, Chapman *et al.* 1978, Lüning 1979, Chapman and Lindley 1980, Fortes and Lüning 1980, Calvin and Ellis 1981, Gagné *et al.* 1982, Dean and Jacobsen 1984, Wheeler and Druehl 1986, Gendron 1989, Dunton 1990, Castric-Fey *et al.* 1999) and this is likely to be the case for the *E. radiata* at West Island, through mechanisms related to seasonal nutrient availability.

Nitrogen (in the form of ammonium) is essential for the synthesis of amino acids and is therefore necessary for metabolic functioning, including the processes needed for photosynthesis and growth. The form of nitrogen most available and important to marine algae is nitrate (Wheeler and North 1981, Gagné *et al.* 1982, Probyn and McQuaid 1985, Gendron 1989, Brown *et al.* 1997), which is then reduced to ammonium in assimilation processes which involve the nitrate reductase and nitrite reductase enzymes (Turpin 1991, Berges 1997). The uptake of nitrate by *Ecklonia maxima* in an enriched upwelling environment was linearly related to ambient nitrate concentrations and was not found to saturate at concentrations >20 μgN l^{-1} (Probyn and McQuaid 1985). The possibility that some of the nitrate absorbed during the period of upwelling is stored for later use was supported by higher tissue nitrogen concentrations and lower C/N ratios recorded during the upwelling period (Probyn and McQuaid 1985). Brown *et al.* (1997) found that the growth of *Macrocystis pyrifera* in New Zealand was nutrient limited in summer, when nitrate concentrations were lowest. The nitrogen content of the blades in that study was highest in winter and lowest in summer and spring.

No work has been done on the uptake and assimilation of nutrients by macroalgae in South Australian waters, or on tissue nutrient status. However, Campbell *et al.* (1999) found evidence of nitrogen limitation over summer in the exotic kelp *Undaria pinnatifida* growing in Port Phillip Bay (Victoria). Low uptake rates of inorganic nutrients during summer and autumn is likely to have a profound influence on the growth of *E. radiata*.

Growth in northern hemisphere kelps, in particular species of *Laminaria*, has been extensively studied and temporal variation in the ambient level of dissolved nutrients is an important factor in many species. In a summer upwelling of nutrients near Cape Town, South Africa,

Dieckmann (1980) observed peak growth of *L. pallida* in summer, but suggested that light was probably the most important factor regulating growth. At several locations in Nova Scotia, Canada, the availability of nutrients was also highly seasonal with inorganic nitrogen abundant only during winter. The growth rate (elongation rate) of *L. longicruris* at these sites increased with nitrogen levels, utilising stored carbon reserves to compensate for the low winter irradiance (Chapman and Craigie 1977, Hatcher *et al.* 1977, Chapman and Craigie 1978, Gerard and Mann 1979, Chapman and Lindley 1980, Gagné *et al.* 1982). Several studies found growth remained high in early summer after ambient nitrogen levels had declined, with growth at this time dependant on accumulated internal reserves of nutrients (Chapman and Craigie 1977, Gerard and Mann 1979, Gagné *et al.* 1982).

A different pattern emerged at sites where inorganic nutrients were abundant for most of the year, particularly when levels were high during summer (due to upwellings etc.). In these cases the annual pattern of growth correlated well to the seasonal changes in irradiance, i.e. growth was fastest during summer (Gagné *et al.* 1982, Gendron 1989). Similarly, Van Tussenbroek (1989) found that the growth of *Macrocystis pyrifera* in the Falklands Islands was correlated with ambient nitrate concentration where nutrient availability fluctuated throughout the year (Stanley Harbour), but where nutrients were always abundant growth rates fluctuated with variation in irradiance or water temperature (Kelly Rocks). Zimmerman and Kremer (1986) also found a correlation between the elongation rate of *M. pyrifera* and ambient nitrate concentration in Californian waters and Dean and Jacobsen (1984) found that while light was the limiting factor for most of the year, periods of low nitrogen availability limited growth of *M. pyrifera*. A summer decline in the growth of *M. pyrifera* in New Zealand was also related to nutrient limitation (Brown *et al.* 1997).

Elongation rates of *Alaria esculenta* in Newfoundland, Canada, also appear to decline in response to nutrient depletion, the lowest rates occurring in summer (Buggeln 1974) when nitrate levels are lowest in the surrounding seawater (Buggeln 1978). More evidence for nitrogen limitation of growth in kelp is found in the studies of Chapman and Craigie (1977) who increased rates of growth of *L. longicruris* in summer by fertilising with nitrate. Also, Chapman *et al.* (1978) found that growth of *L. saccharina* could be linearly related to nitrate concentration in culture conditions. Druehl (1984) also found that elongation rates of *Macrocystis pyrifera* in enriched seawater were 87% faster than in those exposed to ambient seawater.

The ability of *E. radiata* to uptake and store nutrients has not yet been studied, and hence its impact on the growth cycle cannot be directly assessed. Nutrients have, however, been previously implicated in limiting the growth of *E. radiata* (Kirkman 1984). Novaczek (1984a) found, however, that deep water plants actually grew fastest in Goat Island Bay at the time of minimum nitrate concentration, although she noted that these were still relatively high levels. The lower growth rates displayed in autumn compared to summer, in this study, suggest that *E. radiata* may have an ability similar to *Laminaria* in regard to nutrient accumulation (Chapman and Craigie 1977), such that tissue nutrient levels may remain reasonably high throughout summer but become depleted by late summer/autumn. This is clearly an area in which more work must be done before any conclusive statements can be made about the effect of nutrients on the growth cycle of *E. radiata*. It is highly likely however, that given the seasonal nature of nutrient inputs into South Australian waters and the body of work showing nutrient limitation of growth within the Laminariales in general, that the low rates of relative growth in summer and autumn are in part due to a depletion of nutrients in either the surrounding waters or the kelp tissue, or both.

Kirkman (1984) suggested that a tendency for higher water movement in winter may increase nutrient availability by decreasing boundary layers. The effect of slow water movement in increasing diffusion boundary layers (Wheeler 1980a, Hurd *et al.* 1996), which decrease the mass transfer of molecules such as inorganic nitrogen to the thallus surface (Hurd 2000), and the subsequent negative effects of this on photosynthesis and growth have been investigated in kelp (Wheeler 1980a, Sjøtun *et al.* 1998). However, whilst water motion was not quantified in this study, conditions were very rarely calm in Abalone Cove, in summer or winter. Furthermore, evidence of the effects of water motion on kelp growth are conflicting, with other studies reporting slower growth at exposed sites (Gerard and Mann 1979) or no difference between sites with differing exposure (Wheeler and Druehl 1986, Sjøtun *et al.* 1998). More recent experiments have shown that the laboratory conditions used in previous studies (i.e. using laminar flow) are actually very rare in nature (Hurd and Stevens 1997, Hurd *et al.* 1997). Flow visualisation experiments indicated that flow conditions around several kelp species become turbulent at low mainstream velocities (1-3 cm sec^{-1}) (Hurd and Stevens 1997, Hurd *et al.* 1997). The implication being that the size of diffusion boundary layers around a kelp thallus will rarely ever be large enough in the field (under conditions of turbulent flow) to cause the mass transfer of molecules (e.g. inorganic nitrogen and carbon) to be limiting for photosynthesis and growth (Koch 1993, Hurd 2000). However, regardless of the extent of more direct effects of water flow on macroalgal production, the effects of water motion on

other environmental factors which influence rates of production, such as the light climate (e.g. turbidity) will remain important (Hurd 2000).

A combination of factors are likely to be involved in the summer/autumn slowing of growth. The period of putatively low nutrient levels coincides with high seawater temperatures, with water temperatures at West Island increasing in summer and remaining high (>19 °C) until early autumn (Table 2.1 and Appendix D). The effect of high temperature on the growth of *E. radiata* has not yet been assessed experimentally, but Kirkman (1984) found correlative evidence of an inhibiting effect. During the warmer months (October-January) growth of *E. radiata* on Marmion Reef was inversely related to seawater temperature (r = -0.971) and temperatures below 18.5 °C were found to be optimal for growth (Kirkman 1984). Growth of *Macrocystis pyrifera* in California was also found to decrease at temperatures above 18.5 °C (Zimmerman and Kremer 1986). Maximal growth of *E. radiata* in Goat Island Bay occurred when seawater temperatures were low (13-16 °C) (Novaczek 1984a), a similar situation to this study. Hatcher *et al.* (1987) suggested that the critical temperature for *E. radiata* may be 23 °C, above which survival of the species could be reduced. In their study the growth of *E. radiata* was reduced at a lower latitude, where seawater temperatures remained above 20 °C all year, and particularly so during the period when temperatures were above 23 °C. The effect of temperature on the growth of South African *Ecklonia* was assessed by Bolton and Anderson (1987). Both *E. biruncinata*[4] and *E. maxima* sporophytes grew well between 8 °C and 22 °C, and growth was either very poor or absent at 26 °C. The monthly mean seawater temperatures ranged between 13.5 °C and 21.5 °C throughout the distribution of *E. biruncinata*, which is very similar to the temperature range recorded in the current study. The optimal temperature range for growth of *E. biruncinata* was 15 °C to 19 °C. In this study, temperatures only exceeded this range in autumn and summer, when biomass accumulation rates were low.

The need for experimental investigations into the temperature tolerance of *E. radiata*, as suggested by Hatcher *et al.* (1987) remains necessary. The idea that lower seawater temperatures are favourable for metabolism in *E. radiata* is supported in the current study by the fact that both growth and photosynthetic capacity (Chapter 2) were maximal during winter. However, during spring when seawater temperatures remained low, only rates of

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[4] Bolton and Anderson 1987 indicated that *E. biruncinata* is synonymous with *E. radiata*

biomass accumulation are increased, while photosynthetic capacity was similar to that in summer and autumn.

The effect of seasonal changes in the light environment on the growth of macroalgae are well known. In the absence of another limiting factor (e.g. nitrate) the growth cycle often closely follows changes in the light environment (see above), with maximal rates occurring in summer when light levels are high (Dieckmann 1980, Gagné et al. 1982, Gendron 1989, Van Tussenbroek 1989). This relationship is due to the profound influence of light on carbon assimilation rates and of carbon supply on growth rates. In this study, the rates of net productivity (carbon assimilation) remained similar throughout the year (Chapter 3). It therefore seems implausible that the reduced rates of relative biomass accumulation found in summer/autumn result from light limitation, at least for juveniles. It is still possible that growth of adults may be limited in summer/autumn by light availability. Individuals during summer and autumn are of maximal size, whereas in winter and spring thallus erosion (particularly at the distal ends) resulting from the increased frequency of storms reduces plant size (Table 4.1; Collings 1996). Whilst the amount of light reaching juvenile plants (with short laterals) is enough to result in photosynthetic saturation for much of the day for the entire thallus, the irradiance environment experienced by the lower photosynthetically active regions of the adult thallus is considerably different.

Irradiance data recorded above and below the canopy of *E. radiata* at 3 m shows that the irradiance experienced below the canopy is consistently lower and that variability in irradiance is often increased, at least on the time scale presented (minutes) (see Appendix B). The implication of this is that the net productivity of parts of the lower thallus may not be as high as that recorded for the juvenile algae, and thus the rates of net 24 hour production for adults may be lower during the period of the year when the thallus is largest. Self-shading will reduce available levels of carbon and thus limit the growth rate. Lüning et al. (1973) found that shading of the lowermost 10 cm of *Laminaria saccharina* reduced elongation rates by 30%. Conversely, Dromgoole (1987, 1988) showed that the rate of photosynthesis in *E. radiata* increases in response to exposure to irradiance which fluctuated between saturating and limiting light levels at frequencies <300 seconds and increased with decreasing frequencies. Similar findings have been reported for the red algae *Chondrus crispus* (Greene and Gerard 1990), but Kubler and Raven (1996) found no such effect for *Palmaria palmata* or *Lomentaria articulata* (both also Rhodophyta). Thus, if the variability in irradiance environment below the kelp canopy is higher, then this may partly compensate for lower irradiance intensities. Any

effect of self shading is likely to be much lower at 10 m and 12 m due to the significantly lower densities found there (3.9 plants m^{-2} compared with 14.3 plants m^{-2} at 3 m; Appendix E).

The possibility that self-shading by upper necrotic regions of the plant may be causing a reduction in growth during summer was acknowledged by Kirkman (1989). The presence of larger areas of necrotic tissue and epiphyte cover in summer and autumn could potentially influence the calculation of RBA rates if these areas are not as active (photosynthetically) as younger regions of the thallus. For example, the thallus size is larger in summer than in spring, and thus the RBA rate is reduced in summer relative to spring, but rates of biomass accumulation per plant are similar in both seasons. If the RBA was calculated by assuming the necrotic region of the plant does not contribute to growth, then the RBA in both spring and summer may be more similar. However, the dramatic slowing of elongation rates during autumn indicates that other factors (e.g. nutrients, temperature) must be involved at least during autumn. Also, whilst an increase in necrotic tissue and in epiphyte cover (e.g. brown turfs) were observed during summer and early autumn in this study at 3 m, levels of epiphytes were very low and only the very distal ends of the plant were necrotic at 10 m and 12 m. This would suggest that the decrease in RBA rates during summer is not entirely an artefact of the study design, although the decrease in summer RBA rate compared to spring and winter at 10 m is smaller relative to the decrease at 3 m, which suggests that self shading may be involved in the reduction at the more shallow depth.

Evidence against a light limitation during summer and autumn is obtained in the study made by Stewart *et al.* (1961) of the seasonal variation in laminaran and mannitol content in various parts of *E. radiata* growing in Point Lonsdale, in Victoria. If productivity rates remain high during the period of low growth (summer/autumn) then it would be expected that levels of storage carbohydrates would be increased at this time. In fact, the maximal levels of laminaran (the primary storage reserve product in kelps) throughout the thallus were found by Stewart *et al.* (1961) during autumn (May), and minimal levels were observed during winter (August). Levels of mannitol showed a similar pattern with maximal levels occurring in summer (February) in the lamina and autumn (April) in the midrib region. The higher tissue densities (low ww:dw ratios; Table 4.2) recorded in autumn in this study (and the low density in winter) suggest that a similar pattern of accumulation of reserves in summer, and autumn and depletion of stores in winter is occurring in *E. radiata* at West Island.

A linear relationship between thallus length and growth rate of *E. radiata* was reported by Shepherd (1979) in his study of the algal community off Cape Northumberland, South Australia. This appears to indicate that, at least for *E. radiata* at a depth of 15 m, self-shading does not limit growth, as growth rate (elongation rate) increases with thallus length. Indivduals in Shepherd's (1979) study were of a comparable size to those in this study, i.e. ~30-100 cm.

It seems probable that the general growth strategy of *E. radiata* at West Island is caused by some limiting (e.g. low nitrate availability) or inhibiting (e.g. higher seawater temperatures) factor which reduces relative growth during summer and autumn. In spring and winter when environmental conditions are more favourable (nutrient input due to rainfall; lowering of temperatures) growth rates increase, probably through the utilisation of carbon stored during the summer/autumn period.

An annual cycle involving a period of low growth in combination with accumulation of storage carbohydrates (summer months), followed by a period of low productivity but high rates of growth (winter months) has been established for several other kelp species, and in some species the reserves accumulated during summer supplement winter carbon assimilation to support growth (Hatcher *et al.* 1977, Chapman and Craigie 1978, Dunton and Schell 1986, Zimmerman and Kremer 1986, Dunton 1990). The importance to the growth of *E. radiata* of carbohydrate reserves required to complement carbon assimilation in winter is discussed below.

In addition to the influence of environmental factors on growth, the influence of endogenous mechanisms on growth patterns in macroalgae is well established (Lüning 1979, Lüning 1991, tom Dieck 1991, Lüning 1993, Schaffelke and Lüning 1994, Henley and Dunton 1995, Makarov *et al.* 1999). Early evidence against the primary influence of environmental factors on kelp growth was found in the study of Lüning (1979) who found that growth rates of both *L. hyperborea* and *L. saccharina* decreased in summer when both light and nutrients were still abundant in the waters around Helgoland. Calvin and Ellis (1981) found no obvious link between either dissolved nitrate concentration or the irradiance environment and the growth of *L. groenlandica* in Alaska, as elongation rates began to increase in mid winter and peaked in early spring after nitrate concentrations began to decline. Additionally, a summer depression of growth rate occurred in *A. esculenta* despite exposure to nutrient-enriched cold water (favoured for growth) (Buggeln 1978). The growth of several species of kelp in arctic-cold temperate regions resumes in midwinter and ceases in midsummer (see above). Lüning (1993)

observed that this growth strategy allows the algae to take advantage of high nutrient levels before they are depleted by phytoplankton blooms, and also to store enough carbon to survive the dark winter.

A number of more recent studies have used laboratory experiments to investigate endogenous rhythms in kelp (Lüning 1991, tom Dieck 1991, Lüning and Kadel 1993, Schaffelke and Lüning 1994, Makarov *et al.* 1999). Cultivation of *Pterygophora californica* in a constant environment in tanks revealed a "free running" blade production cycle of around 10 months, which included a peak in growth 14 weeks from the beginning of each cycle (Lüning and Kadel 1993). Continuous growth occurred when day-length was kept at 8 hours. Manipulation of the annual cycle of day-length from the natural period of 12 months to periods of 6 and 3 months resulted in the growth rhythm becoming synchronised with the new period, and instead of one growth cycle a year the algae displayed 2 or 4 cycles respectively (Lüning 1991). This experimental evidence indicated that day-length is the synchronising factor in the growth cycle, with new blade growth beginning after the shortest day-length. Additionally, when the day-length cycle was shortened (e.g. to 3 months) there was a lag between shortest day-length and initiation of growth, which indicates a circannual cycle as opposed to control by photoperiodism (Lüning 1991).

tom Dieck (1991) found a similar situation when she grew *Laminaria setchellii* in constant laboratory conditions. A "free running" growth cycle of around 11-17 months was detected under constant "long day" and "night break" conditions, but not under "short day" conditions. Similarly, Schaffelke and Lüning (1994) found that the growth patterns of *Laminaria hyperborea* and *L. digitata* are controlled by endogenous rhythms that are synchronised by the day-length cycle. Recently, Makarov *et al.* (1999) found that in several species of macroalgae from the Barents Sea, growth rates decreased from spring to autumn, regardless of whether they were exposed to field conditions or to a controlled light environment in the laboratory. They suggested that this endogenous rhythm enabled the algae to anticipate the unfavourable conditions of winter.

All the work conducted on growth cycles in *E. radiata* has been conducted in the field. In these conditions an endogenous rhythm would be impossible to detect over the effect of the annual cycles of various environmental factors such as nutrient concentration and irradiance, especially if the annual day-length cycle was the synchronising factor for the circannual rhythm (*sensu* Lüning 1993). Importantly, the work on endogenous rhythms described above was conducted at higher latitudes than that of West Island (e.g. Helgoland, North Sea and

Murmansk, Barents Sea). Lüning (1993) noted that quite different circannual rhythms can occur in closely related kelp species. Until controlled laboratory experiments can be conducted, the existence of circannual cycles in *E. radiata* can only be regarded as likely.

Differences in biomass accumulation rates at shallow and deep sites

This study has shown that rates of growth in *E. radiata* change along the depth profile. The relative biomass accumulation rates (RBA) of *E. radiata* at shallow depths (3 m and 5 m) were higher than those at deep depths (10 m and 12 m), except during autumn when rates at all depths were minimal. Individuals were larger at greater depths and consequently the rates of biomass accumulation per plant (BA) were consistently higher throughout the year. Elongation rates also tended to be faster at 3 m than at 10 m and 12 m, but a clear difference was only apparent during winter. The finding that relative growth rates are faster at shallower depths, but that individuals are smaller, suggests that the processes such as erosion and herbivory may be more significant at these depths.

These findings are consistent with work on *E. radiata* by Kirkman (1989) who found that rates of relative biomass accumulation (g g^{-1} d^{-1}) were higher at depths of 5 m than 10 m, except during summer (December-February). In the current study the difference between depths, whilst still significant, was much less during summer than during spring and winter. Both Hatcher *et al.* (1987) at Marmion Reef, Western Australia (WA) and Novaczek (1980) in Goat Island Bay, New Zealand found that elongation rates in *E. radiata* decreased with depth. Conversely, the rates of elongation at Five Fathom Bank, WA (27 m) were much greater than those at Marmion Reef (5 m and 10 m) and at Abrolhos Reef, WA (4.5 m and 7 m), but the different morphology at that site (longer thallus and stipes but low biomass per unit length) was cited as a possible reason for this difference (Hatcher *et al.* 1987).

In contrast to previous studies (Novaczek 1984a, Hatcher *et al.* 1987, Kirkman 1989) no clear phase shift in phenological events occurred between depths in this study, i.e. the peaks and lows in growth rates occurred in the same season at all depths. Novaczek (1984a) found that phenological events at 15 m occurred about 3 months later compared to those at 7 m, and indicated this suggests that timing of events is controlled by photon flux density. Both Hatcher *et al.* (1987) and Kirkman (1989) also found that deeper *E. radiata* had a later burst of growth. Given the reported lack of variation in other environmental factors (e.g. nutrients) between depths, these studies may represent evidence of an endogenous rhythm in *E. radiata* that is synchronized by day-length. Dieckmann (1980) also found that the onset of rapid

growth in *Laminaria pallida* occurred approximately one month later at 14 m compared with 8 m. The longer interval between sampling times in the current study (i.e. every season compared with every month in the previous studies) may have meant that some detail in the growth patterns was missed.

Allocation of carbon to growth

This study has demonstrated that the historical use of biomass accumulation ("hole-punch") methods to estimate kelp productivity has resulted in large underestimates of annual productivity rates (see Table 4.4). On the other hand, measurements of net productivity on their own will vastly overestimate the production of biomass if it is assumed that all assimilated carbon was incorporated into biomass.

For six months of the year (summer and autumn) the proportion of net assimilated carbon that is incorporated into biomass is only 4-27% across all depths. If a conservative photosynthetic quotient (PQ) of 0.67 is used to calculate net carbon assimilation rates, this proportion raises to 7-41%. During these months the hole-punch method will therefore drastically underestimate net productivity rates.

At 3 m the spring and winter biomass accumulation still only represents 32-41% (or 48-61% if PQ = 0.67) of net assimilated carbon, thus the hole-punch methods will significantly underestimate annual productivity at this depth. Photoassimilates are clearly adequate to support growth at depths of 3 m during all seasons. The proportion of assimilated carbon needed for growth during winter and spring at the deeper depths was 90-128% (or 134-191%). This indicates that, in addition to carbon assimilated at that time, storage carbohydrates, presumably accumulated during summer and autumn, must be utilised to support the high growth rates during these months. On an annual basis, carbon assimilation rates greatly exceed the amount of carbon used for growth at these deeper depths (Table 4.4).

The rates of relative biomass accumulation are lower at 10 and 12 m than at 3 and 5 m (except during autumn). This difference is more pronounced when maximum irradiance is lower during winter and spring compared to summer, when irradiance is higher. This suggests that growth may be light-limited at the deeper sites, particularly during winter and spring. The deficit in assimilated carbon during winter and spring would appear to confirm this notion. Furthermore, while no significant differences were found in net productivity rates at depths of 3 m throughout the year, at 10 m the rates were lower during winter (May) and spring (September), although net productivity rates at 12 m did not differ seasonally (Chapter 3;

Table 4.4 Rates of annual algal net primary production per m² of substrate (based on *in situ* productivity measurements) and production of tissue carbon per m² of substrate (based on variations of the hole punch method; converted from gdwt to gC assuming dry matter is 45% carbon (Drew and Hastings 1992)). For comparison, rates of net primary production by other ecosystem types are also displayed.

Species	Depth	Location	Referenece	Annual Net Production (gC m⁻² y⁻¹).	Annual Tissue Production (gC m⁻² y⁻¹).	Standing Biomass (gdwt m⁻²)
Laminaria longicruris, L. digitata & Agarum cribrosum community	5-15 m	Nova Scotia	Mann (1972)	-	1750	-
Laminaria longicruris	10 m	Nova Scotia	Hatcher *et al.*(1977)	143-428	-	105-315[a]
Ecklonia radiata	5 m	Marmion Reef, W.A.	Kirkman (1984)	-	1575	800-2200[b]
E. radiata	7 m	Goat Island Bay, N.Z.	Novaczek (1984a)	-	2700	-
E. radiata	15 m	Goat Island Bay, N.Z.	Novaczek (1984a)	-	675	-
E. radiata	1.5 m	Fairlight Bay, N.S.W.	Larkum (1986)	-	1305	-
E. radiata	5 m	Marmion Reef, W.A.	Kirkman (1989)	-	1980	1700
E. radiata	10 m	Marmion Reef, W.A.	Kirkman (1989)	-	820	700
Phaeophycean dominated boulders	4 m	West Island, S.A.	Cheshire (1996)	1570	-	500
E. radiata	3 m	West Island, S.A.	this study	5400	1078	911
E. radiata	10 m	West Island, S.A.	this study	920	383	535
Temperate evergreen forest	-	-	Colinvaux (1986)	585	-	-
Swamp and marsh	-	-	Colinvaux (1986)	1125	-	-
Open ocean	-	-	Colinvaux (1986)	57	-	-
Upwelling zones	-	-	Colinvaux (1986)	225	-	-

[a] calculated using conversion factor of 0.005 gdw.cm⁻² based on (Henley and Dunton 1995)

[b] converted using a ww:dw ratio of 7.14

Figure 3.2; Table 3.3). At depths of 10 m these periods of lower net assimilation coincide with the highest growth rates (i.e. winter and spring), suggesting that at this time light limitation may be involved in causing the disproportionaly lower rate of relative growth compared with that at a depth of 3 m (Figure 4.1).

This work is consistent with the that of Kirkman (1989) who compared growth rates of shaded and unshaded *E. radiata* at 5 m. Rates of growth under the shade were reduced during most of year, but were similar to unshaded plants in spring (October). Kirkman (1989) considered that this provided only partial support for a light limitation hypothesis and that the lag in peak growth rates at depth confounded the situation.

In conclusion, the pattern of biomass accumulation by *E. radiata* at West Island is consistent across depths. The reduction in relative growth rates during summer and autumn is likely to be the result of a combination of environmental factors, particularly changes in nutrient availability and seawater temperature, but influences from endogenous rhythms and from reproductive processes may also be important. Annual rates of biomass accumulation are supported by carbon assimilation rates at all depths, but during winter and spring it appears that storage carbohydrates are needed to supplement photoassimilates in order to support growth at deeper sites.

Chapter 5 : Short Term Photoacclimation Response

The previous three chapters have documented the seasonal patterns in photosynthesis (Chapter 2), productivity (Chapter 3) and growth (Chapter 4). This work has highlighted the importance of the acclimation response to seasonal changes in the underwater light environment. This chapter investigates the acclimation response of *Ecklonia radiata* to short term experimental manipulations of the irradiance environment.

Introduction

Macroalgae grow in an irradiance environment which can alter dramatically over an hour, a day, or throughout the year (Kirk 1994, Falkowski and Raven 1997). It is the ability to respond to these changes that allows algae to photosynthesise in a wide range of conditions. The obvious ecological advantage of photoacclimation to seasonal changes in the light environment is that algae are able to maintain high rates of carbon assimilation in both low and high irradiance conditions (Chapter 3). However, changes in irradiance similar to those which occur on a seasonal scale, between summer and winter, can often occur over much shorter time periods.

The nearshore marine environment is currently subjected to various terrigenous inputs, from sources such as rivers or sewage treatment works. These inputs can have a dramatic effect on water quality, and consequently on the irradiance that is able to reach the benthos (Shepherd *et al.* 1989). Other activities, such as sand dredging or marina constructions, have a similar but more prolonged effect on the light environment (Lyngby and Mortensen 1996; Cheshire and Turner 2000). The effect of these inputs on water quality may last for up to a few days or weeks, and thus algae must either acclimate to the lowered irradiance, or potentially suffer from reduced production rates. In addition, if the algae do acclimate to the altered conditions they will then have to respond (acclimate) again if the irradiance environment returns to the previous state (i.e. water quality improves). There is no doubt that *E. radiata* possess the ability to photoacclimate to changes in irradiance, as demonstrated in Chapter 2, but there is currently no knowledge of the time scale over which this acclimation response occurs.

Henley and Ramus (1989c) observed that the acclimation response time must be compatible with the periodicity of irradiance variation in order for the response to be beneficial. The consequence of acclimating quickly (e.g. in a day) to a reduction in irradiance is that once the water quality returns to the previous state (increased irradiance), the algae are likely to experience severe photodamage. Responding to changes in the light environment on a short

time scale may thus not be beneficial. The acclimation response involves the biosynthesis and degradation of a variety of compounds, such as light harvesting components and reaction centre proteins (Sukenik *et al.* 1990, Falkowski and LaRoche 1991). The rate of alteration in the level of these compounds has been related to the magnitude of the irradiance modification (Geider and Platt 1986), and the overall acclimation response rate appears to be species specific. *Ulva rotundata* responded to large changes in irradiance by altering pigmentation and photosynthetic characteristics in 4-5 days (Henley and Ramus 1989c), and in the phytoplankton *Dunaliella tertiolecta* changes were also complete within 4 days during responses to increased and lowered irradiance (Falkowski 1984). The rhodophyte *Palmaria palmata* displayed acclimation to altered light environments in a 14 day period (Sagert and Schubert 2000), although the response may well have been completed before measurements began on day 14. Küster *et al.* (2000) indicates that the charophyte *Lamprothamnium papulosum* is able to acclimate to irradiance variations within a period of hours.

Beardall and Morris (1976) first suggested that algal acclimation to low light predominantly results in the loss of ability to effectively photosynthesise and grow in high light, in addition to the enhanced ability to utilise sub-optimal irradiance. The typical response to lowered light levels is to alter the acclimation state by increasing the capacity to absorb and utilise photons (see Chapter 2). This response is dangerous if the reduction in light intensity is only short lived, as the likelihood of subsequently absorbing damaging quantities of photons is then increased when irradiance returns to the previous high levels. Furthermore, the capacity to avoid photodamage is likely to be decreased in this acclimation state, further increasing the possibility of chronic photoinhibition (see Chapter 3). When measured under the same high irradiance conditions, this results in a midday depression in photosystem II (PSII) efficiency observed in high light acclimated algae that is more likely to be a result of photoprotection, whereas the depression seen in shade grown algae is likely to be the result of photodamage (Henley *et al.* 1992). The negative impact of photodamage and chronic photoinhibition on the productivity of macroalgae is discussed in Chapter 3.

In addition, acclimation to lowered irradiance has a cost in terms of carbon and energy (e.g. manufacturing pigments and proteins) which may impact on the production of other cell components (Raven 1984). Beardall and Morris (1976) found that acclimation to low light, in the phytoplankton *Phaeodactylum tricornutum*, resulted in an increase in chlorophyll content, but they also observed a simultaneous reduction in RuBisCO activity. Furthermore, the efficiency of growth was diminished in *Ulva rotundata* acclimated to low light conditions and then

subsequently placed in a high light environment, which was possibly due to an effect of photoinhibition, or to reduced RuBisCO activity (Henley and Ramus 1989b). Henley and Ramus (1989a) considered that the resource trade-off between light harvesting ability and carboxylation capacity places limits on the acclimation response.

Conversely, the benefit of acclimating to a reduction in irradiance is that rates of productivity will be increased, as the acclimation response will increase the amount of photons that can be absorbed and that will therefore be available for photochemistry, as well as reducing respiratory costs. If the irradiance reduction is long term, such as seasonal reductions over winter, then this benefit is likely to outweigh the cost of any potential photodamage and of increasing the absorption cross-section. Henley and Ramus (1989b) demonstrated experimentally that the efficiency of growth under low light conditions was higher in an *Ulva rotundata* clone (Chlorophyta) which had been acclimated to low light conditions, when compared with the same clone which had been acclimated to high light conditions and then grown in low light conditions. Chlorophyll content increased in *Ulva rotundata* transferred from a high to a low light environment, which increased the light absorption capacity (Henley and Ramus 1989a, Henley and Ramus 1989b).

Chlorophyll *a* fluorescence parameters are frequently used to estimate the photosynthetic efficiency of algae (Henley *et al.* 1991a, Franklin *et al.* 1992, Hanelt 1992, Hanelt *et al.* 1995, Franklin *et al.* 1996). Recent studies have utilised chlorophyll *a* fluorometry to examine the acclimation response of algae to changes in levels of both photosynthetically active radiation (Henley *et al.* 1991a) and ultraviolet radiation (Karsten 2001). These studies have demonstrated that the efficiency of PSII as estimated by chlorophyll *a* fluorescence parameters can be used to identify the changes in acclimation state which occur in response to differing irradiance conditions. The daily cycle of PSII efficiency typically involves a midday depression and recovery of efficiency (Henley *et al.* 1991a, Hanelt *et al.* 1993, Hanelt and Nultsch 1995, Magnusson 1997, Sagert *et al.* 1997, Yakovleva and Titlyanov 2001), and these features can be used to investigate differences in acclimation state. High light acclimated algae will generally show a reversible midday decline in PSII efficiency, whereas low light acclimated algae often show incomplete recovery of efficiency by evening (when exposed to the high light at shallow depths), which reflects a greater degree of photodamage (Henley *et al.* 1992, Hanelt *et al.* 1997a).

The expanding effect of humans on the coastal environment means that an understanding of algal acclimation responses has an increasing importance for coastal management strategies.

The aim of this work was therefore to investigate the timescale of the acclimation response in *E. radiata*. Pilot studies (Appendix F) indicated that a seven day period in a lowered irradiance environment was not sufficient to induce a response in *E. radiata*. An experimental protocol was then set up in order to investigate the response to a longer (~two week) reduction in light levels and also to compare this response with the acclimation response to increased irradiance. Additionally, this work aimed to investigate the seasonal consistency of the acclimation response.

Methodology

General Experimental Procedure

Different experimental designs were used in order to study the acclimation response to both increases and decreases in irradiance. Observing the timescale of the response to increases in light levels was straightforward as plants could be transplanted from a deeper depth and measured for as long as was necessary. Studying the timescale of the response to lowered irradiance was more problematic, as exposing adequate numbers of shallow (high light acclimated) plants to low light for 7, 8, 9, and 10 days etc. and returning them to the high light conditions at the end of each period in order to find out whether acclimation has occurred, was not logistically possible. A time period of 14 days reduction in light levels was therefore selected on the basis of the pilot studies.

Two basic types of experiments were conducted: the first type ("shallow transplant" experiments) consisted of transplantation of *E. radiata* from a depth of 3 m to either 10 m or 12 m. Plants were left at this depth for a period of days, and then transplanted back to 3 m. Experimental controls for the first period of this experiment were plants from 10 m or 12 m, and for the second period (i.e. after the transplants were returned to 3 m) the controls were plants from 3 m. The second type of experiment ("deep transplant" experiments) involved plants from either 10 m or 12 m being transplanted up to 3 m. In this experiment the experimental controls were plants from 3 m. All experimental controls were subjected to the same handling as the transplants (i.e. removed from substrate, transported in bags etc.). In both types of experiment procedural controls were nearby plants that were left attached to the substrate.

Transplant Procedure

Transplants were carried out on the evening before day 1 of each experiment. Adult individuals were randomly selected at each depth on the basis that they were representative of the adult population at that depth. Plants were collected by prising the holdfast off the substrate so that as much as possible of the holdfast remained with the plant. After transportation in large mesh bags, plants were attached to metal grids (10 x 10 cm) which measured 1 x 2.5 m. Rubber preserving-jar rings were twisted around each stipe and these were then attached to the grid by cable ties.

PAM Chlorophyll Fluorescence

The photosynthetic performance of experimental plants was monitored throughout the day by chlorophyll a fluorescence using a Diving-PAM (Walz, Germany). The parameter which was used to determine acclimation state was effective quantum yield ($\Delta F/Fm'$) (Genty et al. 1989). ΔF represents the difference between the steady state (light adapted) fluorescence (F) and the maximal fluorescence in the light adapted state (Fm'). Effective quantum yield was used rather than optimal quantum yield[5] due to the time constraints imposed by SCUBA and also because of the logistical problems encountered using leaf clips in a surgey environment (e.g. movement of the clips during dark adaptation periods), which affected data quality. Diving PAM settings were kept constant throughout the experiments (Measuring Intensity = 12; Saturation Intensity = 8; Saturation Width = 1.0 sec; Gain = 12; Damp = 3). These settings were selected to enable accurate measurement of the low fluorescence signals which were often encountered during high light periods. Measurements for each individual were made ~10cm down from the tip of the second youngest, fully extended lateral on one side of the plant. The lateral was marked by survey tape so that the same lateral was measured throughout the experiment. This ensured that the readings were taken from a similar thallus position each time, however, it was not possible for exactly the same region to be repeatedly measured. Comparisons of F and Fm' values across time were therefore not made.

Evidence of acclimation to the deeper light environment in the shallow transplant experiments (when shallow plants were moved to a deeper depth) was defined as a significant

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[5] Optimal quantum yield is defined as Fv/Fm, where Fv is the difference between maximal fluorescence (Fm occurs when all reaction centres are closed) and initial fluorescence (Fo) which occurs when all reaction centres are open. These measurements require that samples be "dark adapted" for a period, typically 15 minutes, prior to measurement, in order for the primary electron acceptor in PSII to become oxidised i.e. for all reaction centres to "open". The dark adaptation period is required for non-photochemical quenching mechanisms to "relax" and is generally achieved by the use of "leaf clips", which are attached to the algae and completely shade a small portion of the thallus.

difference in yield between the transplants and the controls after the transplants had been transported back up to 3 m. During the deep transplant experiments (deep plants moved to shallow depth) the 10 m or 12 m plants were considered to have achieved the same acclimation state as the controls when they showed similar yield measurements to the controls throughout the daily measurement cycle. The assumption was made that if the transplants displayed a greater midday depression in yield values than the controls, then this was the result of a higher level of photodamage. This assumption can only be validated by also observing evening recovery. Consequently on several days a 24 hour cycle of yield measurements was also made, which enabled recovery of photosynthetic efficiency from the midday depression to be studied.

Photosynthetic Pigments

During the December experiments tissue discs were collected from the same thallus region as that used for chlorophyll *a* fluorescence measurements (see above), but from the opposite side of the thallus, i.e. from a lateral of equivalent age as that used for the chlorophyll *a* fluorometry. The discs were collected using a hole-punch of 1.8 cm diameter. Samples were rinsed in deionised water immediately after collection, then placed into a liquid nitrogen canister. The samples were later transferred to a –80 °C freezer where they remained until the extractions were conducted. Chlorophyll *a*, chlorophyll *c* and fucoxanthin were extracted using dimethyl sulphoxide (DMSO) and methanol (Duncan and Harrison 1982). Concentrations were determined using the equations of Seely *et al.* (1972). The concentration of pigments in transplants were compared with a control group of plants from the original collection depth.

Analysis

The chlorophyll *a* fluorescence data were log transformed to improve variance homogeneity. This transformation was undertaken on "1-Yield value" so that the standard deviations became proportional to the means (Zar 1996). This was necessary because the variation in yield is typically highest during periods of higher light, which is when the lowest yield values are generally recorded. After transformation a series of one-way ANOVA's were used to compare the effective quantum yield of the transplants with those of the controls.

One-way ANOVAs were also used to test for differences between the concentration of chlorophyll *a*, chlorophyll *c* and fucoxanthin in the transplants and in controls.

Experimental Protocol

September Deep Transplant Experiments (10 m to 3 m)

Transplantation took place on the evening of the 14th of September 1999. The irradiance in the low light environment, to which the 10 m plants were acclimated, was around 25% of that at 3 m (116 versus 469 µmol photons m^{-1} s^{-1}; see Table 2.1). Measurements of effective quantum yield were made following transplantation and these were compared to control plants (3 m transplanted to 3 m). Measurements were made every 3 hours for the first two days following transplantation, then at solar noon for the next eight days. This experiment was then repeated on the 22nd of September, however measurements were made only for the first two days following transplantation.

December Deep Transplant Experiments (12 m to 3 m)

The design of this experiment follows the September experiment described above. Transplantation of 12 m plants to 3 m occurred on the evening of 30th of November 1999. During this period the maximum daily irradiance at 3 m was ~6-7 times higher than that experienced at 12 m (705 versus 105 µmol photons m^{-1} s^{-1}; see Table 2.1). Regular yield measurements throughout the daily cycle were made during the first 2 days and also on days 7 and 14. For 17 days following transplantation midday measurements were also made. On day 14 tissue samples were collected for later pigment analysis.

March Deep Transplant Experiment (12 m to 3 m)

The design of this experiment also follows that of those described above. Transplantation to a depth of 3 m took place on the 17th of March 2000. Measurements were made throughout the daily cycle for the next six days. The level of irradiance at 3 m was ~8.5 times higher than that at a depth of 12 m (537 versus 63 µmol photons m^{-1} s^{-1}; see Table 2.1).

December Shallow Transplant Experiment (3 m to 12 m)

This experiment involved transplantation of 3 m plants to 12 m, where they were left for 14 days, and then returned to 3 m. During this period the intensity of maximum irradiance at 12 m was ~15% of the intensity at 3 m (105 versus 705 µmol photons m^{-1} s^{-1}; see Table 2.1). Tissue samples were collected on day 14 , i.e. from 3 m plants after they had experienced the 12 m environment for 14 days.

Photosynthetic electron transport rates (ETRs) were also calculated using the equation:

$$ETR = (\Delta F / Fm') \times PAR \times 0.5 \times AF \quad \text{(Beer et al. 2000)}$$

where PAR is the average incident PAR recorded during the measuring period and AF is the absorption factor (obtained by the methods of Beer *et al.* 2000). These rates enabled an investigation of the impact on productivity of both the 13 day period of irradiance reduction, and the subsequent return to a higher irradiance environment. ETR rates were integrated for each day and those calculated for the shallow transplants are expressed as a percentage of the integrated daily rate of the shallow controls.

Results

Deep Transplant Experiments (Low to High Light)

September Experiments

This experiment demonstrated that the acclimation state of 10 m (low light) *E. radiata* was different from 3 m (high light) *E. radiata*. The deep transplants had significantly lower yield values by 9 am on the first day of exposure to higher PAR (day 1), and these values remained significantly lower throughout that day and the next (Figure 5.1a; p < 0.01, one-way ANOVAs). These results indicate that the deep transplants experienced chronic photoinhibition as, unlike the shallow control group, which showed recovery to high yield values by early evening on day 1, the deep transplants did not recover photosynthetic efficiency, even by the morning of day 2 (Figure 5.1a).

The midday depression in the deep transplants remains significantly lower until day 9 (Figure 5.1b; p < 0.01, one-way ANOVAs), indicating that either this group was experiencing greater photodamage than the controls, or that they quickly developed a superior ability to downregulate. By days 8 & 9 evidence that the photoprotective ability has improved is seen in the almost complete recovery of yield values in the evening, which are not significantly different to the control values (data not shown). On day 10 the midday depression of yield values in the deep transplants is no longer significantly lower than the controls (Figure 5.1b), suggesting that the acclimation response is completed by this time. The irradiance measured on day 10 (670 µmol photons m^{-2} s^{-1}) was the highest of the experiment, and was ~6 times that which the deep transplants would have previously experienced at a depth of 10 m.

Figure 5.1 Photosynthetic efficiency (mean ± se) of *E. radiata* after transplantation of 10 m plants to 3 m (--- = deep transplant treatment; ⎯ = shallow experimental controls; -- = PAR). Data shown in (a) are that measured on days 1 & 2, i.e. the first two days after plants were transplanted to 3 m; the transplants showed a significantly greater degree of photoinhibition when compared to controls, and did not show complete recovery. Data shown in (b) are that measured at midday throughout the experiment; by day 10 the midday photosynthetic efficiency of the transplants was similar to that of the controls. The experiment was conducted in mid September 1999. PAR values are the mean of all values recorded in each measuring time.

When this experiment was repeated (Figure 5.2) both the deep transplant and the control groups experienced chronic photoinhibition on day 1. The controls were able to recover yield values overnight, and while the transplants also displayed recovery (increase in effective quantum yield), this process was not completed by the following morning. Similarly to the first experiment, a reduction in yield values in comparison to the controls occurred from 9am on day 1 and remained significant throughout the next two days ($p < 0.01$, one-way ANOVAs).

Figure 5.2 Photosynthetic efficiency (mean ± se) of *E. radiata* after transplantation of 10 m plants to 3 m (--- = deep transplant treatment; — = shallow experimental controls; — = PAR). Data shown are that measured on Days 1 & 2, i.e. the first two days after plants were transplanted to 3 m. Similarly to Figure 5.3, the transplants were more photoinhibited and were not able to recover photosynthetic efficiency during the evening. The experiment was conducted in late September 1999. PAR values are the mean of all values recorded in each measuring time.

December Experiment

The results of this experiment are consistent with the September experiments described above. During the first two days of exposure to higher light the deep transplants (from 12 m) experienced chronic photoinhibition, displaying incomplete recovery in comparison to the controls, although recovery on day 1 was fairly close to the level seen in the control group

(Figure 5.3a). The levels of irradiance recorded[6] during these two days were very high (maximum levels of 645 & 881 µmol photons m^{-2} s^{-1}), compared to the average maximum irradiance at 12 m during December (105 µmol photons m^{-2} s^{-1}). The differences in means between the two groups were significant by 10am on the first day and remained so throughout the first two days (p < 0.01, one-way ANOVAs).

The acclimation response began to become apparent after one week. On day 7 (Figure 5.3b) the high light depression was still significantly greater in the transplants than in the controls (p < 0.01, one-way ANOVA), but recovery was complete in both groups by early evening. The level of irradiance on this day was not high for the time of year (467 µmol photons m^{-2} s^{-1} at 10am, reduced to 223 µmol photons m^{-2} s^{-1} by 1pm). Similarly, on day 14 the reduction in yield values in the transplant group becomes significantly greater when irradiance increased but there was a complete recovery in photosynthetic efficiency by early evening (Figure 5.3c). Irradiance in the middle of day 14 was high at ~750 µmol photons m^{-2} s^{-1}.

On day 15 the deep transplants had a midday depression in yield values similar to that of the control group (Figure 5.3d). However, the light levels on that day were fairly low (444 µmol photons m^{-2} s^{-1}) and when they increased the next day to 772 µmol photons m^{-2} s^{-1} the midday depression was again significantly greater in the transplant group. Whilst the levels of PAR on day 15 were low, and thus the midday depression may be expected to be smaller, the PAR levels are still similar to the levels experienced during the first two days of the experiment, which at that stage induced a significantly larger midday depression in the deep transplants. This indicates that while the acclimation response may not have been completed by the end of the experiment, the acclimation state of the deep transplants had significantly altered throughout the first two weeks.

The concentration of pigments in the deep transplants, which were measured after 14 days at a depth of 3 m, supports the idea of an incomplete change in acclimation state. These concentrations were compared to the concentration in plants which had remained at 12 m. The levels of chlorophyll *a* & *c* and fucoxanthin were all lower than the deep controls (Figure 5.4). This decrease was significant for both chlorophyll *a* & *c* (p < 0.05, one-way ANOVAs).

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[6] This PAR value (and those reported below) is the average, for the particular measurement period, of all PAR values recorded by the Diving PAM during each fluorescence measurement. The Diving-PAM was held as horizontal as possible during measurements so that the light sensor recorded as accurately as possible the downwelling irradiance. It should be noted that this value is essentially an instantaneous measure and does not provide any information about the history of light exposure.
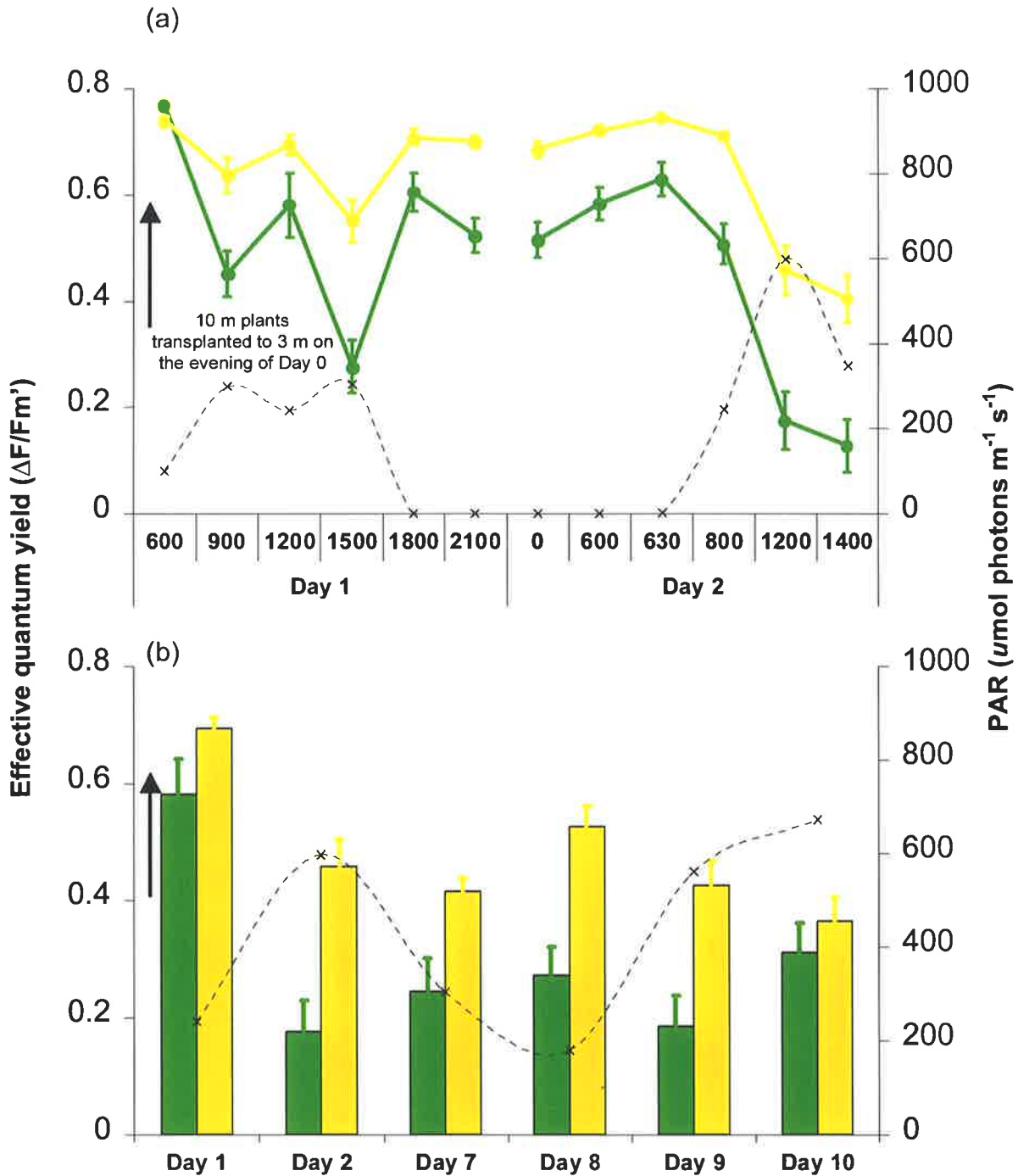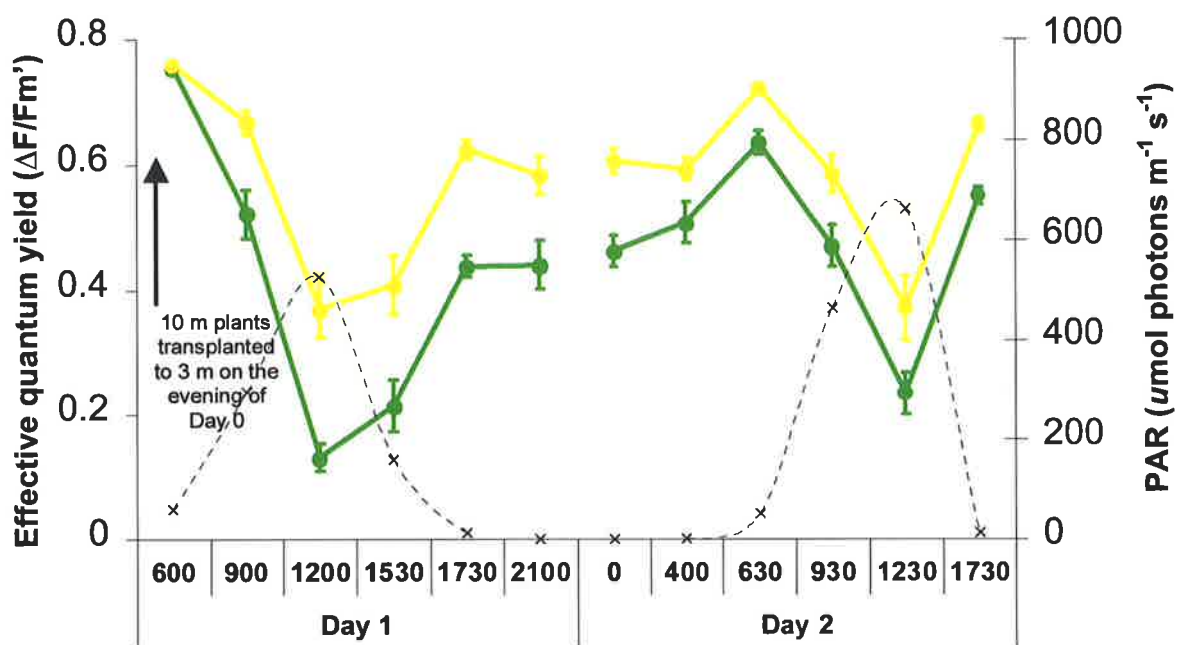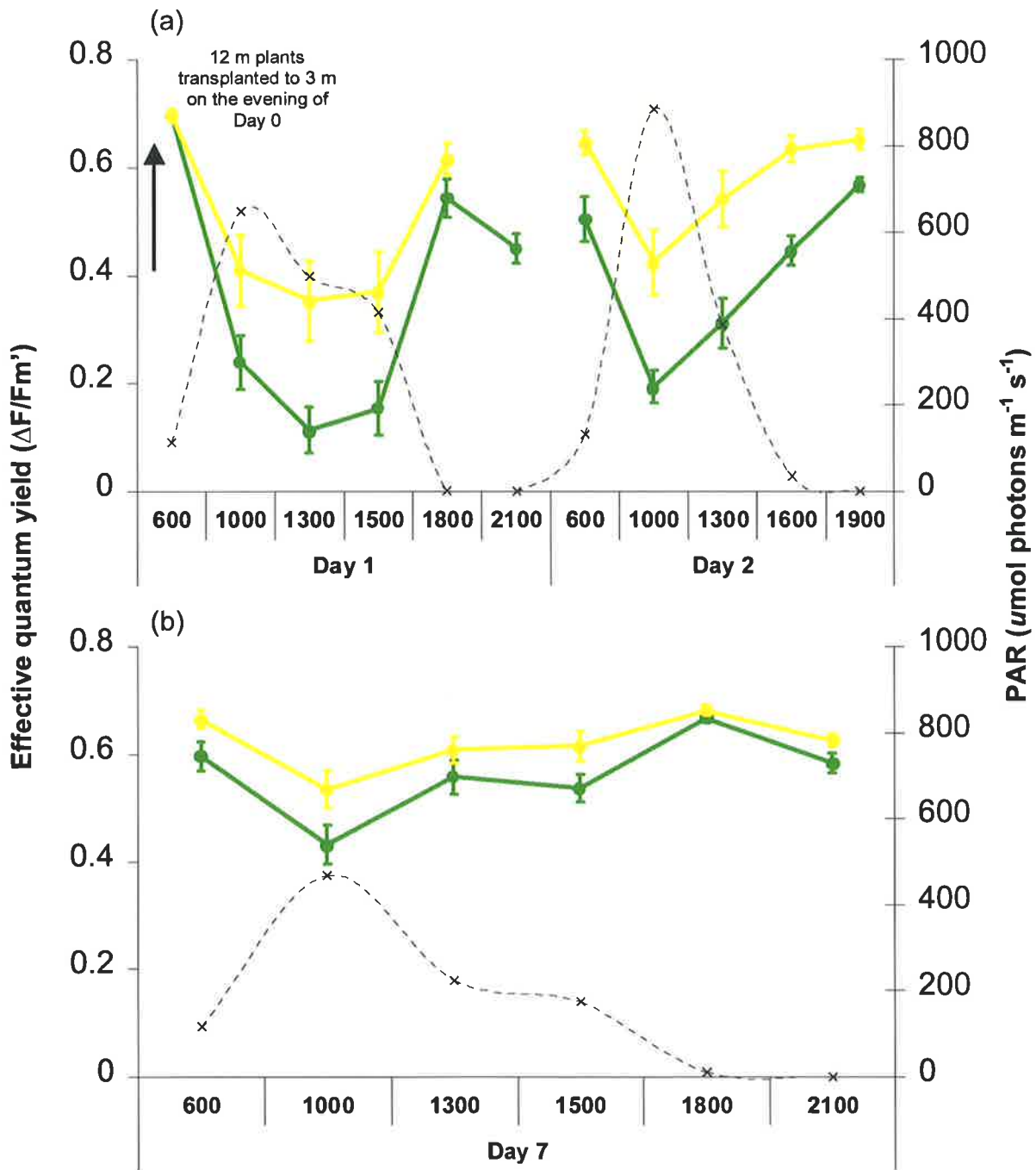
Figure 5.3 Photosynthetic efficiency (mean ± se) of *E. radiata* after transplantation of 12 m plants to 3 m (--- = deep transplant treatment; ⎯ = shallow experimental controls; --- = PAR). Data shown in (a) are that measured on Days 1 & 2, i.e. the first two days after plants were transplanted to 3 m, (b) Day 7, (c) Day 14, and (d) data measured at midday throughout the experiment. The experiment was conducted in early December 1999. PAR values are the mean of all values recorded in each measuring time.
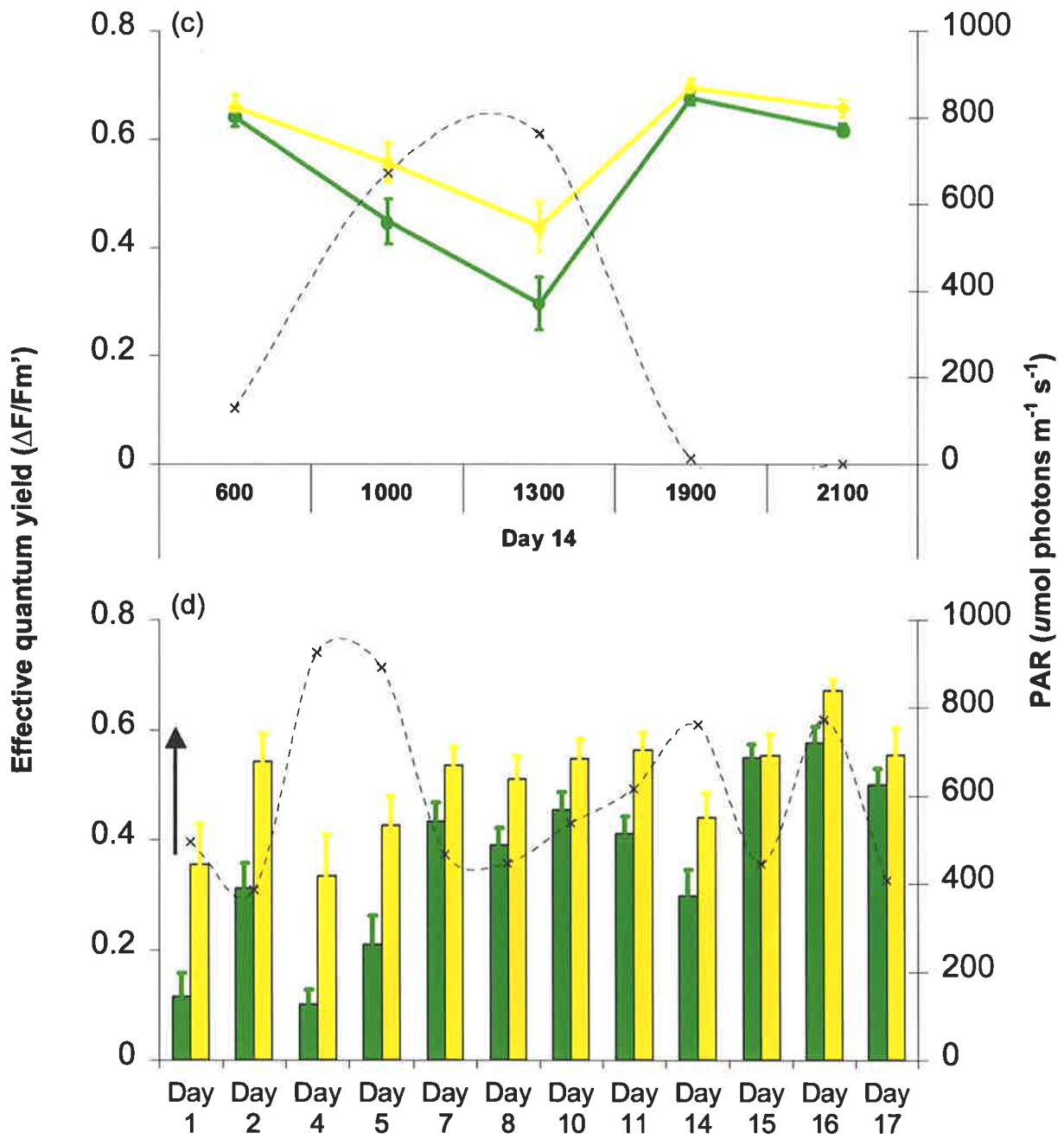
Figure 5.3 continued.

The decrease in pigment concentration in the deep transplants was accompanied by bleaching of the upper thallus. This is indicative of severe photodamage not an acclimation response, as the deep transplants did not become more similar to the shallow control plants (Figure 5.4), which would have involved an increase in concentrations. These results suggest that the time scale of acclimation of the pigment suite is longer (> 2 weeks) than that of the photoprotective mechanisms.
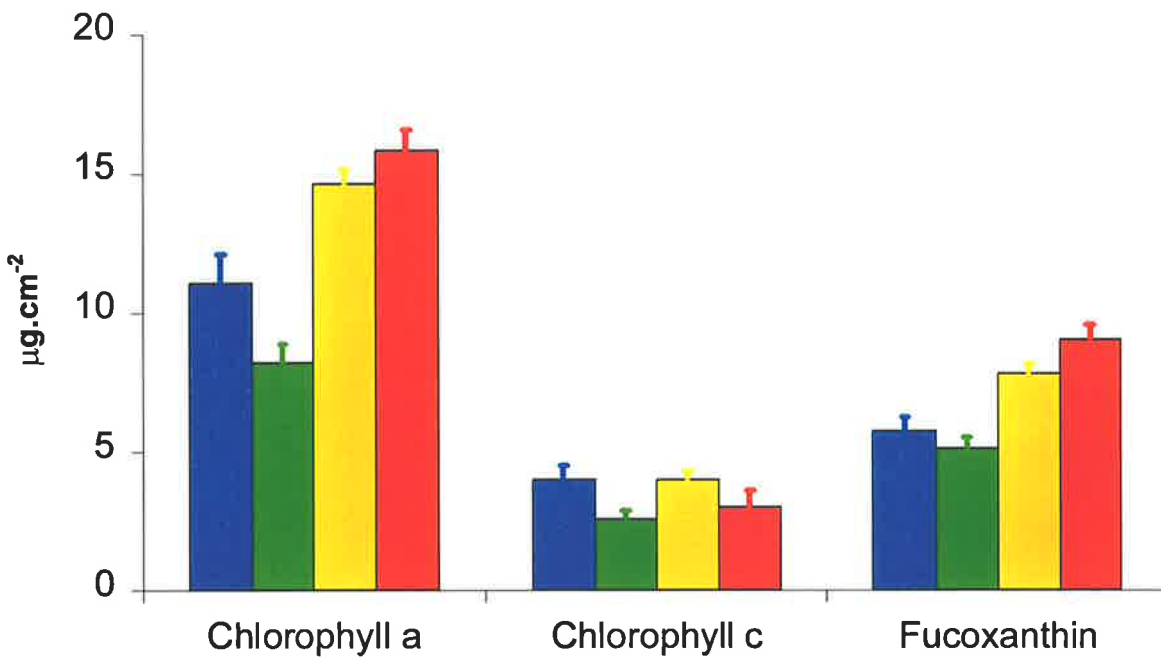
Figure 5.4 Photosynthetic pigment concentration in *E. radiata* during the two experiments in December 1999 (--- = deep experimental controls; --- = deep transplant treatment; — = shallow experimental controls; --- = shallow transplant treatment). Samples were taken 14 days into each experiment, i.e. after "deep transplants" had spent 14 days at 3 m, and "shallow transplants" had spent 14 days at 12 m.

March Experiment

The September and December experiments demonstrated that there were significant differences in the photosynthetic apparatus of shallow (3 m) and deep (10 m and 12 m) *E. radiata*. The March experiment indicates that this difference does not remain constant throughout the year. On day 1 of this experiment the deep transplants had significantly lower midday yield values ($p < 0.05$, one-way ANOVA), and these values did not recover by early evening (Figure 5.5), which is consistent with the previous experiments. However, by day 2

the deep transplants displayed a daily pattern of yield variation similar to the controls (Figure 5.5) and this subsequently remained similar (data not shown). The irradiance at a depth of 3 m during this period was over 8.5 times higher than that at 12 m (Table 2.1). Furthermore, the irradiance measured during this experiment were comparable to those measured during September and December. This result indicates that either by the end of summer the photoprotective and/or photosynthetic capacity of 12 m plants had become much more similar to that of the 3 m control plants, or that the acclimation response is much faster during March than in September or December (i.e. two days compared with two weeks).
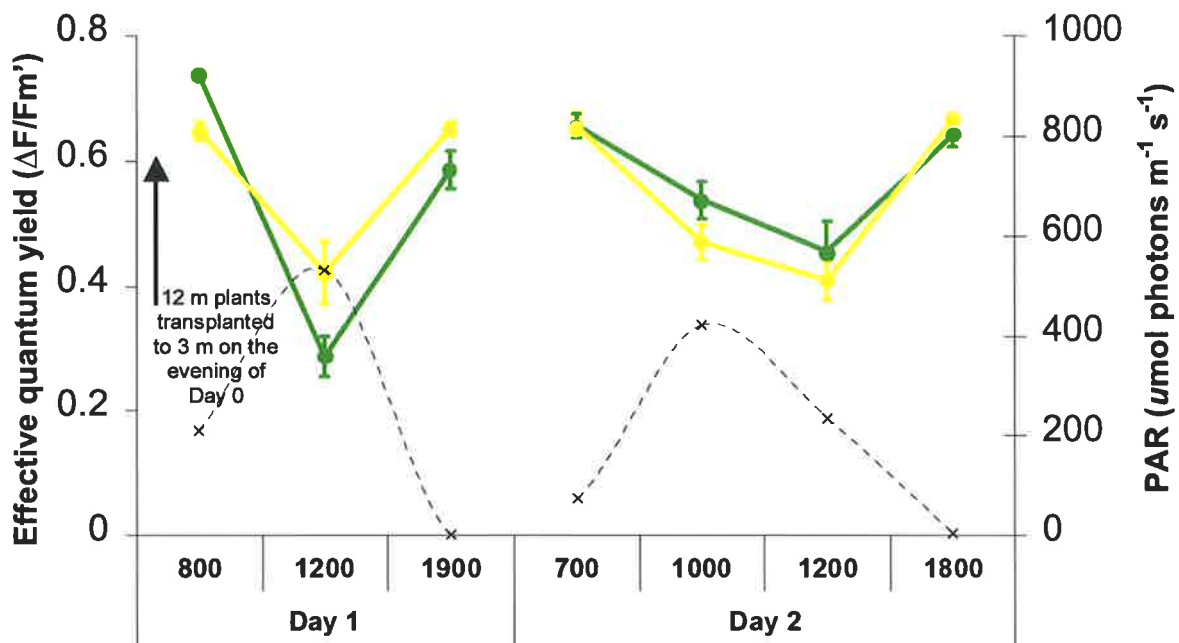
Figure 5.5 Photosynthetic efficiency (mean ± se) of *E. radiata* after transplantation of 10 m plants to 3 m (--- = deep transplant treatment; ▬ = shallow experimental controls; --- = PAR). Data shown are that measured on Days 1 & 2, i.e. the first two days after plants were transplanted to 3 m. The experiment was conducted in mid March 2000. PAR values are the mean of all values recorded in each measuring time.

"Shallow Transplant" Experiment (High to Low Light)

This shallow transplant experiment simulated a reduction in water quality of 13 days duration, by transplanting plants from a depth of 3 m to 12 m for 13 days and then returning them to 3

m. During the 13 days spent at a depth of 12 m the daily cycle of photosynthetic efficiency of the shallow transplants followed that of the deep control plants (see Figure 5.6a for data from the first two days). The levels of light at a depth of 12 m were low in comparison to that experienced at 3 m, and thus with little need for downregulation of PSII efficiency or evidence of effects of photodamage, yield values remained constantly high (>0.6). The exception to this was at 10 am on day 1, when the shallow transplants temporarily displayed a significant reduction in photosynthetic efficiency (Figure 5.6a).

During the 13 days spent at a depth of 12 m, shallow transplants altered their photosynthetic apparatus and moved into an acclimation state that was similar to plants which originated from a depth of 12 m. The daily cycle of photosynthetic efficiency displayed by the shallow transplants when they were returned to a depth of 3 m (Figure 5.6b) was very similar to that observed in the deep transplants when they where initially exposed to the 3 m depth environment (see Figure 5.1a, Figure 5.2 and Figure 5.3a). The significantly lower midday depressions ($p < 0.01$, one-way ANOVAs) and the lower recovery displayed during days 14-16 indicates that the shallow transplants were in a different acclimation state from that of the shallow control plants (Figure 5.6b).

The pigment results indicate, however, that the acclimation response was not completed in 14 days. After the 14 days at the 12 m depth the concentrations of photosynthetic pigments in the shallow transplants were not significantly different from those of the shallow control plants (Figure 5.4). The levels of chlorophyll a and fucoxanthin did increase slightly, which is consistent with the typical acclimation response to lowered irradiance, however chlorophyll c concentrations were actually lower in the transplants. These results are consistent with the deep transplant experiments which suggest that acclimation in the pigment suite occurs over a time scale longer than 2 weeks.

The electron transport rate of the shallow transplants was lower than the controls during the first two weeks as they were exposed to lower photon flux densities. Upon return to the 3 m depth ETR remained lower in the transplants (Table 5.1). The integrated daily ETR rates of the shallow transplants during the period of low light were 29-45% (on days 1 & 2) of the rates calculated for the shallow controls. On day 14, when the transplants had returned to the high light environment the daily integrated ETR rate was only 51% of the rate for the control.
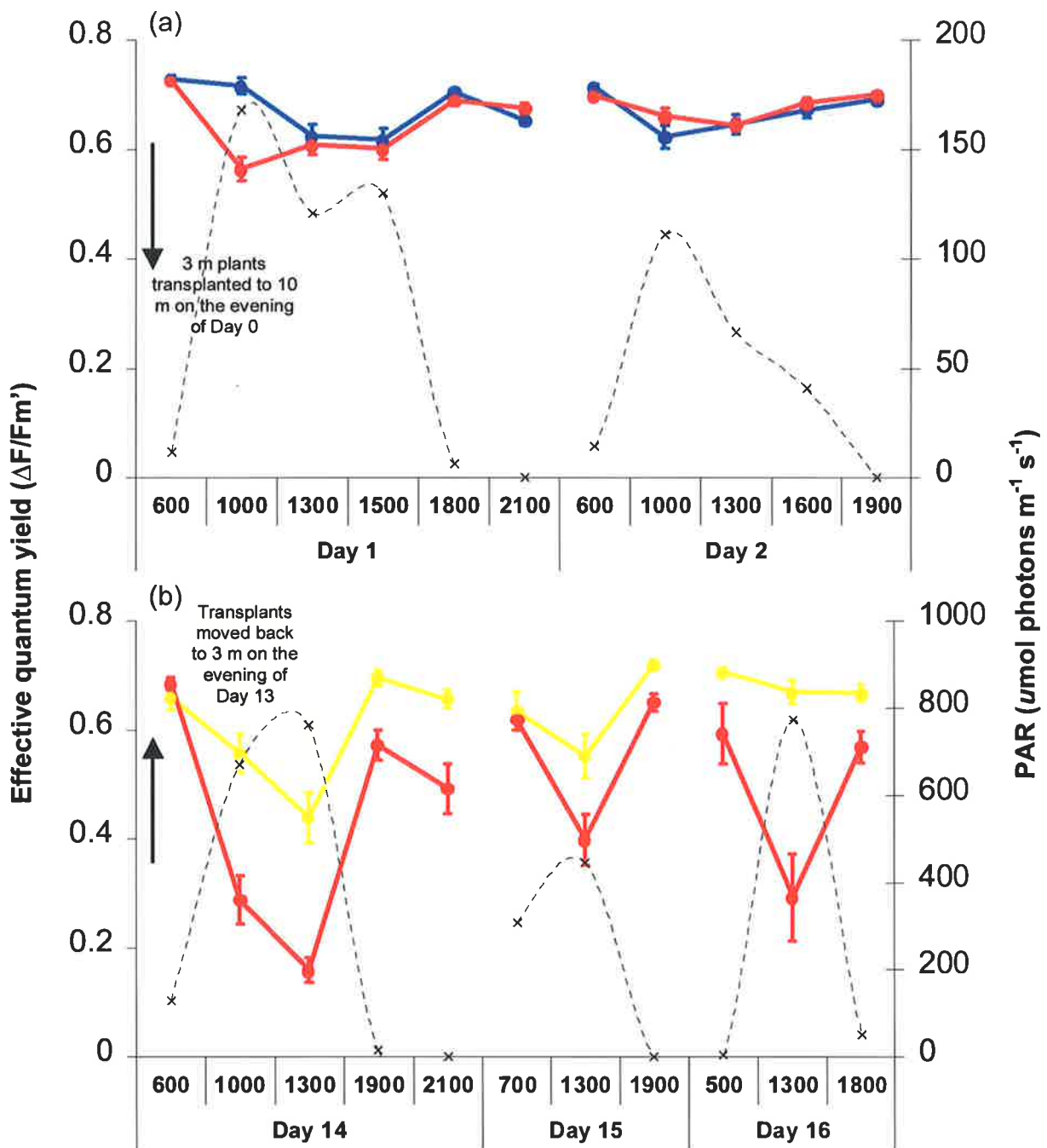
Figure 5.6 Photosynthetic efficiency (mean ± se) of *E. radiata* after transplantation of 3 m plants to a depth of 12 m for 13 days (--- = shallow transplant treatment; — = shallow experimental controls; -- = deep experimental controls; -- = PAR). Data shown are (a) that measured at 12 m on Days 1 & 2, i.e. the first two days after plants were transplanted to 12 m and (b) that measured at 3 m on Days 14 to 16 i.e. the three days following relocation back to 3 m. Upon return to a depth of 3 m the transplants showed a significantly greater degree of photoinihition when compared to controls. The experiment was conducted in early December 1999. PAR values are the mean of all values recorded in each measuring time.

Table 5.1 Electron transport rates (ETR) measured during the December shallow transplant experiment.

Day	Time	Shallow Control		Shallow Transplants	
		PAR	ETR	PAR	ETR
1	6:00	75	24	8	3
1	10:00	428	80	111	29
1	13:00	328	53	80	22
1	15:00	274	46	86	24
1	18:00	1	0.3	4	1
2	6:00	87	26	9	3
2	10:00	584	113	73	22
2	13:00	256	64	44	13
2	16:00	23	7	27	8
7	6:00	77	24	9	3
7	10:00	309	76	48	14
7	13:00	148	41	53	15
7	15:00	115	32	50	15
7	18:00	8	2	4	1
14	6:00	85	26	85	27
14	10:00	444	114	444	59
14	13:00	503	101	503	37
14	19:00	10	3	10	3

Discussion

Deep Transplant Experiments

These experiments demonstrated that in both September and December the acclimation state of low light *E. radiata* was different from high light *E. radiata*. After a period of approximately 10 days the switch between states was significant and the photoprotective and/or photosynthetic capcity had become more similar to the shallow controls. In March both groups of plants were either in the same acclimation state or the acclimation response occurred much faster at that time.

The daily cycle of effective quantum yield displayed by *E. radiata* reflected changes in PAR levels and differences in the state of the photosynthetic apparatus. The characteristic midday depression and recovery is similar to many other studies of macroalgal photosynthesis (e.g. Henley *et al.* 1991a, Hanelt 1992, Hanelt *et al.* 1992, Henley *et al.* 1992, Hanelt *et al.* 1993, Hanelt and Nultsch 1995, Franklin *et al.* 1996, Häder *et al.* 1997, Magnusson 1997, Sagert *et al.* 1997, Häder *et al.* 1998, Yakovleva and Titlyanov 2001). Following transplantation, however, the deep transplants displayed significantly lower midday depressions and incomplete recovery relative to the shallow control plants, which suggests a higher level of photodamage, i.e.

chronic photoinhibition. Chronic photoinhibition results when the rate of photodamage exceeds the rate of repair, and is more likely to occur in the low light acclimated plants, as they typically have a lower capacity for utilizing and dissipating excess energy (Henley *et al.* 1991b, Franklin *et al.* 1992, Hanelt 1992, Franklin *et al.* 1996, Hanelt *et al.* 1997a, Sagert *et al.* 1997, Hanelt 1998, Rodrigues *et al.* 2000)). The high light acclimated *E. radiata* (from a depth of 3 m) would be expected to have a higher concentration of photoprotective pigments (i.e. xanthophylls) and a higher capacity for utilization of absorbed photons (Demmig-Adams and Adams 1992). This would lead to the observed midday depression in effective quantum yield (a downregulation) but reduce the amount of damage to the photosystems, thus yield values recover quickly in the lower PAR of early evening (Huppertz *et al.* 1990, Hanelt *et al.* 1997a, Hanelt *et al.* 1997b, Schofield *et al.* 1998).

The deep transplants originate from a depth which experiences average maximum irradiance of only 25% of that to which they were exposed when transplanted to a depth of 3 m (Table 2.1). On the first two days after transplantation the irradiance measured during the midday period were 3-5 times that which they were exposed to (on average) at a depth of 10 m. The deep transplants were clearly in a different acclimation state and were not able to effectively utilize and/or dissipate the increased flux of photons, as evidenced by the significant and prolonged photoinhibition they experienced when first exposed to the higher irradiance.

Shallow Transplant Experiment

This experiment indicated that *E. radiata* acclimated to low light conditions during the 13 day reduction in irradiance. During period the shallow transplants were at 12 m they displayed the same daily yield cycle as the deep controls (12 m plants). When returned to the high light conditions this acclimation state appeared to result in a level of photodamage that was comparable to the deep transplants.

The shallow transplants were in a different acclimation state by the end of the 13 day reduction in irradiance. The lack of response of photosynthetic pigments indicates that this state was not the same as the deep controls, i.e. that the acclimation response was not completed. The levels of chlorophyll *a*, chlorophyll *a* and fucoxanthin did not differ significantly from the controls. This suggests that the acclimation response requires longer than two weeks to be completed. This result contrasts with several previous studies which have documented increased levels of photosynthetic pigments in algae growing in low irradiance conditions for shorter periods (e.g. Beardall and Morris 1976, Ramus *et al.* 1976a

Ramus *et al.* 1976b, Ramus *et al.* 1977, Henley and Ramus 1989c, Henley and Ramus 1989a, Iglesias Prieto and Trench 1994, Sagert and Schubert 2000).

During the 13 day period of irradiance reduction the integrated daily electron transport rate for shallow transplants was only 29-45% of that calculated for the shallow controls. Whilst the ETR rates are probably not accurate in a quantitative sense, mainly due to the crude estimation of the absorption factor, they are still a strong indication of the significant potential cost to production of a reduction in water quality (and thus irradiance). Furthermore, upon return to the high irradiance environment the integrated daily ETR rate of the shallow controls was still only 51% of the shallow controls (on day 14). This results from the much larger midday depression and the incomplete afternoon recovery in yield values in the shallow transplant group, and is a reflection of the change in acclimation state which occurred during the 13 days of irradiance reduction.

The net 24 hour productivity rates, described in Chapter 3, indicate that primary productivity at 12 m during December is only 17% of that at 3 m, which is lower than the 29-45% reported here for the ETR rates. This discrepancy may be explained by a photoinhibitory reduction in oxygen evolution rates, caused by the measurement of 12 m plants at 3 m (see Chapter 3). The results of the deep transplant experiments support this theory, as they indicated that 12 m plants will experience a higher degree of chronic photoinhibition than 3 m plants (when both are measured at 3 m). Also, the fluorometry measurements only indicate differences in activity around PSII, whereas the productivity measurements integrated carbon metabolism and respiratory processes (Hanelt *et al.* 1997a), which may account for this discrepancy.

Conclusions

This work has demonstrated that the acclimation state of shallow and deep *E. radiata* is different, at least during the spring and early summer months. The time scale required to switch between these states is longer than two weeks, although significant changes occur within a two week period. This knowledge is important in order to gain a better understanding of the impacts of changes in coastal water quality. The results of this work indicated that shallow *E. radiata* began to acclimate within two weeks to a simulated reduction in water quality (i.e. in irradiance). Once returned to high irradiance conditions these individuals appeared to be subjected to a higher level of photodamage. A different situation was observed

in late summer indicating that either the acclimation state of shallow and deep plants is more similar during that time, or that the acclimation response occurs much faster at that time.

The rate of response to both lowered and increased irradiance was similar. This contrasts with the work of Henley and Ramus (1989c) who found that the acclimation response (changes in *Pm*) was much faster when irradiance were increased in comparison to when they were decreased. They suggested that this is because the potential for increased carbon assimilation rates during short periods of high irradiance overrides the benefit of acclimating to maximise assimilation during low irradiance conditions. The long acclimation response time in comparison to other species (Falkowski 1984, Henley and Ramus 1989c) may indicate that a similar strategy exists in *E. radiata*. The cost of maintaining an acclimation state appropriate for high irradiance conditions, and the associated ability to maximize absorption during temporary periods of high light (e.g. when periods of high water quality coincide with solar noon), may only be inefficient after spending several days in a lowered irradiance environment. Perhaps when the cost of maintaining this state begins to involve synthesis rather than maintenance of light harvesting components it may then exceed any benefit. During periods of high resource availability, such as in autumn when levels of storage carbohydrates are elevated (Stewart *et al.* 1961), the influence of the cost of acclimating (e.g. synthesis of xanthophylls) on the time scale of the acclimation response may not be so important, and would explain a rapid acclimation response time during March in comparison to September and December.

The ecological benefit derived by acclimating to the growth irradiance is clearly demonstrated in this study by the higher integrated ETR rates of shallow plants in comparison with the low light acclimated transplants. The lowered ETR rates in the transplants is related to the characteristics of their acclimation state, as the inability to adequately protect the photosynthetic apparatus led to chronic photoinhibition. However, these results also emphasise the importance of an appropriate time scale of acclimation response. The shallow transplants acclimated to lowered irradiance conditions, and this presumably involved some energy cost in terms of biosynthesis which had to be met whilst the rates of production were already lowered in comparison to previous high light levels. After several days in a lowered irradiance environment the benefit of maximizing light utilization apparently exceeded the cost of this acclimation. However, when irradiance was then increased the algae once again underwent an alteration in the acclimation state. In addition, a higher level of photodamage

was experienced during the first few days after the return to high light, which is another cost of this scenario.

Under natural conditions a two-week time scale probably provides *E. radiata* with the best compromise between the cost of acclimating and the benefit derived from an appropriate acclimation response. However, in the experimental situation constructed here, the response time of *E. radiata* meant that a simulated reduction in water quality was probably very costly. Further work assessing the effect of a similar situation on other growth and production parameters is needed before an accurate estimation of the impact can be known. This study has indicated however, that if water quality reductions are kept to less than a week, such as the case for a typical spring storm water influx, then the cost to the algae of acclimating will be kept to a minimum. More prolonged reductions in water quality, such as those caused by channel clearances and marina construction (e.g. weeks to months), are likely to result in significant losses of production.

Chapter 6 : Synthesis

Rocky reefs dominated by *Ecklonia radiata* forests are an important component of the southern Australian nearshore marine environment. Carbon assimilated by *E. radiata* provides an energy source for higher trophic levels (Edmonds and Francesconi 1981, Robertson and Lenanton 1984, Kennelly 1991, Kennelly and Underwood 1992, Kennelly and Underwood 1993) and is released into the system in both particulate and dissolved forms. Previous studies of this species have focussed on tissue production (Kirkman 1981, Mann and Kirkman 1981, Kirkman 1984, Novaczek 1984a, Larkum 1986, Hatcher *et al.* 1987, Kirkman 1989) but this has arguably resulted in an underestimation of the rate of primary production, as neither the amount of carbon released as exudate nor the carbon utilised for respiratory processes is accounted for by such methods (Larkum 1986).In order to comprehend the ecological role of *E. radiata* it is necessary to understand the seasonal patterns in photosynthesis as this process underpins primary production. A comparison of carbon assimilation rates with patterns of tissue production provides a more accurate view of the annual carbon contribution of this species.

In situ oxygen evolution measurements demonstrate that the photosynthetic apparatus of *E. radiata* has distinct changes throughout the year (Chapter 2). This acclimation is primarily related to seasonal variation in the light and temperature regime and enables *E. radiata* to maintain a high level of productivity throughout the year (Chapter 3).

In winter, *E. radiata* plants acclimate to low light levels. The efficiency of photon use at low irradiance (α) is 1.5 to 2 times higher than in summer and the irradiance required for sub-saturation of photosynthesis (Ik) decreases to around 80% of the summer values while the irradiance required for photosynthetic compensation (Ic) decreases to 45% of the summer Ic values (Chapter 2). In addition, the maximum potential rate of photosynthesis (Pm) increases to 1.2 to 1.8 times the summer values which further improves the ability of *E. radiata* to maximise use of all available light (Chapter 2). In summer, with increased irradiance, there is a compromise between maximising the amount of energy available for photochemistry and avoiding the absorption of damaging quantities of photons, which results in a decrease in α and an increase in Ik (Chapter 2).

E. radiata also shows differences in acclimation state along the depth profile (Chapter 2 and Chapter 5). Individuals at deeper depths display characteristics of low light acclimated algae (higher α and lower Ik and Ic) and when transferred to high light environments they are more

susceptible to chronic photoinhibition (Chapter 3 and Chapter 5) as a result of a reduced ability to avoid and repair photodamage.

Changes in pigment concentration and in photokinetic parameters (Chapter 2) indicate that the seasonal photoacclimation strategy of *E. radiata* involves changes in both the number of reaction centres and in the size of the functional absorption cross-section of PSII (*sensu* Falkowski and LaRoche 1991). A response involving an adjustment of reaction centre density is supported by the negative correlation of chlorophyll *a* concentration with irradiance throughout the year, although changes in *Ik* imply that the cross-sectional area is also adjusted (Chapter 2). A combination of responses is also supported by experiments investigating the acclimation of *E. radiata* over short time periods (Chapter 5). During the switch between high and low light acclimation states the changes in photosynthetic pigment concentration are consistent with changes in the number of reaction centres. Changes in photoprotective ability are associated with the acclimation to changing irradiance, which is consistent with alterations in the size of the absorption cross-section.

The time scale of the acclimation response in *E. radiata* extends to more than 14 days (Chapter 5). When irradiance conditions fluctuate markedly on a time scale similar to that required for acclimation *E. radiata* is likely to repeatedly undergo costly acclimation responses. A long response time represents the best strategy to avoid wasting resources but to also respond to long term seasonal changes in the underwater environment.

The increased efficiency of photon absorption and utilisation in winter, when irradiance is low and day-length is shortened, has important ecological implications. It enables the alga to reach photosynthetic compensation for a longer period each day than would be possible given no acclimation and to increase the rate of carbon assimilation relative to the rate at the same irradiance in summer. This acclimation has significant consequences for the rate of daily productivity that are significant. Despite an up to five-fold drop in irradiance and the shorter day-lengths during winter, the level of productivity remains similar to summer recordings (Chapter 3), which contrasts with the seasonal declines in macroalgal productivity reported elsewhere (Hatcher *et al.* 1977, Drew 1983, Drew and Hastings 1992, Cheshire *et al.* 1996).

A comparison of the rates and patterns of productivity and growth (biomass accumulation) in *E. radiata* serves to demonstrate the need to measure both of these aspects of production in order to provide an accurate picture of the carbon flow for this species. Growth rates are highly seasonal in *E. radiata* (Kirkman 1984, Larkum 1986, Kirkman 1989, Chapter 4) and

probably reflect changes in a combination of environmental factors (e.g. nutrient status, temperature) and in the level of available assimilated and stored resources. Rates of growth are low in autumn (0.002 gdwt g^{-1}dwt d^{-1} at both 3 m and 10 m) and summer (0.007 gdwt g^{-1}dwt d^{-1} and 0.004 gdwt g^{-1}dwt d^{-1} at 3 m and 10 m respectively) and increase during spring (0.016 and 0.007 gdwt g^{-1}dwt d^{-1}) and winter (0.015 and 0.008 gdwt g^{-1}dwt d^{-1}). The proportion of carbon allocated to tissue production is generally only a fraction (4-41% at a depth of 3 m) of the amount assimilated through photosynthesis (Chapter 4). In summer and autumn the relative biomass accumulation rates are low while net assimilation rates remain high. This presumably results in an accumulation of stored carbon (i.e. laminaran and mannitol) which are utilised for growth and maintenance processes during times when the carbon demand from growth exceeds the assimilation rate. These stored resources are probably more important at deeper depths where winter carbon assimilation rates are insufficient to support growth (Chapter 4).

Annual Carbon Flow

Quantification of seasonal patterns of productivity and growth allows development of a schema which estimates the carbon flow through a mature *E. radiata* forest. This provides an overview of the processes by which carbon assimilated by *E. radiata* is released into the surrounding system i.e. the amount released as exudate (dissolved organic carbon) or as biomass (particulate organic carbon).

Calculations

An estimate of gross annual production per square metre of substrate was calculated from seasonal daily productivity rates[7] (see Table 3.1), average plant dry weights (Table 4.2) and density measurements (Appendix E) for 3 m and 10 m populations at West Island, South Australia (Table 6.1). The total amount of carbon used in respiratory processes was estimated in the same way. The portion of annual production which is diverted to biomass production was estimated from the average rates of growth (gdwt plant^{-1} d^{-1}) across the seasons (Chapter 4) and plant densities (Appendix E). This rate was converted to carbon units assuming that dry weight consists of 45% carbon (Drew and Hastings 1992).

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[7] Average annual gross productivity rates were calculated by firstly averaging the daily gross productivity rates (μmol O$_2$ g^{-1}dwt d^{-1}) for each season (i.e. the summer rate is the average of December and Feburary rates). The rate across the four seasons was then averaged to provide the average annual rate of gross daily productivity, which when multiplied by 365 gave an annual rate of gross producivity. These rates were then converted to carbon units asssuming a PQ of 1.0.

Table 6.1 Values used for the calculation of annual carbon flow through *E. radiata*.

	3 m	10 m
Density (plants m^{-2})	14.3	3.9
Thallus dwt (g)	63.75	137.38
Standing Biomass (gdwt m^{-2})	911	535
Average Gross Productivity (μmol O$_2$ g^{-1}dwt d^{-1})	1893.60	811.55
Average Respiration Rate (μmol O$_2$ g^{-1}dwt d^{-1})	523.77	419.04
Average BA (gdwt plant^{-1} d^{-1})	0.46	0.60

The work by Novaczek (1984a) on the phenology of *E. radiata* in New Zealand provides an estimate of the proportion of tissue production used for reproductive development. The figures used in this schema are 20% of annual tissue production at a depth of 3 m and 10% at a depth of 10 m, which are based on Novaczek's (1984a) estimates for populations at 7 m and at 15 m at Goat Island Bay. These differ from the 3 m and 10 m populations at West Island in a number of respects (e.g. density and morphology) but are roughly comparable in terms of irradiance environment. The summer I_{max} values in Novaczek's (1984a) study were 500 and 190 μmol photons m^{-2} s^{-1} respectively which compare with 700 and 170 μmol photons m^{-2} s^{-1} at West Island.

The assumption, made by Hatcher *et al.* (1977), that all the carbon diverted into storage is utilised within the same annual cycle was also assumed for these calculations. This enables the proportion of exuded carbon to be calculated by summing the proportions diverted to biomass, reproduction and respiration, and assuming that the amount of gross production left over is lost as exudates.

Schema of Carbon Flow in *Ecklonia radiata*

The results of the analysis of carbon flow through *E. radiata* at West Island population can be viewed as a generalised schema through an *E. radiata* forest (Figure 6.1). This schema enables an understanding of the quantities and form in which carbon is released into the surrounding waters. The main processes depicted in the schema are respiration, carbohydrate storage, vegetative and reproductive growth and exudation, all of which utilise the assimilated carbon pool. The demand for carbon by each of these processes is likely to vary seasonally. For example, this study has demonstrated that biomass accumulation rates are much higher in spring and winter and are probably associated with a depletion (remobilisation) of

carbohydrate reserves. Reproductive growth is also likely to vary in its demand for resources (*sensu* Novaczek 1984a). The presence of a well developed transport system in kelps (Schmitz 1981), means that the breakdown of tissue may result in a return to the carbon pool of some amount of withdrawn carbon. It is not known if this from of remobilisation exists in kelp, or if it is a significant factor in the overall carbon metabolism, but if *E. radiata* is able to withdraw nutrients and carbon from necrotic tissue it may contribute to the carbon pool at certain times of the year. The proportions of carbon indicated by this schema may therefore not be accurate at any one time of the year, and can only be viewed on an annual scale.

The schema indicated that the proportion of carbon used for tissue production by *E. radiata* (B_{3m} and B_{10m}) is low at only 11-16% of annual carbon assimilation and represents the majority of the carbon made available to the consumer population as particulate matter. In addition to a constant stream of detrital matter this particulate carbon is released when whole plants are dislodged from the substrate. The West Island population releases biomass as particulate carbon (POC) at a rate of 863 $gC\ m^{-2}\ y^{-1}$ at 3 m and 307 $gC\ m^{-2}\ y^{-1}$ at 10 m, and as dissolved organic carbon at a rate of 4391 $gC\ m^{-2}\ y^{-1}$ at 3 m and 537 $gC\ m^{-2}\ y^{-1}$ at 10 m (Table 6.2). Breakdown of reproductive tissue (RS_{3m} and RS_{10m}), which is produced at 216 $gC\ m^{-2}\ y^{-1}$ at a depth of 3 m and 77 $gC\ m^{-2}\ y^{-1}$ at 10 m, will also contribute to POC release, as only a fractional amount of this tissue is actually reproductive cells that are recycled within the forest.

The rates of POC release (Table 6.2) were comparable with other *E. radiata* populations, which have annual tissue production rates in the range of 675-2700 $gC\ m^{-2}\ y^{-1}$ across a range of depths (see Table 4.4). The particulate contribution is also similar to the annual POC production by *Laminaria pallida* beds in South Africa of 773 $gC\ m^{-2}\ y^{-1}$ (Branch and Griffiths 1988). Jackson (1987) modelled the harvest yield of *Macrocystis pyrifera* in North America and from a gross production of 1567 $gC\ m^{-2}\ y^{-1}$ it was determined that tissue production was 537 $gC\ m^{-2}\ y^{-1}$. The contribution of POC by a square metre of southern Australian *E. radiata* forest is therefore equal to that of kelp forests at similar latitudes elsewhere in the world.

Table 6.2 Gross annual production by *E. radiata* and the amount of carbon diverted to respiration, reproduction, biomass and exudation.

$gC\ m^{-2}\ y^{-1}$	3m	10m
Carbon Pool	7561	1904
Respired Carbon	2091	983
Reproductive Tissue	216	77
Biomass	863	307
DOC	4391	537
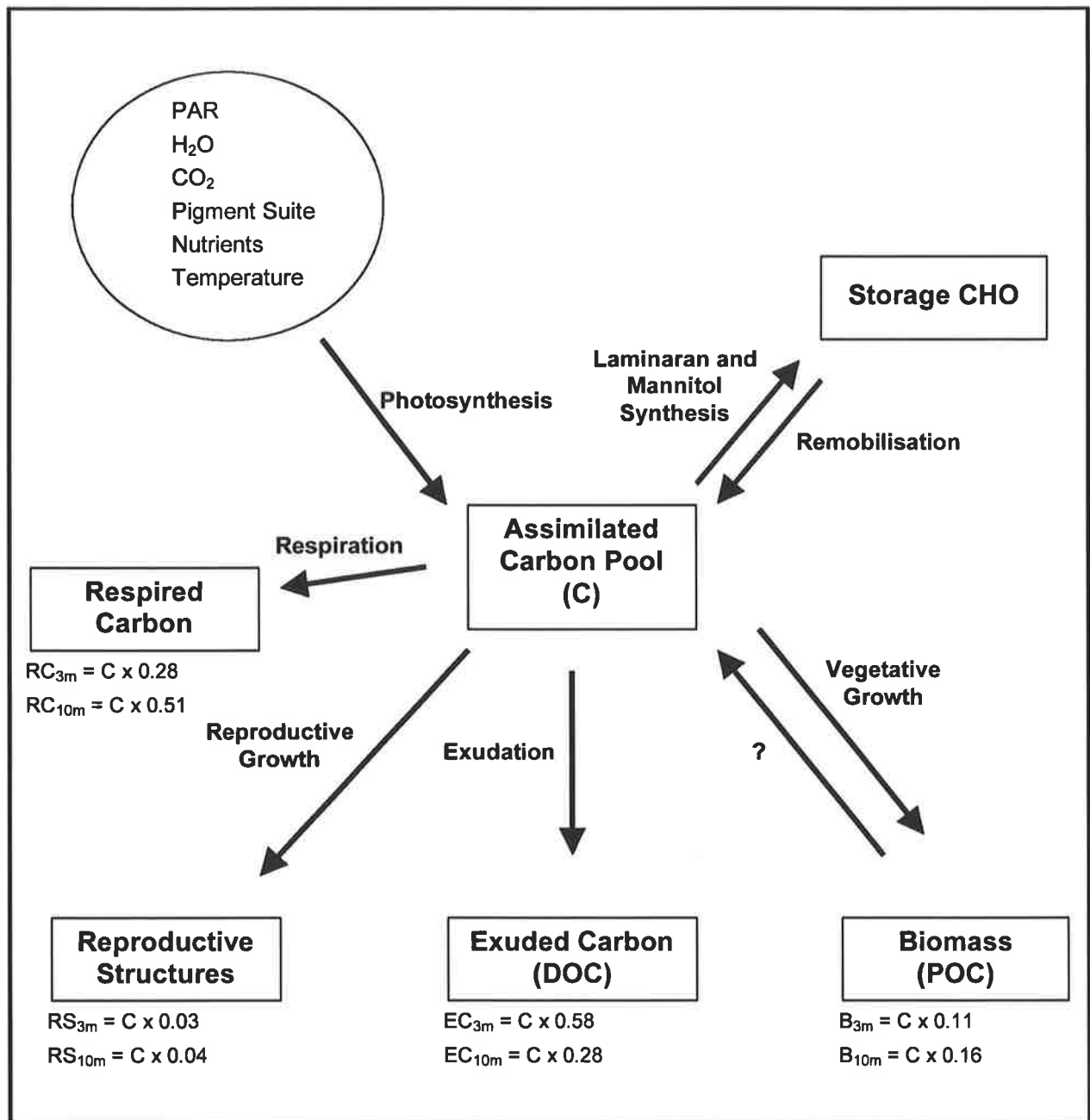
Figure 6.1 Schema of the annual carbon flow through a mature *Ecklonia radiata* population.

By contrast, rates of exudation by *E. radiata* are high at 28-58% of gross annual production (EC_{3m} and EC_{10m}). Previous estimates of exudation in brown algae range from 1-40% of net annual production (Khailov and Burlakova 1969, Sieburth 1969, Brylinsky 1977, Hatcher *et al.* 1977). Branch and Griffiths (1988) estimated that South African *Laminaria pallida* beds

produced only 328 gC m^{-2} y^{-1} of DOC which compares with the 4391-537 gC m^{-2} y^{-1} by *E. radiata* at West Island. Jackson (1987) did not include a parameter for exudation in his model of *M. pyrifera* production, as rates have been found to be minimal in that species. The role of exudates in many species is not known (Lobban and Harrison 1994), however, the composition of exudate in *E. radiata* includes a large component of phlorotannins which are known to have a chemical defence role (Steinberg 1989).

The higher proportion of DOC released at 3 m compared to 10 m and visa versa for the respired carbon suggests that either the role of the exudates (e.g. as protection against herbivores) may be more significant at shallower depths, or simply, that the 10 m population needs to divert a higher proportion of assimilated carbon in order to meet respiratory demands. Regardless of the role of exudation, the amount of DOC released by *E. radiata* on an annual basis is high (0.5-4.3 kgC m^{-2} y^{-1}) and must represent an important energy source for marine consumers.

Carbon release by *E. radiata* differs from other co-occurring canopy dominants. Hotchkiss (1999) found that 87-91% of total biomass was diverted in reproductive biomass in the *Cystophora* species studied in locations close to West Island. This compares with only 3-4% of gross production in *E. radiata*. This finding is consistent with the vastly different reproductive strategies of kelp and fucoids (Womersley 1987). More work is needed before comparisons can be made between the allocation to other processes (i.e. growth and exudation).

The dominance of *E. radiata* on southern Australian rocky reefs (Shepherd and Womersley 1970, Shepherd and Womersley 1976, Kirkman 1981, Kennelly 1983, Larkum 1986, Kennelly 1987b, Collings 1996) means that it plays an important role in terms of providing habitat, shelter and substrate for a range of marine organisms. This study has quantified another aspect of the ecological role of *E. radiata*, and has demonstrated that on an annual basis the contribution of energy to consumers in the nearshore marine environment is profound.

Future Directions

There is considerable potential for future research in this area. A preliminary study comparing *in situ* photosynthetic response of mature and juvenile *E. radiata* was included in this thesis, but a more comprehensive study is necessary in order to validate the extrapolation of juvenile rates of productivity to adults. Incorporation of seasonal changes in storage carbohydrates would also further improve our understanding of the growth strategy of *E. radiata* and thus

the annual carbon flow. Similarly, a study of the reproductive phenology of southern Australian *E. radiata* is necessary in order to understand seasonal variations in carbon allocation. The primary importance of irradiance regimes on seasonal changes in photosynthesis was highlighted by this study but the role of nutrient and temperature fluctuations are also likely to be important and need to be investigated. There is also considerable scope for research on the ecological impact of water quality changes. This work has indicated that considerable changes in acclimation state occur in a two week period but the time scale required for a completed acclimation response in *E. radiata* is unknown. Controlled laboratory experiments investigating the kinetics of the acclimation response to lowered and increased irradiance could be combined with field experiments documenting the impact on carbon assimilation to provide an understanding of the potential impact of human activities on macroalgal production.

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Appendix A

Respirometry data (photokinetic data (mean and standard error), sample sizes, r² values, wet weight:dry weight ratio) for each depth and trip (year;month).

Trip	Data used	Depth	n	Pm_{gross}	se	Pm_{net}	se	Ik	se	Ic	se	Rd	se	α	se	r^2	se	ww:dw	se
9810	ALLDAY	3	6	175.15	11.55	160.27	11.26	146.41	5.11	13.12	1.20	-14.89	1.47	1.20	0.08	0.98	0.01	6.12	0.47
9810	AM	3	6	177.16	11.50	162.34	11.31	152.33	2.82	13.42	1.19	-14.82	1.45	1.17	0.08	0.97	0.01	6.12	0.47
9902	ALLDAY	3	9	227.66	40.61	196.00	32.95	160.90	12.20	22.29	3.69	-31.66	8.07	1.41	0.20	0.98	0.01	5.20	0.17
9902	AM	3	8	246.45	42.87	210.84	34.95	138.73	7.42	21.38	3.08	-35.62	8.42	1.72	0.22	0.98	0.01	5.18	0.19
9905	ALLDAY	3	14	266.61	17.05	250.91	15.92	96.69	6.13	6.07	0.84	-15.70	2.09	2.90	0.23	0.97	0.01	7.02	0.32
9905	AM	3	14	266.61	17.05	250.91	15.92	96.69	6.13	6.07	0.84	-15.70	2.09	2.90	0.23	0.97	0.01	7.02	0.32
9909	ALLDAY	3	11	236.97	15.50	221.17	15.23	127.90	9.84	8.74	0.59	-15.80	1.25	1.90	0.13	0.99	0.00	5.94	0.20
9909	AM	3	11	244.29	16.20	228.21	15.97	126.33	9.39	8.55	0.60	-16.09	1.28	1.99	0.14	0.99	0.00	5.94	0.20
9912	ALLDAY	3	9	179.49	18.30	156.63	16.61	129.26	8.36	17.98	1.90	-22.86	2.44	1.44	0.17	0.96	0.02	5.73	0.14
9912	AM	3	9	189.31	18.28	166.38	16.58	116.68	6.91	15.49	1.61	-22.93	2.41	1.63	0.15	0.99	0.00	5.73	0.14
0003	ALLDAY	3	14	191.66	8.49	169.52	8.47	125.21	8.56	15.72	1.83	-22.14	2.22	1.61	0.10	0.99	0.00	5.59	0.08
0003	AM	3	14	191.53	7.27	169.39	7.22	123.55	8.47	15.51	1.81	-22.14	2.23	1.64	0.12	0.99	0.00	5.59	0.08
0006	ALLDAY	3	7	312.25	29.67	283.52	28.54	178.88	12.36	17.99	1.99	-28.73	2.31	1.79	0.21	0.94	0.02	6.51	0.24
0006	AM	3	7	278.48	25.26	253.31	24.97	110.57	10.19	10.70	1.25	-25.17	1.85	2.62	0.30	0.99	0.00	6.51	0.24
9810	ALLDAY	5	8	162.69	17.05	144.73	15.85	123.30	10.60	14.38	1.08	-17.95	1.91	1.41	0.20	0.98	0.01	5.64	0.24
9810	AM	5	8	164.72	17.07	147.29	16.01	121.67	8.23	14.02	1.31	-17.43	1.90	1.45	0.24	0.98	0.00	5.64	0.24
9902	ALLDAY	5	9	158.50	20.77	136.31	18.37	130.51	14.26	21.81	4.07	-22.19	2.97	1.36	0.22	0.94	0.01	5.17	0.37
9902	AM	5	8	177.82	27.37	150.41	21.30	111.42	12.50	18.16	3.17	-27.42	7.47	1.75	0.31	0.95	0.02	5.21	0.41
9905	ALLDAY	5	10	377.03	43.88	361.26	41.96	91.08	5.71	3.85	0.42	-15.78	2.46	4.14	0.43	0.98	0.01	7.15	0.49
9905	AM	5	10	377.03	43.88	361.26	41.96	91.08	5.71	3.86	0.42	-15.78	2.46	4.14	0.43	0.98	0.01	7.15	0.49
9909	ALLDAY	5	7	192.29	15.83	172.74	12.78	114.18	15.18	11.26	2.32	-19.55	4.26	1.90	0.32	0.94	0.02	6.03	0.15
9909	AM	5	7	196.83	14.53	178.36	11.91	113.35	14.88	10.39	2.27	-18.47	3.95	2.01	0.42	0.93	0.03	6.03	0.15
9909	ALLDAY	7	8	168.90	13.92	154.09	12.88	130.94	14.03	12.25	1.78	-14.81	1.88	1.41	0.19	0.96	0.02	6.11	0.14
9909	AM	7	7	185.07	16.20	170.07	15.60	127.54	14.54	10.56	1.19	-15.00	2.01	1.56	0.21	0.97	0.01	6.15	0.15

Appendix A: continued.

Trip	Data used	Depth	n	Pm_{gross}	se	Pm_{net}	se	Ik	se	Ic	se	Rd	se	α	se	r^2	se	ww:dw	se
9810	ALLDAY	10	9	132.79	11.39	119.99	10.98	138.81	11.49	14.68	1.64	-12.80	0.82	1.02	0.14	0.98	0.00	6.24	0.94
9810	AM	10	7	132.70	14.83	119.78	14.26	142.17	15.27	15.41	2.08	-12.91	0.89	1.04	0.22	0.98	0.01	6.39	1.22
9902	ALLDAY	10	5	131.90	21.95	117.76	20.83	107.25	9.92	12.53	4.10	-14.13	4.85	1.26	0.25	0.92	0.02	5.04	0.10
9902	AM	10	5	160.81	26.02	145.56	23.15	101.43	7.20	10.12	2.34	-15.25	4.70	1.60	0.27	0.90	0.03	5.04	0.10
9905	ALLDAY	10	8	348.13	29.29	328.07	27.48	80.51	5.69	4.83	0.93	-20.05	3.53	4.33	0.24	0.99	0.00	6.17	0.23
9905	AM	10	8	348.13	29.29	328.07	27.48	80.51	5.69	4.83	0.93	-20.05	3.53	4.33	0.24	0.99	0.00	6.17	0.23
9909	ALLDAY	10	7	140.67	8.14	125.41	8.47	137.44	20.42	16.83	4.09	-15.25	1.78	1.18	0.18	0.94	0.02	6.19	0.14
9909	AM	10	7	149.75	11.86	134.62	12.25	128.61	25.50	13.62	2.39	-15.13	1.42	1.36	0.21	0.95	0.01	6.19	0.14
9912	ALLDAY	10	10	186.12	19.99	166.89	18.86	130.08	5.81	15.05	1.27	-19.24	1.33	1.46	0.17	0.99	0.00	5.10	0.20
9912	AM	10	10	183.52	20.41	163.78	19.28	112.47	6.30	13.63	1.23	-19.74	1.35	1.67	0.20	0.99	0.00	5.10	0.20
0003	ALLDAY	10	6	186.48	25.58	171.33	22.45	149.12	23.94	11.24	1.88	-15.15	3.97	1.52	0.43	0.96	0.01	4.80	0.62
0003	AM	10	6	190.57	29.62	172.19	25.14	104.88	16.77	9.35	1.05	-18.38	4.96	2.15	0.59	0.99	0.00	4.80	0.62
0006	ALLDAY	10	1	349.47		326.50		246.64		16.76		-22.96		1.42		0.82		6.60	
0006	AM	10	1	278.58		258.75		87.39		6.46		-19.84		3.19		0.98		6.60	
9909	ALLDAY	12	7	152.53	16.09	138.33	16.65	104.85	15.33	10.07	1.42	-14.20	1.23	1.66	0.27	0.96	0.03	6.09	0.07
9909	AM	12	7	164.65	15.93	150.33	16.28	107.46	17.63	9.27	1.13	-14.32	1.23	1.85	0.40	0.98	0.01	6.09	0.07
9912	ALLDAY	12	10	96.61	7.29	82.74	6.51	109.44	11.66	17.47	2.88	-13.86	1.29	1.01	0.16	0.93	0.02	5.50	0.15
9912	AM	12	10	108.30	6.88	93.53	6.04	94.63	9.91	14.46	2.59	-14.77	1.40	1.21	0.09	0.98	0.01	5.50	0.15
0003	ALLDAY	12	10	181.96	11.65	164.89	11.15	113.92	10.42	11.10	1.03	-17.07	1.34	1.67	0.12	0.97	0.01	5.51	0.12
0003	AM	12	10	187.44	10.81	170.27	10.32	97.26	7.56	9.27	0.75	-17.17	1.23	1.97	0.09	0.98	0.00	5.51	0.13
0006	ALLDAY	12	4	319.30	26.09	297.90	26.28	99.58	9.82	7.03	1.84	-21.40	4.95	3.26	0.32	0.90	0.03	6.97	0.05
0006	AM	12	5	317.60	30.78	306.15	32.20	89.07	14.81	3.32	0.84	-11.45	2.64	3.86	0.61	0.97	0.02	6.98	0.04

Appendix B

Simultaneous recording of PAR (μmol photons.m^{-2}.sec^{-1}) above the canopy of *E.radaita* and below the canopy (approx. 10 cm off the substrate). Measurements were made at the 3 m site in Abalone Cove throughout May 1999. Data presented here is typical of all days, a) recorded on the 2nd of May and b) on the 6th of May. Measurements were made every 5 sec (using LiCor underwater quantum sensors) and the average of each minute is presented.
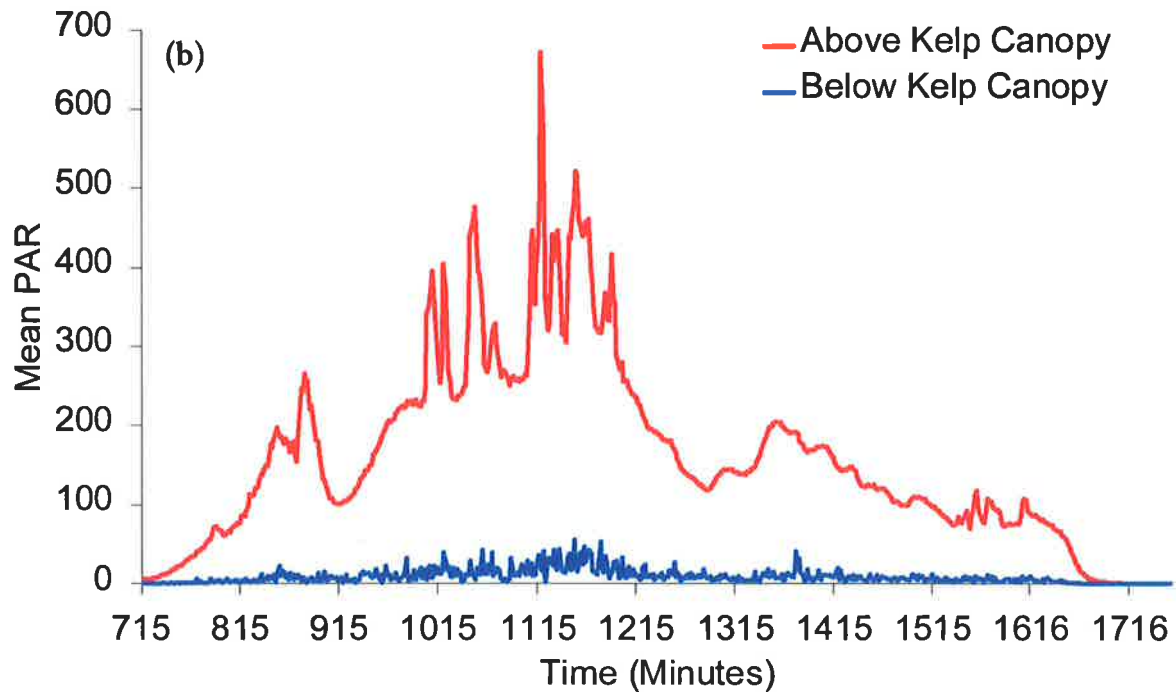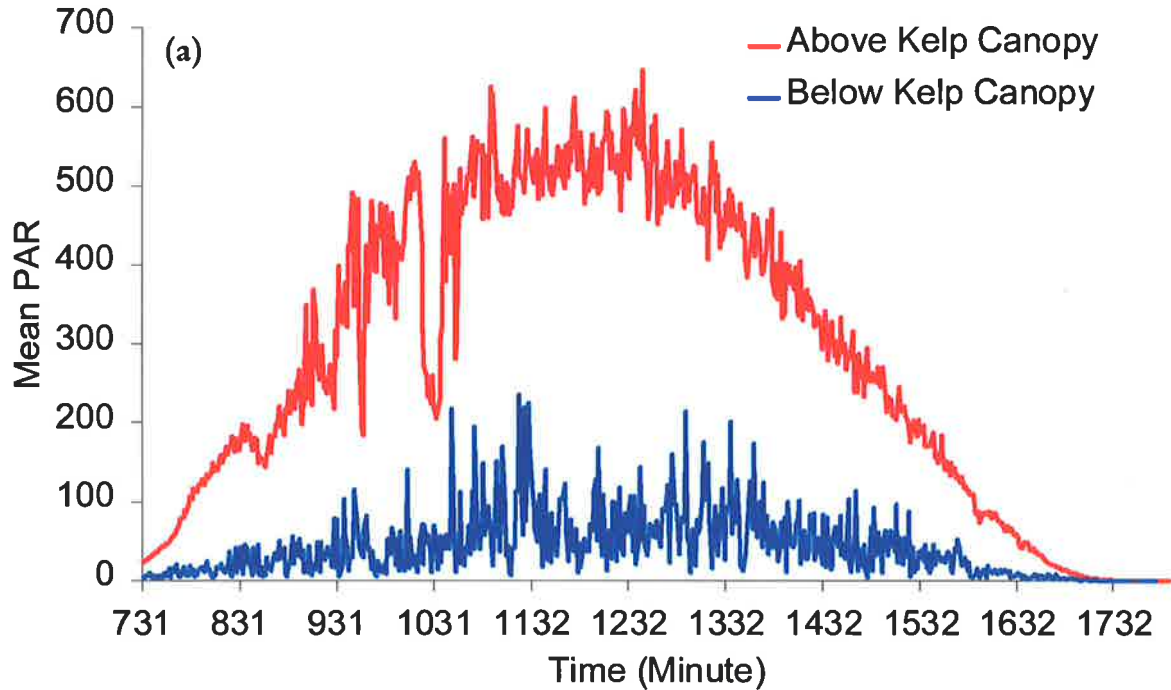
Appendix C

Total monthly precipitation (mm) recorded by the Buerau of Meterology, at Victor Harbour 1 km NE of West Island. Filled symbols indicate months in which photosynthesis-irradiance data was collected and symbols with red outlines indicate months in which biomass accumulation data was also collected.
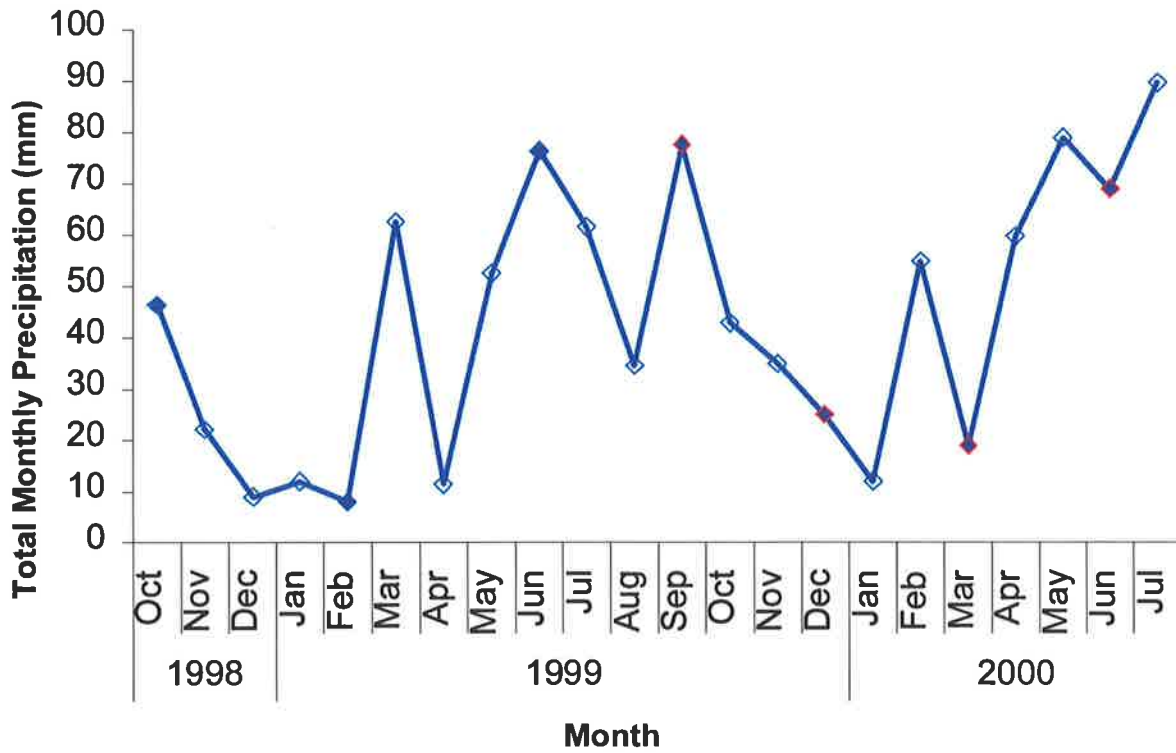
Appendix D

Light and temperature averages (*se*) recorded in Abalone Cove, West Island. Data courtesy of A.Cheshire ('92- '94) and T.Kildea ('96-'98).

Month	n	Daylength	I_{max}	Max Temp	Min Temp
Jan '94	5	-	646.20 (*38.51*)	20.67 (*0.37*)	19.30 (*0.04*)
Feb '94	1	-	390.00	20.89	20.00
Feb '97	1	13.41 (*0.09*)	605.00	22.50	20.00
Feb '98	4	13.29 (*0.00*)	444.56 (*87.15*)	20.79 (*0.08*)	19.99 (*0.10*)
Mar '93	5	-	485.40 (*28.99*)	19.54 (*0.11*)	18.97 (*0.08*)
Mar '94	3	-	356.67 (*53.99*)	20.42 (*0.04*)	19.63 (*0.03*)
May '93	3	-	131.00 (*15.04*)	17.93 (*0.10*)	17.54 (*0.07*)
May '96	1	10.08	172.67	16.57	16.13
May '97	3	10.09 (*0.07*)	137.53 (*61.85*)	15.84 (*0.09*)	15.52 (*0.06*)
Jun '93	5	-	168.40 (*14.45*)	15.38 (*0.06*)	15.04 (*0.04*)
Jun '98	3	9.67	189.10 (*42.59*)	14.07 (*0.07*)	13.80 (*0.05*)
Jul '96	1	10.06 (*0.14*)	249.33	14.26	13.95
Aug '92	3	-	425.67 (*35.67*)	17.13 (*0.83*)	16.96 (*0.84*)
Aug '93	1	-	290.00	13.40	13.10
Aug '97	3	10.38 (*0.06*)	232.22 (*76.51*)	13.39 (*0.06*)	12.99 (*0.03*)
Sep '94	3	-	431.67 (*56.00*)	14.15 (*0.16*)	13.42 (*0.13*)
Oct '92	1	-	510.00	17.66	12.05
Oct '96	3	12.92	318.22 (*64.38*)	15.66 (*0.14*)	15.15 (*0.18*)
Oct '97	2	13.43 (*0.16*)	665.10 (*107.90*)	17.27 (*0.13*)	16.34 (*0.36*)
Nov '94	3	-	803.00 (*18.77*)	16.77 (*0.29*)	15.97 (*0.14*)

Appendix E

Primary blade (thallus) length (mm), stipe length (mm) and density (plants.m^{-2}).

Trip	Depth	No.1x1m quadrats sampled	Juvenilles					Adults				
			No.plants measured	Stipe Length	sd	Blade Length	sd	No.plants measured	Stipe Length	sd	Blade Length	sd
May 99	3	14	28	39.3	39.3	317.1	132.4	132	66.8	39.6	418.1	167.5
	5	6	6	26.7	4.7	336.7	57.4	44	54.7	20.8	411.0	131.7
	10	12	7	45.7	25.0	348.6	105.0	38	78.6	40.8	481.3	168.5
Sep 99	3	11	32	49.6	51.6	425.8	202.7	190	97.0	78.0	588.8	250.3
	5	9	19	32.9	17.9	383.7	157.9	98	51.1	28.2	460.3	166.0
Dec 99	3	8	26	33.5	26.7	343.8	198.5	109	62.2	36.8	507.8	174.3
	10	5	18	22.5	14.3	253.5	127.6	18	74.2	47.8	564.5	200.8
	12	5	5	31.6	10.4	373.2	201.2	18	57.0	18.0	574.5	125.5
Jun 00	3	5	6	21.7	3.7	230.8	90.7	75	55.5	38.2	431.3	153.7
	10	5	5	32.0	6.8	474.0	149.2	17	62.9	25.9	567.6	149.6
	12	10	6	27.5	7.5	481.7	118.8	21	60.5	41.8	475.7	150.0

Appendix E: continued.

Trip	Depth	No.of quadrats	Adults		Juvenilles	
			Plants.m^{-2}	sd	Plants.m^{-2}	sd
May	3	14	12.9	4.5	3.8	3.5
	5	13	6.6	3.8	1.1	1.8
	10	12	3.3	2.4	0.7	0.8
Sep	3	11	16.1	7.3	4.0	5.8
	5	9	10.4	1.7	2.6	2.3
Dec	3	8	13.3	7.0	3.3	2.6
	10	5	3.6	1.0	3.4	2.4
	12	5	3.6	2.1	1.0	0.9
Jun	3	5	14.8	2.1	1.6	1.9
	10	25	4.7	2.6	0.2	0.6
	12	10	1.9	1.4	0.6	1.0

Appendix F

This work had an original aim of investigating the effect of a short term (7 day) reduction in irradiance on the photosynthetic activity of *E. radiata*. This time period is fairly typical of the duration of water quality changes associated with events such as river flushing or sand dredging which occur along the South Australian coastline.

This experiment aimed to determine what acclimation response would result from 7 days in a lowered irradiance environment. Individuals were transferred from 3 m to 10 m on the evening of 21st February 1999, left at 10 m for a period of one week, then were returned to 3 m (on the evening of 28th February 1999 i.e. day 7). Measurements of the effective quantum yield of the transplants were compared with measurements of control plants, i.e. plants from 3 m that were transplanted to 3 m. These measurements were made on day 8, the first day after the transplants had returned to 3 m. Tissue samples were collected on the evening of day 7 for later analysis of photosynthetic pigment content.

The shallow transplants (from 3 m) showed no measurable acclimation response to a 7 day period of lowered irradiance at 10 m. During February the intensity of maximum irradiance at 10 m was only around 15% of that which would have been experienced at 3 m. Upon return to 3 m the midday depression in effective photochemical yield ("yield") in the shallow transplant group was almost identical to that displayed by the control plants (Figure F.1). The average PAR intensity recorded during the midday measurement period was 755 μmol photons.m^{-2}.sec^{-1}, which is over 7 times higher than the average maximum irradiance calculated for 10 m at that time (Table 2.1). If the transplants had acclimated to the lower PAR levels the expectation would be that this level of PAR would provoke a greater midday depression in this group than the control group. More particularly, a greater degree of "chronic" photoinhibition would be expected, which would be evidenced by an only partial recovery of yield values by evening (Häder *et al.* 1996, Hanelt *et al.* 1997a). In this experiment recovery of yield values is clearly completed by evening in both the control and transplant groups, and the actual midday depression is small in both groups. In addition, no significant changes were observed in photosynthetic pigments (Figure F.2). The typical acclimation response to lowered irradiance would be for an increase in the amounts or alteration the stoichiometry of photosynthetic pigments (Ramus *et al.* 1976a, Ramus *et al.* 1976b, Ramus *et al.* 1977, Falkowski and Owens 1980, Falkowski *et al.* 1981, Henley and Ramus 1989a, Sukenik *et al.* 1990, Falkowski and LaRoche 1991, Iglesias Prieto and Trench 1994).

An alternative explanation for the lack of acclimation response displayed by the shallow transplants is that the deep (10 m) and shallow (3 m) *E. radiata* are already in the same acclimation state. This idea is supported by the study of photokinetics in Chapter 2. No significant differences in any of the photokinetic parameters (e.g. Pm_{gross}, Rd, Ik) were found during the February deployment period (Table 2.2), which coincided with this experiment. The experiments described in Chapter 5 utilise plants which are definately acclimated to low irradiance conditions (i.e. plants from 10 m), and test whether these plants are in fact in the same acclimation state as the 3 m plants. These experiments also investigate what the time scale for the acclimation response is in *E. radiata*, as the current experiment indicates that this response may take longer than 7 days to complete.
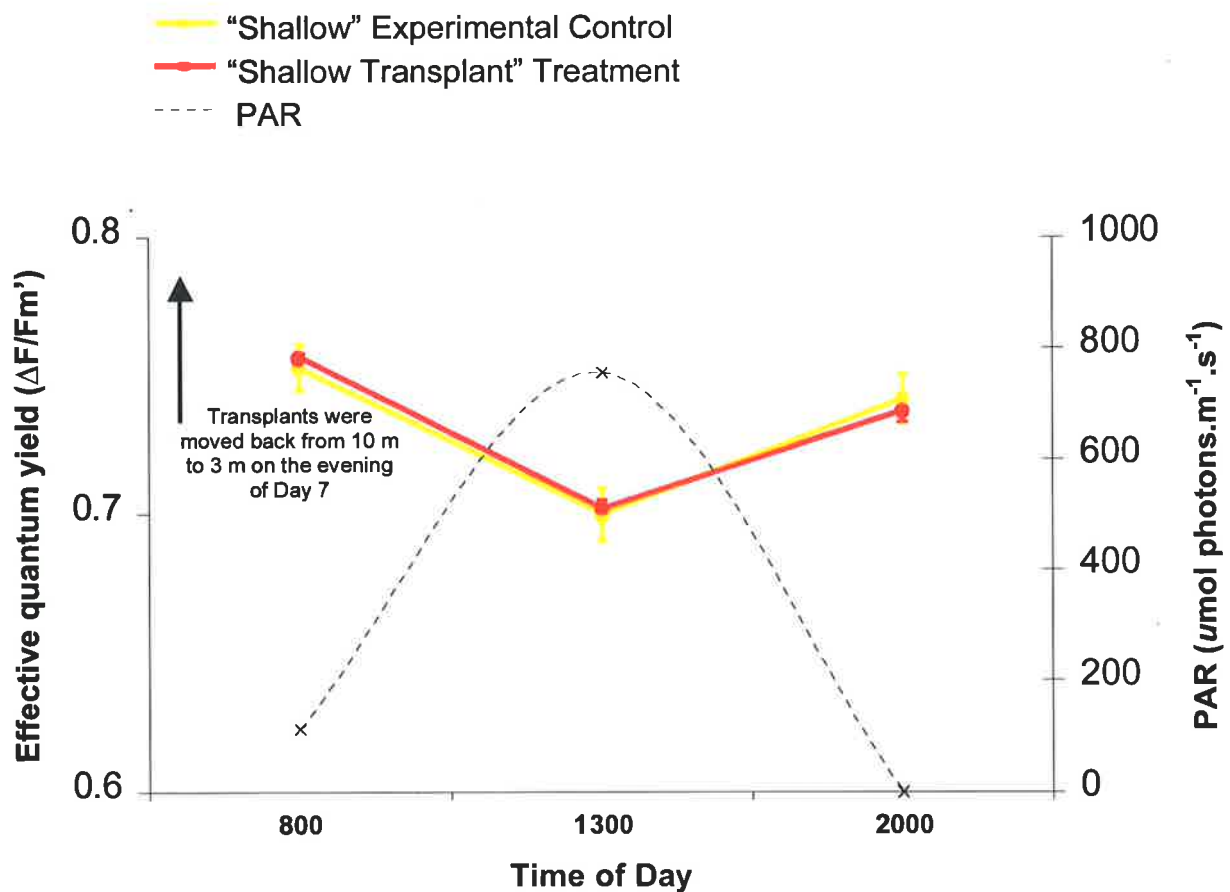

Figure F.1 Photosynthetic efficiency (mean ± se) of *E. radiata* after transplantation of 3 m plants to 10 m for 7 days. Data shown is that measured on Day 8, i.e. the day after plants were returned to 3 m. The experiment was conducted in mid Feburary 1999. PAR values are the mean of all values recorded in each measuring time.
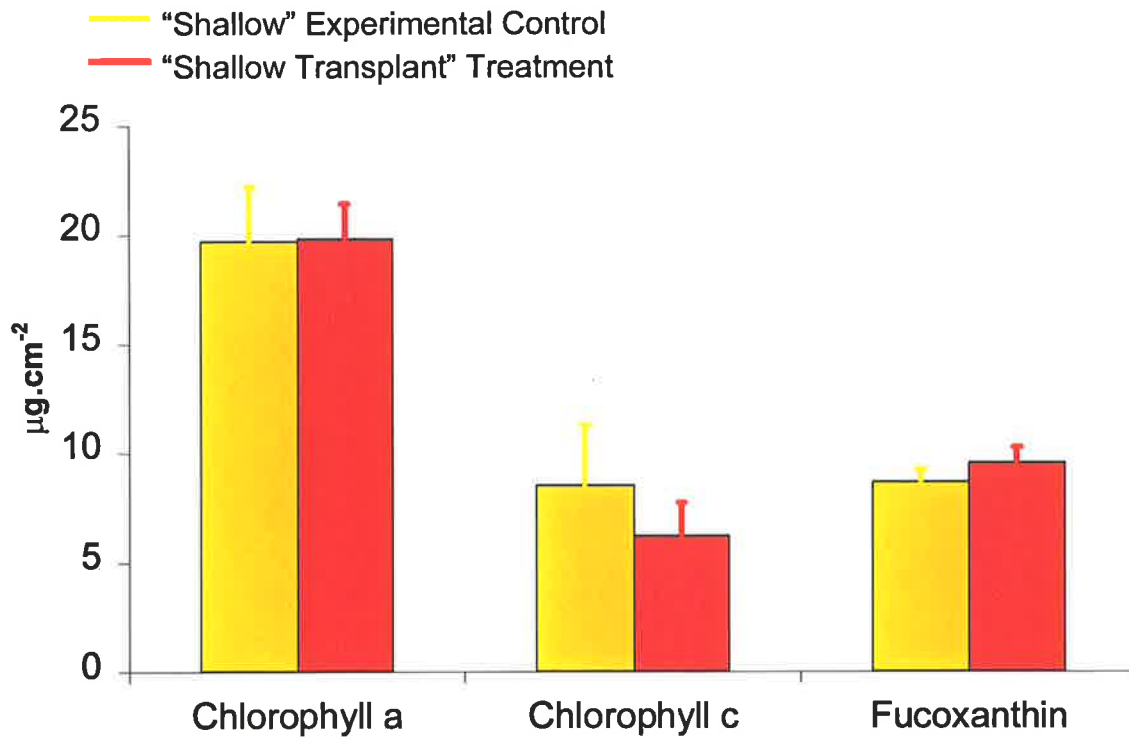
Figure F.2 Photosynthetic pigment concentration during Feburary in 3 m *E. radiata* ("controls") and 3 m *E. radiata* after 7 days at 10 m ("shallow transplants"). No significant differences were found between the two groups.