

Modelling kelp forest primary production using *in situ* photosynthesis, biomass and light measurements

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ABSTRACT: Kelp forests are among the most productive ecosystems in the world. Accurately quantifying net primary productivity (NPP) of kelps is challenging, as the carbon being produced is continually being lost through erosion of tissue and as dissolved organic carbon. Here, we use a physiological model that incorporates *in situ* estimates of photosynthesis vs. irradiance (*P-E*) parameters, biomass and underwater irradiance to estimate NPP of a subsurface *Ecklonia radiata* kelp forest in northern New Zealand over the seasonal cycle and depth range. Model testing found that predicted gross primary production (GPP) based on seasonal and depth-specific *P-E* parameters, biomass and underwater irradiance levels was strongly related to rates of GPP measured on individual kelp in the field ($r^2 = 0.83$). Sensitivity analysis indicated that NPP estimates were most sensitive to variation in biomass and photosynthetic parameters. Using this approach, estimated annual production (\pm SE) at 6 m ($615 \pm 183 \text{ g C m}^{-2} \text{ yr}^{-1}$) was found to be 1.6 \times greater than at 14 m depth ($374 \pm 102 \text{ g C m}^{-2} \text{ yr}^{-1}$), which was proportional to the difference in biomass between depths. This indicates that the greater photosynthetic abilities (higher maximum photosynthetic rates and photosynthetic efficiency) of deeper kelp offset the effects of reduced irradiance on overall NPP at depth. This study demonstrates how *in situ P-E* curves of adult kelp can be incorporated with biomass and irradiance data to estimate NPP of kelp forests, and highlights the importance of understanding depth-related variation in photosynthetic performance when estimating primary production of subsurface kelp forests.

KEY WORDS: Primary productivity · Macroalgae · Modelling · Photosynthesis · Respiration · Biomass · Irradiance · *Ecklonia radiata*

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INTRODUCTION

Kelp (Order: Laminariales) comprise the majority of macroalgal biomass on subtidal reefs in temperate latitudes (Dayton 1985, Steneck et al. 2002) and are among the most productive ecosystems in the world (Mann 1973, 2000, Reed et al. 2008). Kelp forests maintain ecosystem function by structuring biodiversity (Graham 2004, Christie et al. 2009) and ameliorating environmental stress (Bruno et al. 2003, Bennett et al. 2015). The carbon fixed by kelp contributes not only to local reef food webs, but also to adjacent inter-

tidal, deep water and terrestrial habitats (Duggins et al. 1989, Krumhansl & Scheibling 2012); thus, changes to the functioning or distribution of kelp beds could have widespread effects on marine ecosystems. Accurately quantifying spatial and temporal patterns of kelp primary production is fundamental to the understanding of ecosystem functioning, energetics and tropho-dynamics in coastal marine ecosystems (Reed et al. 2008, 2009), and of increasing importance in assessing the potential consequences of global and regional climate change on primary production (Melillo et al. 1993, Schneider et al. 2008, Reed et al. 2009).

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Kelp and seaweed productivity has typically been estimated based on methods that measure growth and yield or standing biomass (Mann 1973, Mann & Kirkman 1981, Gerard & North 1984, Kirkman 1984, Dunton 1990, Reed et al. 2008, 2009). In most cases, those methods are complicated by the inability to account for loss of dissolved organic carbon (DOC) by exudation, and tissue loss from erosion. The hole-punch method for estimating growth and biomass production can account for erosion, but not rates of exudation. Estimates of the amount of carbon lost through exudation are highly variable and species dependent, and are influenced by a variety of abiotic and intrinsic factors as well as the level of stress exposure (Hurd et al. 2014). Standing biomass has been used to provide accurate estimates of net primary production (NPP) of the Californian giant kelp *Macrocystis pyrifera* forests, assuming biomass within a sampling period was produced and lost at rates proportional to the existing standing crop (Reed et al. 2008, 2009). Recent estimates have shown DOC production by *M. pyrifera* to be highly temporally variable, but averaging 14% of total NPP on annual timescales (Reed et al. 2015). The long-term, high-frequency (monthly) sampling program in the southern Californian kelp forests has provided a very comprehensive and unique data set that has allowed for the investigation of all the factors that influence NPP, including resource supply, disturbance, standing crop, recruitment and growth (Rassweiler et al. 2008, Reed et al. 2008, 2009, 2011). However, this approach is extremely labour intensive. Such comprehensive data sets are not available for other kelp populations, and it is unknown how applicable particular population variables for estimating production in floating kelp, such as *M. pyrifera*, are to estimating production of subsurface kelps. This is because they fundamentally differ; most of the biomass of floating kelp is at the surface where it receives high irradiance, whereas subsurface kelps can form extensive forests spanning a range of depths that are exposed to a range of lower light levels depending on depth.

Measurements of photosynthetic rates, obtained by measuring oxygen evolution or carbon fixation in enclosed chambers during incubations of individual taxa (Hatcher et al. 1977, Littler & Arnold 1982, Dunton & Jodwalis 1988, Fairhead & Cheshire 2004a, Staehr & Wernberg 2009, Richards et al. 2011) or multispecies assemblages (Cheshire et al. 1996, Miller et al. 2009, Tait & Schiel 2010), provide a more direct measure of primary production under a given set of physical conditions. This instantaneous measurement of carbon production is not affected by exu-

dation of dissolved carbon or tissue loss and is therefore a measure of the overall primary production of an individual of a given biomass and point in time. Photosynthetic parameters derived from photosynthetic-irradiance ($P-E$) curves can then be incorporated into physiological models with biomass and physical information (e.g. light and temperature) in order to scale up estimates of primary production of benthic macrophytes over larger spatial or temporal scales (Jackson 1987, Duarte & Ferreira 1997, Miller et al. 2012). Such approaches can also be used to provide insights into the important drivers of variation in primary production and provide a framework to predict future changes in primary production. For example, is production related solely to biomass and growth, or is photosynthetic performance an important factor? Models can range from simple physiologically-based models incorporating light, biomass and physiological parameters of photosynthetic response to light (Brinkhuis 1977, Jackson 1987, Burd & Dunton 2001, Binzer & Sand-Jensen 2002, Miller et al. 2012), to more complex models incorporating physiological responses to multiple environmental variables (Duarte & Ferreira 1993, 1997). To date, a modelling approach incorporating photosynthetic response of kelp to light (parameters from $P-E$ curves), kelp biomass and annual light conditions has not been applied to estimating areal primary production of kelp forests, in part due to difficulties in measuring photosynthetic performance of adult kelp *in situ*. However, a newly developed photorespirometry chamber system that allows measurement of *in situ* $P-E$ parameters of adult kelp (Rodgers et al. 2015) provides an opportunity to use a physiological model to estimate NPP of kelp forests over different temporal and spatial scales.

Many subtidal benthic macroalgae, including Laminarians, exhibit strong seasonal variability in growth, photosynthesis and respiration rates due to seasonal changes in environmental factors including light, temperature and nutrient availability (Kirkman 1984, Hatcher et al. 1987, Kain 1989, Cheshire et al. 1996, Fairhead & Cheshire 2004a, S. Miller et al. 2011), and consequently primary productivity can vary temporally between seasons (Hatcher et al. 1977, Cheshire et al. 1996, Fairhead & Cheshire 2004a, R. Miller et al. 2011). Understanding this seasonal variability is essential to estimating annual NPP. Similarly, for subsurface kelp species, growth, photosynthesis and respiration rates can be highly variable between different depths (Novaczek 1984, Kirkman 1989, Fairhead & Cheshire 2004a). Kelp at greater depths may acclimate to lower light levels,

for example by increasing photosynthetic efficiency (Ramus et al. 1976, Fairhead & Cheshire 2004b, Rodgers et al. 2015), which may mean that deeper kelp contributes disproportionately to NPP relative to overall biomass. Quantifying photosynthetic performance over the depth gradient is an important step towards understanding spatial patterns of productivity of subsurface kelps and seaweeds that occur across a depth range, unlike for floating canopy kelp forests (i.e. *M. pyrifera*) where depth is not as important a factor, given that most of the biomass is at the surface.

In this study, we used a simple physiologically-based model (Miller et al. 2012) to estimate NPP of the widespread subsurface kelp *Ecklonia radiata* using seasonal and depth-related measurements of *P-E* parameters, biomass and underwater irradiance. We evaluated the model by comparing modelled estimates of primary production for individual kelps to *in situ* measurements, and performed sensitivity analysis to determine whether the productivity estimates were more sensitive to changes in biomass, irradiance or photosynthetic parameters. Based on the model, we provide seasonal and annual estimates of NPP at 2 depths and compare these estimates to relative differences in biomass between depths.

MATERIALS AND METHODS

Study system and species

All field measurements were carried out at Goat Island (36° 17' S, 174° 48' E) in northeastern New Zealand (Fig. 1). The subtidal reef communities at this site are typical of moderately exposed coasts in northeastern New Zealand (Shears & Babcock 2004), with the stipitate kelp *Ecklonia radiata* forming continuous monospecific stands at depths >5 m. Photosynthetic measurements were carried out at 2 sites approximately 220 m apart on the west side of Goat Island, at 6 and 14 m depth. Average daily water temperature at these depths ranged from ~14.5°C in winter to ~21°C in the summer (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m553/p067_supp.pdf). The water column at this location is well-mixed over the year, and daily average temperature is

only marginally warmer (0.09°C on average) at the shallower 6 m site. While measurements of nutrient concentrations are not available from these 2 depths, the nutrient status of kelp from these sites indicates that kelp at both depths receive similar amounts of nutrients from the same source (% tissue N: 1.82 ± 0.14 [SE] at 6 m and 1.88 ± 0.10 at 14 m; $\delta^{15}\text{N}$: 6.99 ± 0.14 at 6 m and 6.52 ± 0.20 at 14 m, based on monthly samples from August 2013 to July 2014; N. Shears unpubl. data). Wave exposure at the 2 sites is comparable; the 6 m site is protected from prevailing north-easterly swells by Goat Island and the 14 m site is on the sheltered side of North Reef, which is a large submerged reef located northwest of Goat Island (Fig. 1).

In situ measurement of *P-E* parameters

In situ photosynthetic and respiration rates of adult *E. radiata* sporophytes were measured using photorespirometry chambers (see Rodgers et al. 2015 for full description of chamber and methodology). Kelp were incubated over 4 seasons at 6 m depth: summer (Dec to Feb 2013, n = 7), autumn (Mar to May 2012,

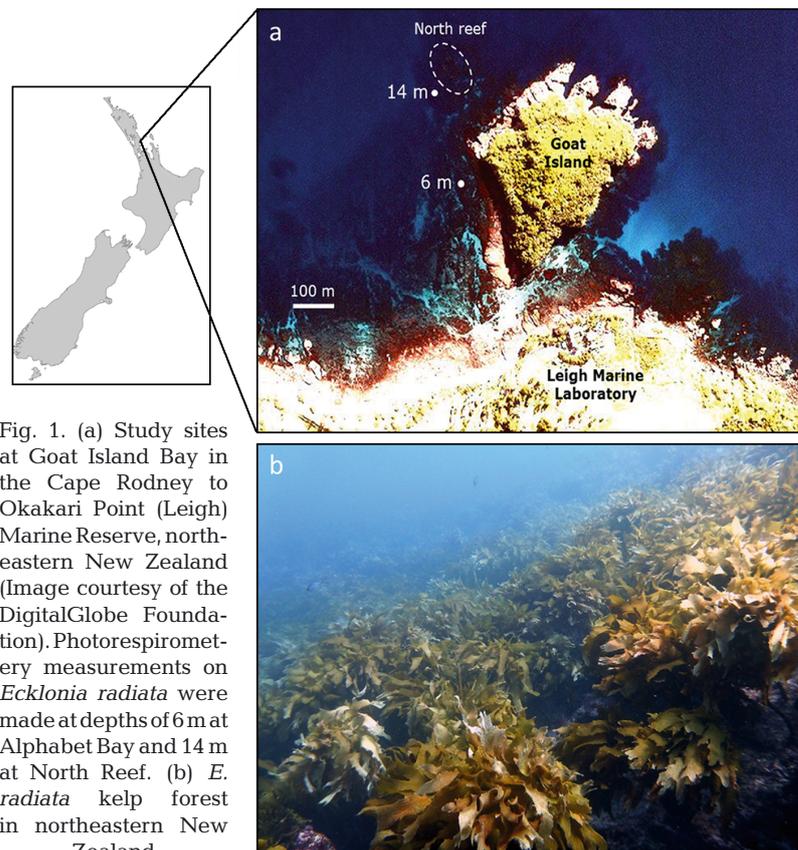


Fig. 1. (a) Study sites at Goat Island Bay in the Cape Rodney to Okakari Point (Leigh) Marine Reserve, northeastern New Zealand (Image courtesy of the DigitalGlobe Foundation). Photorespirometry measurements on *Ecklonia radiata* were made at depths of 6 m at Alphabet Bay and 14 m at North Reef. (b) *E. radiata* kelp forest in northeastern New Zealand

n = 5), winter (Jun to Aug 2013, n = 6) and spring (Sep to Nov 2013, n = 10), and in summer (n = 5) and winter (n = 6) at 14 m depth. Adult canopy individuals were randomly selected for chamber incubations. Typical canopy kelp were ~55 cm stipe length with ~15 to 40 cm primary lamina length and fit in the chamber with blades naturally arrayed. In some cases, very large individuals were not incubated so as to avoid any effects of self-shading from excessive constriction of the laminae.

All measurements were carried out between 11:00 and 16:00 h using 2 replicate chambers that were sampled simultaneously. Measurements were made on clear, cloudless days to utilize the highest available light levels, ensuring that maximum photosynthetic rate was achieved, and to minimize fluctuations in light over the duration of the incubations due to variable cloud cover.

During each incubation, photosynthetic rates of an individual kelp were measured at 5 irradiances (achieved through the use of varying shade cloth layers and lifting the kelp to shallower, higher light depths on a lift frame) in order to generate a P - E curve for that individual, in addition to a respiration (dark) measurement, each being measured over a 10 min interval (60 min total). A duration of 10 min for each irradiance, with measurements every 1 min, was found to be sufficient to show linear changes in oxygen concentration from which to calculate rates of respiration and photosynthesis, these were not different from linear changes over longer time periods (30 to 40 min). The short time period minimized fluctuations in light intensity during each irradiance level and meant a P - E curve could be generated for 2 individuals in a single dive. At the end of the photosynthetic measurements kelp were collected, and volume, wet weight (WW) and dry weight (DW; dried at 60°C for 48 h) of the lamina were measured in the laboratory. Tissue samples (~5 g WW) were collected from secondary laminae from the basal third of the primary lamina for chlorophyll (chl) a and c analysis (see Text S1 in the Supplement).

Respiration and photosynthesis rates were calculated from the linear slope of oxygen concentration over the dark and each light phase of the incubation period. Linearity of slope within each phase was inspected for any indication of changing rate (non-linearity), e.g. as a result of oxygen supersaturation, nutrient and carbon dioxide limitation, photoinhibition or enhanced post-illumination rates of dark respiration. There was no evidence of non-linearity. A total of 10 min of data were used for each phase, with the minute spanning the transition excluded. Irradi-

ance was averaged over the same time period. Rates of respiration (R_d) and photosynthesis were expressed per unit dry biomass per hour ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$).

For each individual a P - E curve was fitted using nonlinear regression in R (R Core Team 2013), following (Webb et al. 1974); nonlinear regression of net photosynthesis (normalized to DW) on irradiance (E), following Webb et al. (1974):

$$P = P_{\max}(1 - e^{-\alpha E/P_{\max}}) \quad (1)$$

where P is the net photosynthetic rate at any irradiance (E), P_{\max} is the maximum net photosynthetic rate at saturating irradiances, α is the photosynthetic efficiency (i.e. the slope of the linear light-limited part of the curve). Additional parameters calculated were E_k (saturation irradiance, which is the onset of light saturation estimated as P_{\max}/α), and E_c (the compensation irradiance at which photosynthesis balanced respiration, estimated as R_d/α).

Biomass and underwater irradiance monitoring

Seasonal variation in kelp biomass was estimated at the 2 depths by multiplying the density of adult canopy-forming individuals measured from 1 m² quadrats (at 6 m, summer n = 5, winter n = 13; at 14 m, summer n = 7, winter n = 6), by the mean biomass of incubated individuals. Biomass was estimated for summer and winter at both depths, but only at 6 m depth for spring and autumn.

In situ irradiance at 6 and 14 m depth was recorded over a 1 yr period (Jan to Dec 2013) using integrating data loggers with cosine-corrected sensors (Odyssey Photosynthetic Irradiance Recording System, Dataflow Systems). The loggers were mounted approximately 30 cm above the seafloor on metal rods attached to heavy iron mooring bases located in small cleared patches within the kelp forest. Irradiance at the surface was also recorded nearby at the Leigh Marine Laboratory. Loggers were calibrated on land prior to deployment, over a full range of irradiances from full sunlight (up to 2100 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) to very low light (<10 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$), and darkness. Individual logger calibration curves were constructed using linear regression of raw logger values against values recorded by a LI-190 quantum sensor (LI-COR Biosciences). Integrated photon flux density (PFD, $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) was recorded every 5 min. Mean hourly PFD ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) over the course of the day was calculated for every day of 2013.

Loggers were deployed for 1 to 2 mo before being replaced by a clean logger. Fouling of the sensor by algae occurred during some deployments; the difference in irradiance recorded by the fouled logger and the clean replacement logger was used to calculate attenuation of the fouling community (Gallejos et al. 2005). Irradiance values were then corrected as an exponentially increasing function of time after deployment. Average and maximum daily PFD ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) was calculated over the year at the 3 sites (surface, 6 and 14 m depth).

Physiological model of primary production

A physiologically based model incorporating average seasonal photosynthetic performance measured from *in situ* *P-E* curves, average seasonal biomass and an annual irradiance budget was used to estimate areal NPP ($\text{g C m}^{-2} \text{ h}^{-1}$) following the equation of Webb et al. (1974):

$$\text{NPP} = P_{\max} \times 1 - e^{(-\alpha E/P_{\max})} \times b - R_d \quad (2)$$

where P_{\max} is the gross photosynthetic rate at saturating irradiance calculated from *P-E* curves measured *in situ* ($\text{g C g DW}^{-1} \text{ h}^{-1}$), α is the photosynthetic efficiency (i.e. the slope of the linear light-limited part of the curve) ($\text{g C g DW}^{-1} \text{ h}^{-1}$), E is incident irradiance on the seafloor averaged over 1 h ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$), and b is the macroalgal standing crop ($\text{g DW lamina m}^{-2}$). Gross primary production (GPP) was converted to NPP using mass-specific respiration rates, R_d ($\text{g C g DW}^{-1} \text{ h}^{-1}$), measured in the dark during the *in situ* incubations. Oxygen evolution rates were converted to carbon using a photosynthetic quotient of 1 (Rosenberg et al. 1995).

To evaluate how well the model predicted production of *E. radiata*, a subset of data from spring 2013 (6 m depth; 10 ind.) was used to compare modelled GPP with measured rates from the field. Average *P-E* parameters were first calculated based on a random selection of 5 ind. These parameters were then used to estimate GPP for the remaining 5 kelp ind. for each photosynthetic measurement made in the field ($n = 6$ measurements per kelp), by incorporating individual biomass of the lamina and irradiance at the time of incubation. These modelled estimates were then compared to the measured rates of GPP from those 5 ind. This process was repeated 10 times on a random selection of 5 kelps, and in each case modelled GPP was compared against the measured rate of GPP using linear regression. To investigate

how well the model performed with season and depth, the measured rates of gross photosynthesis from all of the individuals incubated across the different depths and seasons at each of the different irradiances ($n = 246$ measurements on 44 ind.) were compared to predicted GPP based on mean *P-E* parameters specific to each season and depth, individual biomass of the lamina and the irradiance at the time of incubation. While this is not strictly independent, as the *P-E* parameters used were derived from the same individual kelps averaged across seasons and depths, it provides an indication of variation in model performance across seasons.

Estimating seasonal and annual NPP

Photosynthetic parameters were obtained from *P-E* curves measured *in situ* at 6 m during summer, winter and spring 2013 and autumn 2012, and at 14 m during summer and winter 2013. Autumn 2012 rates were used in the seasonal comparison for 6 m depth because data was not collected in autumn 2013 for logistical reasons. This was justified by the similarity of *P-E* parameters measured in winter 2012 to those measured in winter 2013, supporting the use of autumn 2012 as a substitute for autumn the following year. Due to the lack of measurements from autumn and spring at 14 m depth, photosynthetic parameters and respiration rates for those seasons were estimated as the average of summer and winter rates. The rationale for this approach was based on previously documented clear seasonal patterns in photosynthetic parameters for *E. radiata* at 5 and 12 m depth, with P_{\max} and α being highest in winter, lowest in summer and generally intermediate in autumn and spring (Fairhead & Cheshire 2004b). However, the relative effects of the decision to use intermediate values for the seasons without *in situ* measurements were examined by calculating the percent change in the seasonal estimates of NPP if measured values from adjacent seasons had been used. Biomass values for autumn and spring at 14 m were also estimated as intermediate between summer and winter at each depth. This was supported by seasonal biomass patterns recorded at the sites between summer 2012 and spring 2013 (K. Rodgers unpubl. data) and at the same sites over several years in the late 1970s (Novaczek 1984).

The physiological model was used to calculate daily NPP at both depths from January to December 2013. For each day, GPP was calculated for each hour of the day using hourly underwater light measure-

ments (from *in situ* loggers), and the seasonal (as defined by the solar solstices and equinoxes) estimates of kelp biomass and *P-E* parameters. Hourly GPP values were summed and total respiration over the 24 h period subtracted to obtain NPP. Respiration rates were assumed to be constant over the 24 h cycle (Sadro et al. 2014). All sources of error in the model were propagated to calculate error (SE) for the seasonal and annual estimates of NPP.

Simple sensitivity analysis was performed to determine which factors (biomass, irradiance or the photosynthetic parameters P_{\max} and α) most influenced the estimates from the model, following the methods applied by Miller et al. (2012). The annual model was re-run using the field-collected irradiance, biomass and photosynthetic parameters, and each time one parameter was varied $\pm 25\%$. Consistently varying parameters and combinations of parameters by 25% was considered a realistic variation to be ecologically meaningful, and also to allow comparison to Miller et al. (2012), who applied the model to an understory algal community. The resulting output was expressed as percentage change from the original modelled values.

Data analysis

Two-way ANOVA was used to compare the effect of depth and season (summer and winter) on biomass and *P-E* parameters. At the shallower site where there was data for all 4 seasons, the effects of season on biomass and *P-E* parameters were analysed separately using 1-way ANOVA. Data was log transformed to fulfil the assumption of equal variance. Post hoc Holm-Sidak pairwise multiple comparison procedures were used to determine differences among seasons. Analyses were performed in SigmaPlot v.11.0 and R v.3.0.

RESULTS

Biomass

Biomass varied between seasons and depths, and there was a significant interaction (Table 1). Biomass was significantly different between depths in summer ($p < 0.001$), but not in winter ($p = 0.585$), and biomass significantly differed within depths between summer and winter (6 m: $p < 0.001$; 14 m: $p = 0.027$) (Fig. 2a). Biomass of kelp in shallow water (6 m) differed among seasons ($F_{3,24} = 33.167$, $p < 0.001$), with

Table 1. 2-way ANOVA of dry weight of the lamina, respiration rate (R_d), and photosynthetic parameters of *Ecklonia radiata* at Goat Island Bay, New Zealand, over 2 seasons (summer and winter) and between depths (6 and 14 m) ($df = 1$). P_{\max} : maximum rate of net photosynthesis ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$); α : slope of the linear light-limited part of the curve; E_k : saturation irradiance; E_c : compensation irradiance

Source of variation	<i>F</i>	<i>p</i>
Dry weight		
Season	76.14	<0.001
Depth	19.62	<0.001
Season \times depth	27.13	<0.001
P_{\max}		
Season	0.28	0.605
Depth	28.12	<0.001
Season \times depth	5.31	0.032
R_d		
Season	1.86	0.189
Depth	5.78	0.027
Season \times depth	2.54	0.128
α		
Season	2.98	0.100
Depth	6.21	0.022
Season \times depth	0.54	0.472
E_k		
Season	3.41	0.079
Depth	2.79	0.110
Season \times depth	1.08	0.312
E_c		
Season	8.29	0.010
Depth	17.29	<0.001
Season \times depth	0.31	0.586

significantly greater biomass in summer than in the other seasons. Biomass was highest in summer and lowest in winter at both depths, although there was a much less pronounced difference between the 2 seasons at 14 m (Fig. 2a). Average biomass across seasons was 1.6 times higher at 6 than at 14 m.

Relationship between kelp size and *P-E* parameters

There was no clear relationship between biomass (lamina DW) and photosynthetic parameters of individuals measured (see Fig. S2 in the Supplement at www.int-res.com/articles/suppl/m553p067_supp.pdf). Only during summer at 6 m depth was there a significant negative relationship between lamina weight and P_{\max} ($r^2 = 0.63$, $p = 0.03$), with larger individuals having a lower P_{\max} . At this time canopy plants were larger than in other seasons and also exhibited a wider range in kelp biomass (71.1 to 131.7 g

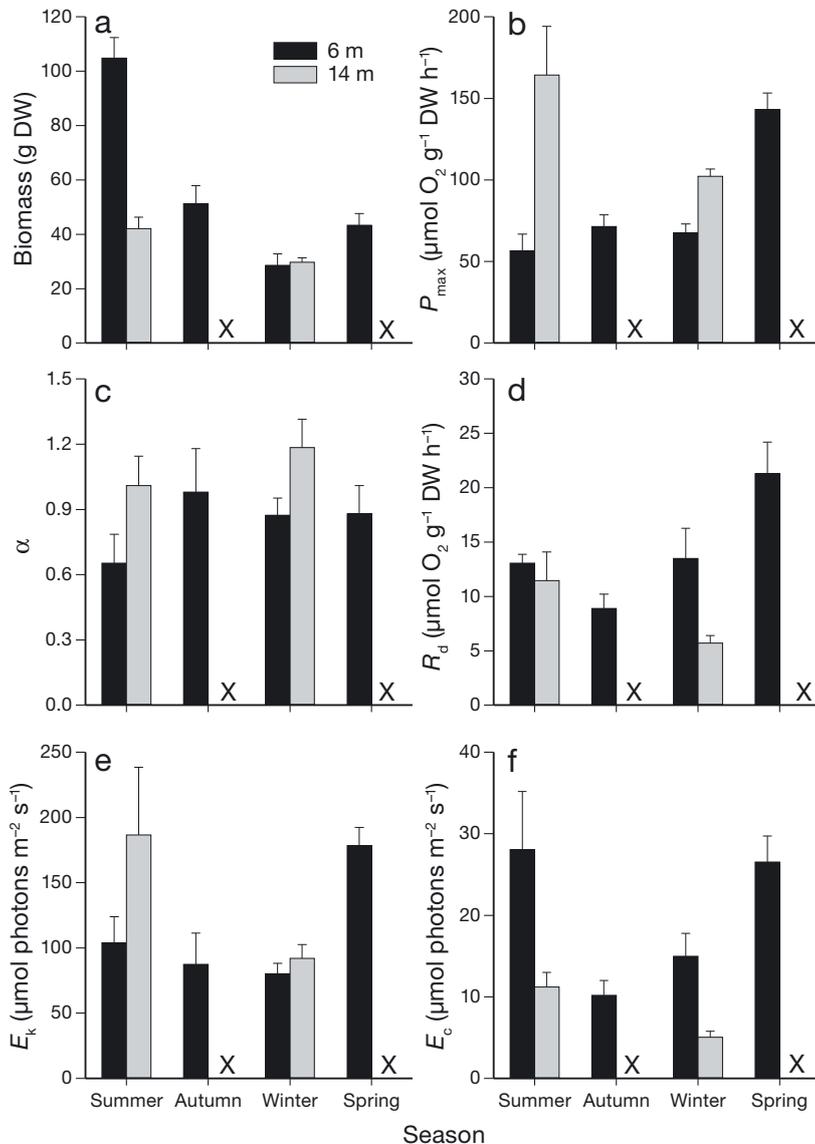


Fig. 2. *Ecklonia radiata*. Mean (\pm SE) of (a) biomass (g dry weight [DW] of lamina); (b,c,e,f) photosynthetic parameters; and (d) respiration rate (R_d) at Alphabet Bay (6 m depth) in summer 2013 (n = 7), autumn 2012 (n = 5), winter 2013 (n = 6) and spring 2013 (n = 10), and at North Reef (14 m depth) in summer 2013 (n = 5) and winter 2013 (n = 6). X indicates that no measurements were made at 14 m depth in those seasons. P_{max} : maximum rate of net photosynthesis (expressed in terms of net primary productivity [NPP], $\mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$); R_d : respiration rate ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$); α : slope of the linear light-limited part of the curve; E_k : saturation irradiance ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$); E_c : compensation irradiance ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)

lamina DW). This relationship between P_{max} and lamina weight was not found at 14 m during summer ($r^2 = 0.07$, $p = 0.66$) where kelp were smaller. There was no relationship between P_{max} and size in winter at either depth. None of the other P - E parameters (α , R_d , E_k or E_c) varied significantly with kelp size (lamina DW) at either depth during any season.

Seasonal and depth-related patterns in P - E parameters and photosynthetic pigments

There was a significant interactive effect of season and depth on P_{max} (Table 1, Fig. 2b). P_{max} did not differ between summer and winter at 6 m, but was higher in summer compared to winter at 14 m. P_{max} was significantly higher at 14 m in both seasons compared to 6 m (Fig. 2b). P_{max} ranged from 27.7 to 209.3 $\mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$ at 6 m depth and 72.0 to 251.5 $\mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$ at 14 m. At 6 m, P_{max} did differ among the 4 seasons ($F_{3,24} = 18.910$, $p < 0.001$) with a significantly higher mean value in spring compared to all other seasons (Fig. 2b). α varied with depth, and was higher at 14 m (Fig. 2c). Season did not have a significant effect on α , although it did tend to be lower in summer compared to winter and spring (Table 1, Fig. 2c). R_d varied with depth (Table 1), with higher mean R_d at shallower depth (Fig. 2d). Respiration rates did vary seasonally at 6 m ($F_{3,24} = 5.400$, $p = 0.006$), with significantly higher rates in spring compared to all other seasons (Fig. 2d). E_k did not vary with season and depth (Table 1), although mean E_k was higher in summer compared to winter at both depths (Fig. 2e). At the 6 m site, E_k differed across the 4 seasons ($F_{3,24} = 7.214$, $p = 0.001$), with higher E_k in spring compared to all other seasons (Fig. 2e). E_c varied with season and depth (Table 1). Mean E_c declined with depth, and was lower in winter compared to summer at both depths (Fig. 2f). At 6 m depth, E_c differed among all seasons except between summer and spring ($F_{3,24} = 10.407$, $p < 0.001$) (Fig. 2f). Seasonal averages of photosynthetic parameters used to parameterize the productivity modelling for kelp forest at both depths are given in Table S1 in the Supplement.

Chl *a* content in *Ecklonia radiata* was higher in winter compared to summer (2-way ANOVA, $F_{1,27} = 5.213$, $p = 0.032$), but did not vary with depth (2-way ANOVA, $F_{1,27} = 0.070$, $p = 0.793$). Chl *c* was higher in winter compared to summer at 6 m, and higher in summer compared to winter at 14 m, although the differences between seasons within depths were not

significant (2-way ANOVA, $F_{1,27} = 0.066$, $p = 0.800$). Chl *c:a* ratios varied with season (2-way ANOVA, $F_{1,27} = 16.450$, $p < 0.001$) but not depth (2-way ANOVA, $F_{1,27} = 0.315$, $p = 0.580$), with higher chl *c:a* ratios in summer compared to winter at both depths (Fig. S3 in the Supplement).

In situ irradiance

There were clear seasonal and depth-related patterns in average daily PFD (Fig. 3a). On average, daily PFD was 2.5× higher at 6 than 14 m. On average, 20% of the surface irradiance reached 6 m and 8% reached 14 m during summer, whereas 10% reached 6 m and 3% reached 14 m depth during winter.

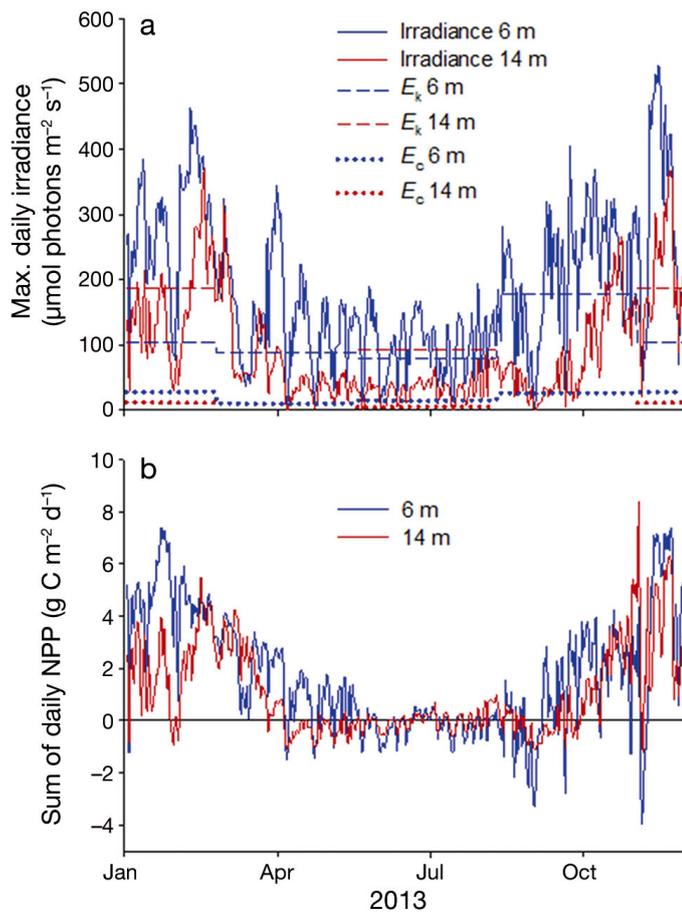


Fig. 3. (a) Maximum daily irradiance at 6 and 14 m depth in Goat Island Bay during 2013 (solid lines) and average seasonal saturation irradiance (E_k , dashed lines) and compensation irradiance (E_c , dotted lines) of *Ecklonia radiata* and for all 4 seasons at 6 m depth and for summer and winter at 14 m depth. (b) Sum of daily net primary productivity (NPP) for the same period, estimated by modelling, shown for 6 and 14 m depths

Maximum hourly irradiance exceeded E_c for some part of the day every day during summer (90 d) at both 6 and 14 m depths (Fig. 3a). During winter, however, maximum irradiance was below E_c for 3 full days at 6 m and 7 full days at 14 m, and for 1 full day during autumn and 2 full days during spring at 6 m (E_c and E_k not available at 14 m for autumn and spring) (Fig. 3a). Maximum hourly irradiance exceeded E_k for some part of most days during summer at 6 m (85 d), and for under half of the days at 14 m (41 d). During winter, maximum irradiance was below E_k for 23 full days at 6 m and all (92) days at 14 m, and for 15 full days during autumn and 23 full days during spring at 6 m (Fig. 3a).

Seasonal and annual estimates of productivity

Modelled GPP was strongly related to *in situ* measurements of GPP for all subsets of kelp randomly selected from spring 2013 ($r^2 = 0.71$ to 0.95, mean \pm SE = 0.82 ± 0.03 , $n = 10$ iterations). When GPP was estimated for all individuals using the seasonal and depth related *P-E* parameters it was also strongly related to the measured GPP across all seasons and depths ($y = 1.05[\pm 0.02 \text{ SE}]x$, $r^2 = 0.83$). The overall fit did vary with season ($r^2 = 0.66$ to 0.95; Fig. 4), with lower r^2 in summer and spring when rates were highest (Fig. 4). These results indicate that the model performed well at estimating instantaneous rates of primary production in *E. radiata*.

Modelled NPP of the *E. radiata* canopy exhibited a strong seasonal pattern and clear differences between depths (Table 2, Fig. 5). Daily rates were highest in summer at both depths and lowest in winter when NPP was estimated to be ~ 0 at both depths (Fig. 3b). Averaged over the year, daily NPP (\pm SE) was higher at 6 m ($1.7 \pm 0.1 \text{ g C m}^{-2} \text{ d}^{-1}$) compared to 14 m ($1.0 \pm 0.1 \text{ g C m}^{-2} \text{ d}^{-1}$). The majority of annual production (64% at 6 m, 62% at 14 m) occurred in summer (Table 2). The pattern between depths was reversed during winter, where marginally negative production was estimated at 6 m depth (Table 2). Estimated annual production at 6 m ($614.5 \pm 183.2 \text{ g C m}^{-2} \text{ yr}^{-1}$) was 1.6× greater than at 14 m depth ($373.5 \pm 102.3 \text{ g C m}^{-2} \text{ yr}^{-1}$) (Table 2).

NPP estimates were most sensitive to changes in biomass and photosynthetic parameters (P_{max} and α simultaneously) (Table 3). Proportional changes in biomass, and P_{max} and α simultaneously resulted in equivalent changes in modelled GPP. The model output was less sensitive to changes in irradiance or in P_{max} or α separately. For 14 m depth, using mean *P-E*

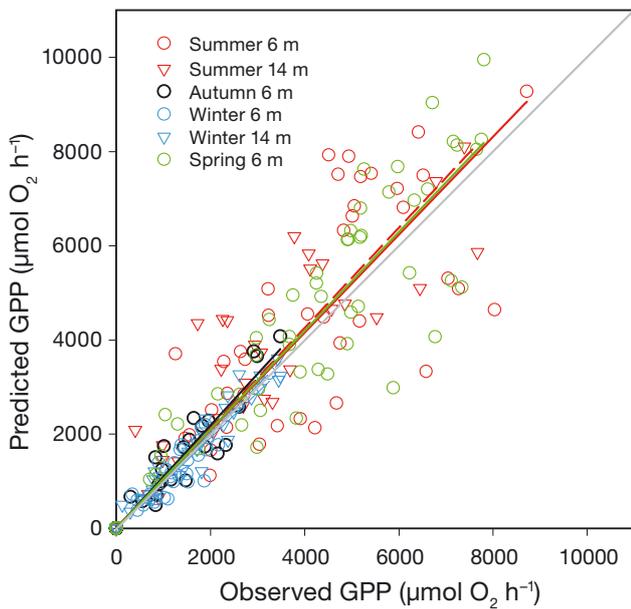


Fig. 4. Modelled estimates of gross primary productivity (GPP) versus *in situ* measurements of GPP of individual kelp (*Ecklonia radiata*) at varying light levels for each depth and season. The *in situ* measurements were those that were used to generate *P-E* curves and based on between 6 and 11 ind. for each depth and season. Overall: $y = 1.05(\pm 0.02 \text{ SE})x$, $r^2 = 0.83$; summer 6 m: $y = 1.04(\pm 0.05 \text{ SE})x$, $r^2 = 0.66$; summer 14 m: $y = 1.06(\pm 0.05 \text{ SE})x$, $r^2 = 0.78$; autumn 6 m: $y = 1.09(\pm 0.04 \text{ SE})x$, $r^2 = 0.91$; winter 6 m: $y = 0.96(\pm 0.03 \text{ SE})x$, $r^2 = 0.88$; winter 14 m: $y = 1.01(\pm 0.02 \text{ SE})x$, $r^2 = 0.95$; spring 6 m: $y = 1.05(\pm 0.05 \text{ SE})x$, $r^2 = 0.84$

Table 2. Sum (\pm SE) of net primary productivity (NPP, g C m^{-2}) of *Ecklonia radiata* kelp forest at 6 and 14 m depths seasonally (3 mo) and annually, expressed as carbon production m^{-2} (g C m^{-2})

Season	Depth (m)	
	6	14
Summer	392.4 (190.9)	231.1 (119.2)
Autumn	139.1 (74.7)	70.0 (45.3)
Winter	-15.6 (39.4)	1.4 (13.6)
Spring	98.6 (96.3)	71.0 (44.7)
Annual	614.5 (183.2)	373.5 (102.3)

parameters (P_{max} and α), respiration rate and biomass from summer instead of the estimated intermediate values for autumn resulted in a 42.8% lower estimate of NPP for autumn, and if winter values were used instead it resulted in a 15.4% higher estimate. Similarly, if summer values were used instead of the estimated intermediate values for spring it resulted in a 33.1% lower estimate of NPP for spring, and if winter values were used instead it resulted in a 15.9% higher estimate.

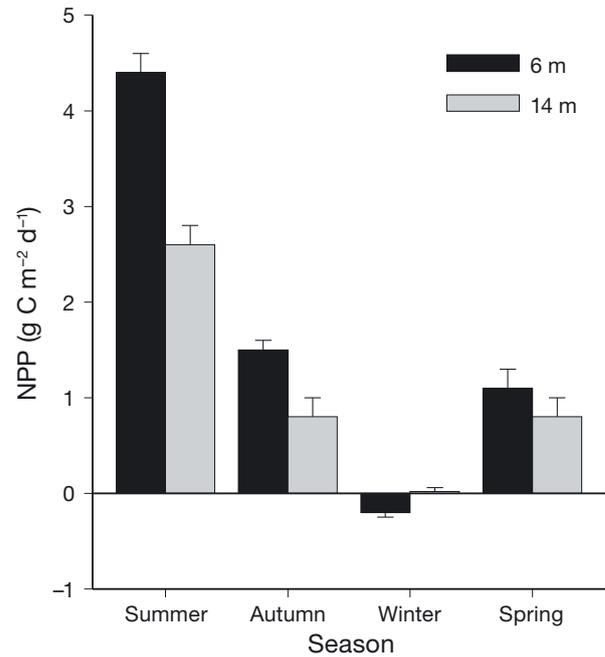


Fig. 5. Mean (\pm SE) daily net primary production (NPP, $\text{g C m}^{-2} \text{ d}^{-1}$) of *Ecklonia radiata* kelp forest for each season at 6 and 14 m depths

Table 3. Percentage change from modelled gross primary production (GPP) when biomass, hourly irradiance or production rates (P_{max} and α separately or together) were changed by 25%. *B*: biomass; *E*: hourly irradiance; P_{max} : maximum rate of photosynthesis; α : slope of the linear light-limited part of the curve. Values represent percent change averaged over an entire year (365 d)

Depth (m)	Parameter change (%)	<i>B</i>	<i>E</i>	P_{max}	α	P_{max} and α
6	-25	-25.1	-14.4	-14.2	-14.4	-25.1
	+25	24.8	11.1	11.0	11.1	24.8
14	-25	-25.0	-19.1	-8.7	-19.1	-25.0
	+25	25.0	16.6	6.2	16.6	25.0

DISCUSSION

Comparison of predicted versus *in situ* measurements of GPP indicates that the simple model framework used in this study effectively predicts the photosynthetic rates of individual kelp under varying light levels and over an annual cycle. The same model had previously been applied to understory multispecies macroalgal communities in giant kelp *Macrocystis pyrifera* forests (Miller et al. 2012). The present study shows that this type of model can be applied to estimate production of a canopy-forming kelp species that achieves higher standing biomass

and daily NPP than understory macroalgae (R. Miller et al. 2011).

Sensitivity analysis indicated that variation in biomass and P - E parameters contributed equally to modelled estimates of production, and varying those factors resulted in proportional changes in production. This mirrors the findings of Miller et al. (2012) for understory macroalgae; however, in multi-species communities the largest or most abundant species in terms of biomass largely determine GPP, despite having lower biomass-specific photosynthetic rates (Copertino et al. 2005, Miller et al. 2009, 2012). The sensitivity of the model to changes in P - E parameters differed with depth: for shallower kelp it was more sensitive to P_{\max} and for deeper kelp it was more sensitive to α . This is because irradiance is seldom saturating at the deeper depth and therefore photosynthetic efficiency is more important, whereas at the shallower depth it is more often saturating and thus a change in P_{\max} has a larger influence on estimated NPP. The model was less sensitive to varying irradiance and changed less with added light compared to subtracted light due to the saturating nature of the P - E relationship (Miller et al. 2012). The effects also varied with depth; change in irradiance at deeper depth had a larger effect on NPP because the kelp there receive much less light. At 14 m depth, kelp received sub-saturating irradiance for much of the time (~50 and 100% of days in summer and winter respectively), whereas at 6 m depth, irradiance was rarely at sub-saturating levels (5 and 25% of days in summer and winter respectively). Despite the model showing less sensitivity to changes in irradiance, higher levels would undoubtedly have led to higher NPP considering the extent to which it is light-limited at greater depths.

The model presented here provides a useful approach to estimating NPP and gaining insight into factors influencing production. However, uncertainty around model parameterization is a limitation of the approach. In this example, sources of uncertainty were around estimates of P - E parameters and biomass for seasons where *in situ* measurements were unavailable, the representativeness of the biomass estimates, and the necessity to extrapolate rates measured at particular times of the day to the entire 24 h cycle. The uncertainty around NPP estimates for the 2 seasons where P - E parameters and biomass were estimated for the deeper population was explored by calculating the difference in NPP if P - E parameters from adjacent seasons were applied. The relatively larger uncertainty that would result from the use of summer compared to winter values for

autumn and spring in the model can be explained by high P_{\max} and R_d and low α in summer interacting with decreased light availability in autumn and spring. The much lower estimates of NPP based on summer values compared to when seasonal acclimation was taken into account highlights the importance of incorporating algal physiology into productivity modelling. Uncertainty around the representativeness of biomass estimates was a concern because if larger or smaller individuals than those measured varied in photosynthetic response, a model based on a limited size range would over- or underestimate NPP. Analysis of the relationship between size and photosynthetic parameters did indicate that the largest individuals sampled (in summer, 6 m depth) tended to have lower P_{\max} and α . It is possible that there is increased self-shading of larger individuals in the chamber and this requires further investigation. If P - E parameters do vary in a predictable manner with size this could be incorporated to further refine NPP estimates.

Extrapolating measured rates over the 24 h cycle is also a potential source of uncertainty because some algae exhibit diurnal variations in photosynthetic performance that do not parallel diurnal changes in environmental variables (specifically irradiance) (Lobban & Harrison 1994, Kirk 2011). Furthermore, diurnal variation in respiration rates is typically unknown, and although enhanced post-illumination respiration rates have been observed in some algae, this was not observed for *E. radiata*. Preliminary investigation into respiration rates over a 24 h cycle in the laboratory indicated that rates did not significantly change throughout the night, and were not significantly different from those measured in the dark at midday. Accordingly, respiration rates were assumed to be constant over the 24 h cycle (in the model), but this question warrants further investigation.

This study also demonstrates how this approach can provide important insights into how differing photosynthetic performance of subsurface kelps across depths can influence overall annual productivity, and shows that increased photosynthetic performance offsets the effects of lower light in deeper water. *E. radiata* exhibited acclimation of photosynthetic performance to lower irradiance in deeper water, with higher α and P_{\max} and lower E_c compared to kelp in shallower water. Reduced E_c in deeper water and lower light has been reported for several other macroalgal species (Gómez et al. 1997, McGlathery & Pedersen 1999, Johansson & Snoeijs 2002, Terada et al. 2016). The high P_{\max} and α observed in deeper *E. radiata* also agrees with the

often observed positive correlation between P_{\max} and α in phytoplankton species (Harding et al. 1987) and macroalgae (Sand-Jensen 1988, Enríquez et al. 1995, McGlathery & Pedersen 1999), where those with high photosynthetic efficiency at low light also tended to exhibit high maximum photosynthetic rates. Similar to the responses observed with depth, seasonal changes in P - E parameters were consistent with reduced irradiance in winter, with increased α and reduced E_k and E_c during winter compared to summer. Increased chl a and lower ratios of chl c : a during winter compared to summer at both depths is consistent with adaptation to low light conditions, whereby chl a production is maintained at the expense of the accessory pigment chl c (Wheeler 1980, Gómez & Wiencke 1996). The changes in P - E parameters with depth and season are indicative of photoacclimation.

The methods used here can also be used to validate estimates of NPP from tissue measurement methods. This is illustrated by the fact that we found the difference in annual production between depths to be proportional to the difference in annual biomass (1.6× greater at 6 vs. 14 m depth) despite the lower light levels at 14 m. Although this may suggest that simply measuring standing stock is a good proxy for overall NPP across depths, the physiologically based method used in this study provides additional insights into primary production and how it varies over an annual cycle and depth. For example, it revealed that the proportional difference between NPP and biomass varied seasonally; in summer, biomass was 2.5× higher but NPP was only 1.7× higher at 6 m compared to 14 m depth due to the greater efficiency of deeper kelp. This acclimation of the photosynthetic response to lower light conditions in deeper water (and in winter) is critical for allowing the population to remain productive over the annual cycle in low light conditions (Ramus et al. 1976). Other factors that may influence the photosynthetic performance of kelp, such as temperature and nutrient availability, did not substantially differ between depths at our closely located sites, meaning we are confident that light availability is the important environmental factor driving the variation in photosynthetic response. However, it is important that variation in these factors is considered between sites, seasons and depths when applying this approach.

The daily production rates (\pm SE) of *E. radiata* (average 1.4 ± 0.1 g C m⁻² d⁻¹ across the entire study period and both depths) revealed that production of this species was near or slightly above the median published value for macroalgae (Duarte & Cebrian

1996). Daily NPP of subsurface *E. radiata* at 6 m depth was greater than that of the floating kelp *M. pyrifera* in summer and autumn, but lower in winter and spring (R. Miller et al. 2011). *M. pyrifera* is often used as an example of the extremely productive nature of kelp forests, but averaged over the year, daily NPP of *E. radiata* (1.7 ± 0.1 g C m⁻² d⁻¹) at 6 m depth is comparable to that of *M. pyrifera* (1.9 ± 0.4 g C m⁻² d⁻¹) (R. Miller et al. 2011). These findings highlight that the production of subsurface kelp forests such as *E. radiata* can be similar to, if not higher than that of the more well-documented and symbolic floating kelp forests.

CONCLUSIONS

This study is the first to quantify areal primary productivity of a subsurface kelp forest by incorporating P - E parameters measured on canopy-forming individuals *in situ* into a physiological model. A key advantage of the method presented here is that unlike tissue measurement methods, this procedure accounts for all carbon produced, including carbon released as DOC. Seasonal measurements of photosynthesis and respiration on the widespread kelp *Ecklonia radiata* identified depth-related variation, and this information was combined with biomass and underwater irradiance data to estimate NPP. This approach provides insights into how the different photosynthetic performance of kelp at depth can influence overall annual productivity. In particular, modelling revealed that the difference in annual production between depths was proportional to the difference in annual biomass, despite lower light, indicating that increased photosynthetic performance offsets the effects of lower light in deeper water. The approach used in this study provides an experimental framework to further investigate production over the depth range of subsurface kelps and seaweeds, and the relative importance of the various drivers of productivity. This is critical to improving our understanding of how these important coastal ecosystems are likely to be affected by global change.

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