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An *in situ* study of production from diel oxygen modelling, oxygen exchange, and electron transport rate in the kelp *Ecklonia radiata*

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ABSTRACT: Macroalgal forests provide the foundation for most shallow reef ecosystems in temperate environments; hence tools for accurately measuring primary productivity are integral for ecosystem management. This study compares estimates of production/potential production in an *Ecklonia radiata* kelp forest in Tasmania, Australia, using diel oxygen gross primary production (GPP) models, benthic exchange chambers, and electron transport rate in photosystem II measured using PAM fluorometry. Two approaches to modelling GPP show good fit with environmental dissolved oxygen (DO), with gross oxygen production of the kelp bed ranging between ~0–20 for one model and ~0–8 µmol O_2 m^{-2} s^{-1} for the other, with total daily GPP (±SE) of 464 ± 28 and 347 ± 7 mmol O_2 m^{-2}, respectively. The oxygen production rate of *E. radiata* in benthic chambers ranged between 0 and 9.6 µmol O_2 m^{-2} s^{-1}, with total daily production as 204 ± 13 mmol O_2 m^{-2}, half that estimated from modelling DO. The peak value for maximum relative electron transport rate was 49 µmol e^- m^{-2} s^{-1} at PAR of 208 µmol m^{-2} s^{-1}. Oxygen evolution from benthic chambers and electron transport rates from PAM fluorometry were well correlated; however, the latter may overestimate oxygen production. Water column DO can measure GPP of the benthic communities; however, additional measurements/more sophisticated models may be necessary. Benthic exchange chambers and PAM fluorometry can potentially estimate the contribution of *E. radiata* to total daily production provided that the measurements can be calibrated with other methods to obtain actual productivity. Additionally, upscaling requires reliable biomass estimates.

KEY WORDS: Diel oxygen modelling · PAM fluorometry · Benthic chambers · Oxygen exchange · *Ecklonia radiata* · Kelp forests · Primary productivity

1. INTRODUCTION

Macroalgal beds provide the ecological foundation for most shallow reef ecosystems in temperate marine environments. Overexploitation and the effects of coastal activities have resulted in significant habitat loss in coastal ecosystems (Jackson & Sala 2001), and human-induced climate change is now seen as a major threat to ecosystem health in many marine systems (Richardson & Poloczanska 2008, Wernberg et al. 2011). Primary production is an integral aspect of system function, and can provide a real-time indication of system health. Hence, suitable tools are required for accurate measurement in space and time. As a result of the diversity of measurement methods, estimates of primary production for temperate reefs are numerous and variable (Madsen et al. 2001). This can lead to challenges for ecologists attempting to amalgamate research findings to facilitate long-term, broad-scale perspectives, or to compare research be-

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tween different studies that are spatially or temporally separated. However, to date there has been little research to quantify and compare differences in productivity estimates from multiple techniques applied simultaneously to the same system.

Perhaps the oldest and most extensively utilised method of measuring primary production in aquatic ecosystems uses diel changes in 'free water' dissolved oxygen (DO) to calculate rates of production and respiration (Cole et al. 1998, Gelda & Effler 2002, Lauster et al. 2006). Although first applied in coral reef systems (Van de Bogert et al. 2007), the free-water oxygen method (FOM) became widely accepted after work by Odum & Odum (1955) and Odum (1956, 1957) broadened application from coral reef metabolism into river and lake systems. The technique has now been used extensively in aquatic ecosystems (e.g. Smith & Key 1975, Kemp & Boynton 1980, Gattuso et al. 1993, Cole et al. 1998, Hanson et al. 2003, Van de Bogert et al. 2007, Staehr et al. 2010). At their simplest, FOM models estimate gross primary production (GPP) from DO measurements through time, factoring ecosystem respiration (estimated from night time changes in DO), exchange of O_2 from the atmosphere (typically modelled as a function of the concentration gradient between water and atmosphere, dependent on temperature, with a wind-derived coefficient), and vertical and horizontal advection (Hatcher 1977).

Development in technology has made it easy to continuously measure DO concentrations and relevant physical and chemical parameters accurately, allowing for detailed description of temporal variability and calculation of metabolism. However, despite the obvious advantages, questions remain about the extent to which free-water measurements actually represent whole-system metabolism (Lauster et al. 2006, Van de Bogert et al. 2007, Coloso et al. 2008). In particular, assumptions associated with advection, quantification of the air–water exchange and respiration estimates require consideration (Hatcher 1977). Also, depending on the scale and precision at which advective and diffusive processes are captured, these models can be numerically complex.

Other open system techniques exist, most notably the 'eddy covariance' method (Berg et al. 2003). This approach relies on measuring vertical water column velocity and O_2 concentration in a ~1 cm^3 volume located 5 to 30 cm above the benthos. The underlying assumption is that all O_2 transported vertically toward or away from the benthos is facilitated by turbulent motion, hence the vertical flux can be derived from these 2 variables (Berg & Huettel 2008). However, a number of challenges remain, including deployment considerations as well as requirements on sensor response time (McGinnis et al. 2011). Most notably, technology constraints and microelectrode breakages mean that deployments are relatively short, thereby limiting the scalability of productivity estimates (Glud et al. 2010). The 'eddy covariance' method has thus far been successful in measuring O_2 flux over relatively simple habitats in less dynamic environments, such as sheltered soft sediment and seagrass systems (Berg & Huettel 2008, Glud et al. 2010, Long et al. 2015). Moreover, flux estimates using this approach have been limited to small space and time scales. Thus, at this point in time, the dynamic physical environment in which most macroalgal systems occur and the need to estimate production over meaningful ecological space (meters to 100s m) and time (days) scales precludes the application of this approach for this purpose.

Another widely used method for measuring photosynthetic rate in macroalgae involves enclosing entire individuals in chambers to measure changes in DO or, more rarely, carbon dioxide (CO_2). *In situ* measurements to estimate the initial slope (α) of the irradiance-dependent O_2 evolution curve, the rate of maximum photosynthesis (i.e. oxygen production), irradiance where α intercepts the maximum rate of oxygen production under light saturation (P_{max}), and dark respiration rates were made possible with the design of data-logging oxygen exchange devices (Hatcher 1977, Carpenter 1985, Cheshire et al. 1995, 1996, Fairhead & Cheshire 2004, Rodgers & Shears 2016). Since respiration can also be estimated, the method can determine both GPP and net primary productivity (NPP) over periods of 24 h. Using this kind of apparatus, primary productivity and photosynthesis have been measured for kelp and other macroalgae (Hatcher 1977, Cheshire et al. 1997, Longstaff et al. 2002), seagrass (Sargent & Austin 1949), invertebrate symbioses (Cheshire et al. 1997, Hoegh-Guldberg & Jones 1999), and turf algae (Odum 1957, Staehr et al. 2010). This method allows specific measurement of the primary productivity of a species/individual of interest. However, the need to enclose the algae inside a chamber substantially limits scale, and results are sensitive to the level of stirring/water movement in the chamber.

Simplicity and convenience have led to the increasing use of pulse amplitude modulation (PAM) fluorometry as a non-invasive method to monitor the functional state of photosynthetic organisms in real-time. PAM fluorometry measures chlorophyll *a* (chl *a*) fluorescence associated with photosystem II (PSII)

(Rosenqvist & van Kooten 2003) as a measure of photosynthetic potential and is increasingly used to assess the physiology of macroalgae *in situ* under varying environmental conditions (Franklin & Badger 2001, Longstaff et al. 2002, Kim & Garbary 2006, Edwards & Kim 2010). Fluorescence measurements can provide estimates for a number of different photosynthetic characteristics which indicate various aspects of an organism's photophysiology (Ralph & Gademann 2005). Electron transport rate (ETR) or, when an absorbance factor is not used, relative electron transport rate (rETR), is measured at increasing light intensities to produce rapid light curves (RLCs). Curves fitted to raw rETR data facilitate derivation of the saturating light intensity (*Ek*), relative maximum electron transport rate or photosynthetic capacity (rETRmax), and the initial slope of the curve, known as the light harvesting efficiency of photosynthesis (α).

Collectively the parameters derived from PAM fluorometry have been interpreted as a measure of potential photosynthetic performance. ETR has been found to relate to photosynthetic activity as measured by CO_2 uptake or oxygen evolution (Beer et al. 1998), and so PAM fluorometry is often interpreted as a comparable method of measuring photosynthetic performance, or at least potential photosynthetic performance, with the benefit of providing virtually instantaneous (90 s) measurements. However, there are indications that PSII activity estimated from PAM fluorometry only correlates well with photosynthetic rates estimated using respirometry chambers at low irradiances, with increasing discrepancies at higher irradiances (Beer et al. 1998, 2000, Häder et al. 1997, Longstaff et al. 2002, Colombo-Pallotta et al. 2006, Enríquez & Rodríguez-Román 2006, Nielsen & Nielsen 2008). In addition, measurements are focused on a small piece of tissue on a single leaf blade and so results cannot be indicative of overall physiology of the individual. Moreover, at a basic theoretical level, there are many reasons why activity in PSII — at the beginning of the photosynthetic pathway — need not equate to production of O_2 or photosynthate, or thallus growth. For example, there are alternative electron sinks which may consume O_2 (Mehler reaction and chlororespiration) (Consalvey et al. 2005).

There are fundamental dissimilarities in the nature of the measurements made using each of these methods. PAM fluorometry gives an instantaneous measure of ETR in PSII from a single (and very small) location on the surface of the thallus; it says nothing about the downstream molecular machinery between that point and the fixation of carbon or production of photosynthate or the state of PSII elsewhere on that thallus. Oxygen exchange measured in closed chambers *in situ* provides an integrated measure of oxygen evolved under a complex natural light environment for a sample (comprising a thallus portion, whole plant, or even a part of an algal assemblage). Open system models estimate GPP over an entire community, with the estimated productivity in an area often attributed to the largest and most populous species despite the presence, usually, of diverse sub-canopy and understorey species. We question whether these methods can be used to assess *in situ* photosynthesis in comparable situations, what the limitations are, and how they can be overcome.

The present study compares these most widely used methods for measuring productivity or aspects of photosynthesis in macroalgae in field research during the Austral summer, 2012 (when productivity is high). We used benthic chambers in a shallow-water temperate reef environment in Tasmania, Australia, to measure oxygen exchange in the kelp *Ecklonia radiata*, the most important habitat-forming marine macroalga species in temperate Australia. Concurrent diurnal PAM fluorometry measurements were taken to estimate *Ek*, rETRmax, and α. In addition, diel changes in 'free water' DO at various heights in the water column were recorded to facilitate estimating rates of production and respiration for the entire system by fitting 2 kinds of diel GPP models.

2. MATERIALS AND METHODS

The experiment ran over the austral summer period 12 to 23 February 2012. A transect was placed along the ~7 m contour line in Canoe Bay (43.12583° S, 147.96056° E), Tasmania, Australia, which supports a sheltered and dense *Ecklonia radiata* forest over dolerite reef. The relatively calm setting of the site provided stable environmental conditions (including low tidal variation, minimal wave action and horizontal flushing, and low anthropogenic activity), for the duration of the experiment. The average density of adult *E. radiata* sporophytes at the site was 7.9 ± 0.5 m^{-2} (±SE), of average individual size 499 ± 26 g (±SE). Density values were determined from 20 randomly positioned quadrats (1 m^2) at the site, and average individual size was determined from laboratory measurments taken of 40 randomly sampled individuals. Over the experimental period, vertical profiles of DO, temperature, turbidity, and salinity were measured using a hand-held sensor (YSI Sonde 6-series model 6600 V2) at varying

times of the day (n = 12). Deployment of all other equipment was by divers, with sampling occurring within 10 m of the experimental transect. The tidal range was <0.90 m during the experimental period.

2.1. Modelling ambient dissolved oxygen

DO was measured at 10 min intervals from midday on 12 to 23 February 2012 by a series of sensors deployed in the water column (~7.2 m depth). Two sensors (D-Opto Logger, Zebra-Tech) were placed at 0.5 and 3.0 m depth on an inelastic line attached to a large surface float. This arrangement was attached to a heavy, taut but elasticised 'string' fixed to a large anchor, which ensured that sensors remained in the same position at a constant depth from the surface through the tidal cycle. A further 3 sensors were fixed at positions 0.30, 0.50, and 0.80 m above the benthos (NexSens SDL500 data logger with Ponsel conductivity/salinity sensor; Aanderaa oxygen fast optode Y330F). A sensor (Licor 192SA Underwater Quantum Sensor) to measure photosynthetically active radiation (PAR) and the associated data logger were situated at a depth of 1.2 m above the benthos, at the top of the kelp canopy. Temperature and salinity in the water column were recorded at 10 min intervals at depths of 0.5 and 3.0 m from the surface ('string') and 0.70 m above the benthos. A weather station was mounted onshore (~110 m from transect, ~1 m above sea level) to continuously record wind speed and direction.

Two models were developed that book-end a spectrum of possible approaches. The first involved fitting a Fourier series to the DO data ignoring any DO–PAR relationship. The Fourier elements were then fitted back to the periodic DO data using least squares in a linear model to estimate forcing (O_2 production) from the kelp layer. The second model also utilised the periodic DO data; however a DO–PAR relationship was assumed. The parameters of this relationship were estimated by fitting to the DO data using least squares and from this the forcing (O_2 production) from the kelp layer was estimated.

For both models, it was assumed that the area was horizontally isotropic, with uniform coverage of macroalgae. It was also assumed that there was no vertical stratification in the water column (as supported by empirical data from the sonde profiles) and no significant effect of waves and tide. Again, the many instruments we deployed did not indicate influence of different water masses through the tidal cycle, which is not surprising given that the site was shallow (6–7 m), close to shore, at the sheltered distal end of the bay, that the tidal range was low (<0.90 m), and weather benign during the experimental period. Thus, any horizontal flux was discounted and the system was treated as 1-dimensional in the vertical. A coordinate system was constructed so that $z = 0$ at the benthos, $z = h$ at the top of the macroalgae canopy and $z = H$ at the sea surface. Assuming that vertical advection can be ignored, the concentration of dissolved oxygen $\Psi_{(z,t)}$ satisfies a diffusion equation in the form:

$$\frac{\partial \psi(z,t)}{\partial t} = F(z,t) + K\nabla^2\psi(z,t) \quad (1)$$

where $F(z,t)$ represents the generation and consumption of O_2 at height z and time t, K is a diffusion constant, and ∇ is the Laplacian operator. Assuming that oxygen is generated and consumed uniformly within the macroalgal bed, there may also be a small constant consumption throughout the water column, so that F takes the form:

$$F(z,t) = f(t)u(h - z) \quad (2)$$

where u is the Heaviside step function, and f represents the rate of uniform generation throughout the kelp layer.

We disregard any respiration in the rocky reef, and so there is no flux at the lower boundary:

$$\left.\frac{\partial \psi}{\partial z}\right|_{z=0} = 0 \quad (3)$$

At the sea surface we have the condition:

$$\left.\frac{\partial \psi}{\partial z}\right|_{z=H} + k\left(\psi(H-l,t) - \psi^{(sat)}(t)\right) = 0 \quad (4)$$

where $k = k_b/\mathrm{K}$ (see Baird et al. 2014), and the transfer rate k_b (m s^{-1}) is:

$$k_b = \frac{0.0283}{360000}u^3\left(\frac{S_c}{660}\right)^{-1/2} \quad (5)$$

where u is the wind speed (m s^{-1}), and S_c the Schmidt number (from Wanninkhof 1992, Baird et al. 2014). A periodic condition was adopted for the initial condition:

$$\psi(z,0) = \psi(z,1) \quad (6)$$

Initial conditions for the model assumed that consumption and generation of oxygen were periodic over the experiment. Given the experimental period of only a few days, there was no seasonal component to variables such as day length and temperature. To make the observed time series indefinitely periodic, the ends of the 10 d time series were joined. To do

this, an initial segment of data was replaced with a weighted average of itself and a corresponding segment at the end of the data that smoothly transitioned between the two, and then the end segment was dropped. Thus DO for the first 12 h is an amalgam of the actual first 12 h and the last 12 h, and the last 12 h has been discarded. The oxygen concentrations for the exact probe heights were calculated by linearly interpolating the finite difference solution.

Finite differences were used to solve the system for a given forcing (Smith 1985). A simple implicit scheme was adopted:

$$\frac{\psi_{i,j} - \psi_{i,j-1}}{\Delta t} = F_{i,j} + \frac{K}{(\Delta z)^2}(\psi_{i-1,j} - 2\psi_{i,j} + \psi_{i+1,j}) \quad (7)$$

The system was solved on a grid offset in the vertical to span both the upper and lower boundaries so that at the surface the boundary condition takes the form:

$$-rK_j\psi_{i-1,j} + (2rK_j + 1)\psi_{i,j} - rK_j\psi_{i+1,j} - \psi_{i,j-1} = \Delta t F_{i,j} \quad (8)$$

where:

$$r = \frac{\Delta t}{(\Delta z)^2} \quad (9)$$

In Model 1, the forcing is expressed as a sum of Fourier components:

$$f(t) = a_0 + \sum_{k=1}^{N} a_k \sin(2k\pi t) + b_k \cos(2k\pi t) \quad (10)$$

The finite difference solver was used to determine the expected DO concentrations at the probe heights for each Fourier (sine or cosine) component of the forcing, and the unknown coefficients (the a_i and b_i) were determined by fitting the expected DO concentrations to the observed concentrations by least squares.

In Model 2, the forcing is assumed to be a function of the observed PAR:

$$f = a + b[1 - \exp(-c\mathrm{PAR})] \quad (11)$$

which defines the relationship between O_2 production and PAR (after Platt et al. 1980). Again, the coefficients a, b and c are determined by fitting the expected DO concentrations determined by finite differences to the observed concentrations by least squares. However, in this case the problem is nonlinear and the unknown coefficients were determined by numerical minimization.

For both models, the vertical profiles of dissolved oxygen measured during the experiment were compared to the expected concentrations predicted by the model to further evaluate the validity of the forced solutions. After compensating for respiration determined during the nighttime periods, oxygen generated in the macroalgae bed and canopy was expressed per m^2 of benthos (canopy height 0.40 m) and plotted against the average incident photon flux density (PAR; µmol photons m^{-2} s^{-1}) for each model. Daily productivity rates were calculated from the daily sum of productivity for each of the models.

2.2. Benthic chambers

Benthic oxygen evolution chambers were deployed on 5 days during the experimental period (13, 15, 19, 21 and 23 February 2012). Each chamber (Chamber 1 and 2) was situated in close proximity to the transect at a depth of 7–8 m (depending on tide) and contained a single, complete adult *E. radiata* sporophyte of average size and condition. Thalli were sourced from within 10 m of the transect from 7–8 m depth. Each individual was placed in the chamber with intact holdfast, but holdfast fauna were first removed. Chambers were cylindrical (0.145 m diameter × 0.6 m high) clear Perspex with a volume of 40 l, constructed at the University of Tasmania based on the design of Carpenter (1985). Each chamber cycle lasted 24 h, with flushing of the internal seawater every 2 h, and chambers contained a battery-operated stirring mechanism to ensure mixing in the chamber to minimise establishment of a boundary layer on the algae and avoid stratification of oxygen in the water.

On completion of the experiment, the wet weight of each individual was recorded and surface area of the thallus estimated. Estimates of thallus area were based on the thallus area to weight ratio calculated for *Ecklonia radiata* in the Canoe Bay site. To estimate this ratio, 20 individuals chosen to encompass the full size spectrum present in the study area were returned to the laboratory where mass was recorded and thallus surface area measured by tracing the kelp outline onto grid paper. The relationship (R^2 = 0.94) between mass (m, g) and surface area (s, m^2) is given as:

$$s = 0.0019m + 0.0308 \quad (12)$$

Background photosynthesis by phytoplankton in local waters during this period is typically very low due to depleted nutrient concentrations (at nearby Maria Island [42° 34′ 38.41″ S, 148° 3′ 45.65″ E] during February 2012 and 2013, production in chambers containing only seawater was <2 µmol O_2 h^{-1} in each benthic chamber), and so was not considered further. Respiration was measured during the night and assumed to be constant over a 24 h cycle. In this way gross oxygen production could be calculated for daylight hours by

compensating for respiration. Average photosynthetic rates for each flushed cycle were expressed per unit of estimated algal surface area (considering both sides of the thallus) and plotted against the average incident photon flux density (PAR) for each cycle to produce a photosynthesis/irradiance curve.

In order to calculate daily production estimates comparable to those calculated by the FOM models, the daily sum of productivity for each m^2 of tissue in each chamber was used. After scaling for the density of adult sporophytes on the benthos and average sporophyte size at the study site (as measured from 28 randomly selected individuals), a total surface area of tissue (7.824 ± 0.403 m^2, SE) was calculated for each m^2 of benthos. This was used to calculate daily production rates for each m^2 of benthos.

2.3. PAM fluorometry

PAM measurements occurred on 5 days during the experimental period (13, 15, 19, 21 and 23 February 2012). On each day, sampling was undertaken in the periods 05:00–06:00, 07:00–08:00, 10:00–11:00, 13:00–14:00, 16:00–17:00 and 19:00–20:00 h. For each period, measurements were taken from a set of 10 healthy mature sporophytes selected randomly within 10 m of the transect (7–8 m depth). The sampled area on each thallus was on a lateral (secondary lamina) located at one-third the length of the lamina from the top of the stipe and one-third along the branch/lateral from the centre of the thallus midrib.

Activity of PSII was estimated *in situ* by chl *a* fluorescence using a blue LED Diving PAM (Walz). A 'dark leaf clip' was connected to the algal thalli to ensure consistent spacing of the PAM fiber optic cable from the surface of the tissue and to enable fluorescence measurements without ambient light interference. RLCs were produced for ambient light-acclimated tissue using a built-in software routine, where actinic light intensity was increased in 8 steps (reaching a maximum of 463 µmol photons m^2 s^{-1} at 650 nm) of 10 s in duration. Before light-acclimated RLCs were commenced, tissue was quasi-dark adapted for 5–10 s to allow re-oxidation of the primary electron acceptor (e.g. Schreiber 2004, Stirbet 2011). All RLCs were conducted on fresh tissue *in situ*, with the area first gently wiped to remove epiphytic growth.

Because large variation in tissue light absorption could be expected in the macroalgae (see Section 4 for further details), we used the approach recommended by Saroussi & Beer (2007) and did not attempt to approximate actual ETR by using an absorption factor to represent the fraction of incident light absorbed by thalli. Curves were fitted to the raw ETR data to derive *Ek*, rETRmax, and α as a measure of 'quantum yield' or the light-harvesting efficiency of PSII. The empirical double exponential decay model of Platt et al. (1980) was selected as it effectively describes both the initial linear response and allows for photoinhibition at high light intensity:

$$\mathrm{rETR} = P_s\left[1-\exp\left(\frac{-\alpha E_d}{P_s}\right)\right]\times\exp\left(\frac{-\beta E_d}{P_s}\right) \quad (13)$$

where α is the light harvesting efficiency as measured by the initial slope of the RLC before light saturation, E_d is the downwelling actinic irradiance of the PAM's internal halogen light, β is the negative slope of the RLC at high irradiance, and P_s is a scaling factor defined as the maximum potential rETR in the absence of any photoinhibition (if β = 0, this is equal to rETRmax). The nonlinear least-squares function in the 'R' software environment (v. 3.0.0) was used to fit the model to each set of RLC data, and the parameters rETRmax and *Ek* were estimated according to equations given in Ralph & Gademann (2005). The following parameters were used in the curve-fitting routine to ensure convergence: iterations = 100; step-size = 1/1024; tolerance = 10^{-5}; initial seed value for rETR = maximum rETR derived from raw data, α = slope of linear regression fitted to first 3 points of raw data (typically in the range 0.7–1.0).

3. RESULTS

3.1. Estimating production using the ambient DO model

Both models provided estimates of DO that matched well with those recorded in the environment, particularly for the depths matching the near-bottom sensors within or just above the kelp canopy (Fig. 1A,B: P3–P5). For the sensors close to the surface (P1, P2) the match was less accurate, with the models underestimating oxygen in the water column. Small-scale perturbations in ambient DO were not reflected in either model (e.g. P2, Day 3 peak; Fig. 1). There was a tendency for the models to overestimate DO during nighttime periods for the 3 sensors near the seafloor.

The agreement between the DO sonde profiles and the DO predicted by both models at the 5 sensor depths was variable. For some profiles for both models there was a good fit (Profiles 2, 5, 7, 9 and 10; Fig. 2; shown here for Model 1). No predicted value

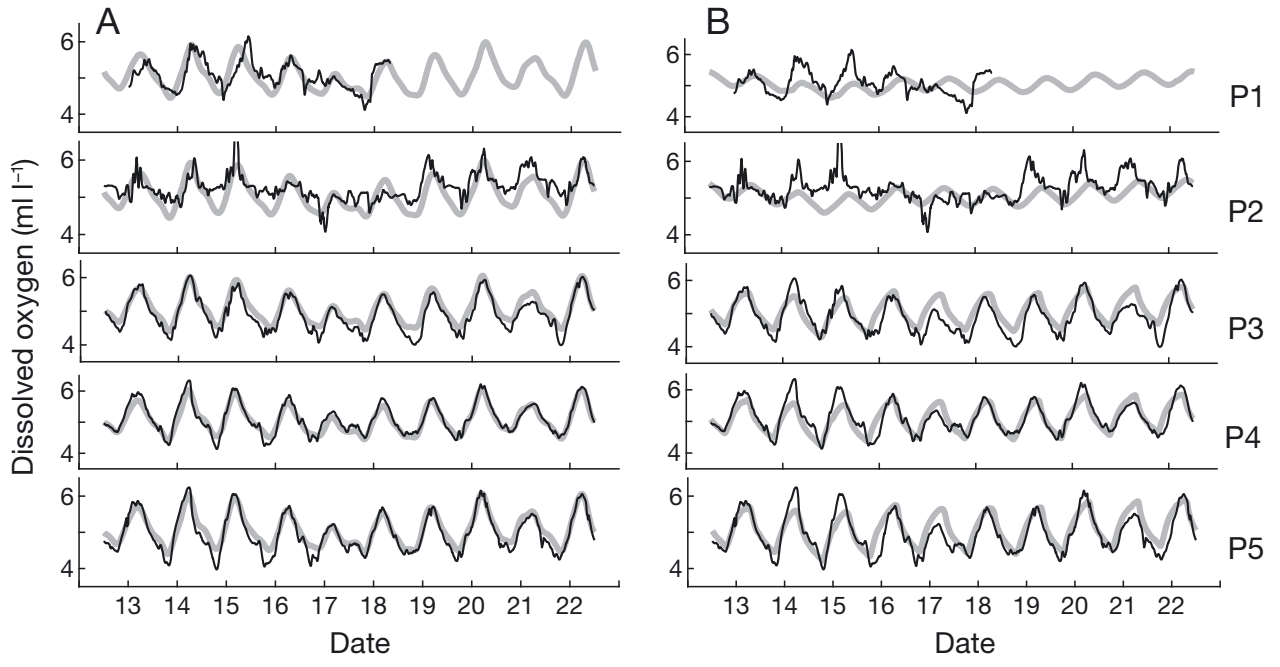

Fig. 1. Dissolved oxygen recorded at each probe (black line) and the dissolved oxygen predicted by the diel oxygen method (grey line) for (A) Model 1 and (B) Model 2 over the period 12 to 23 February 2012. P1–P5: dissolved oxygen sensors at depths corresponding to 0.5 and 3.0 m from the surface, and 0.8, 0.5, and 0.3 m from the seafloor, respectively

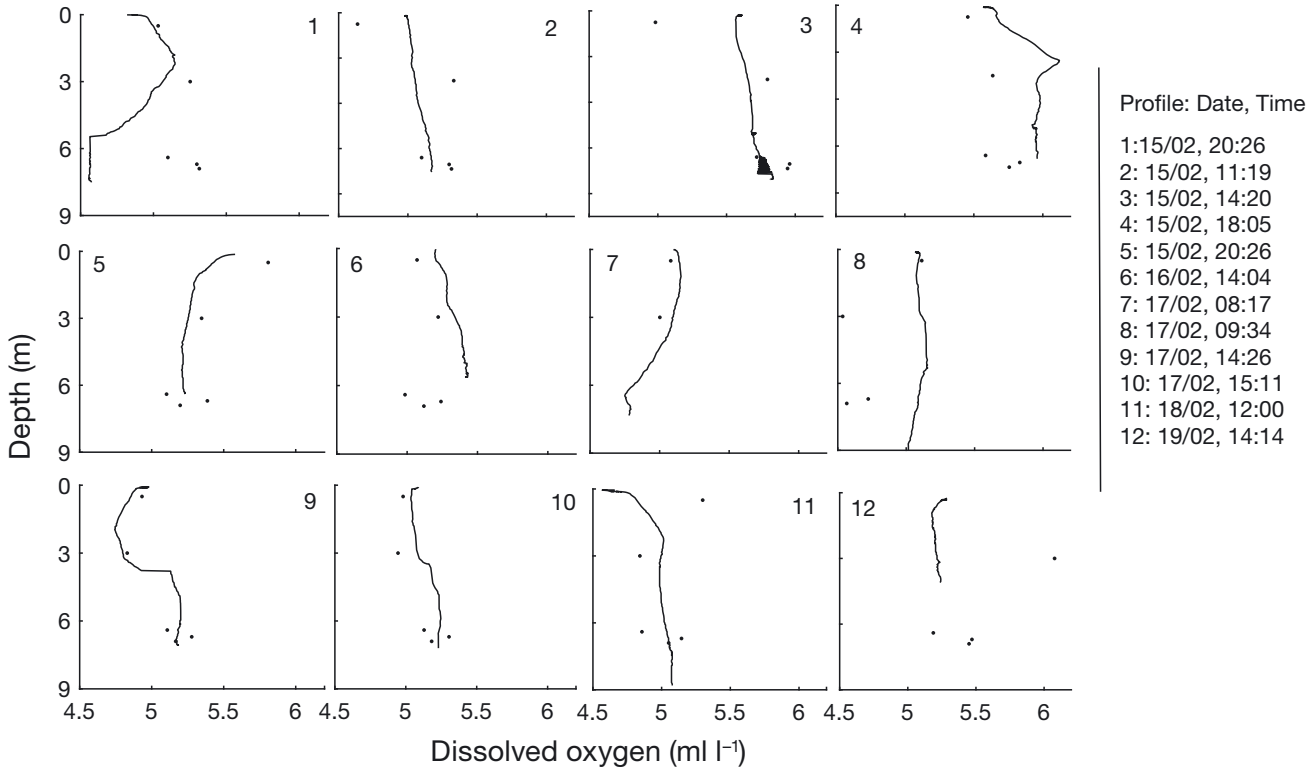

Fig. 2. Dissolved oxygen (DO) measured as vertical profiles using a sonde unit (solid lines) over the period 12 to 23 February 2012, predictions of DO from Model 1 (shown as dots) at depths corresponding to the position of DO sensors in the water column. Dates are given as d/mo

was >0.75 ml l^{-1} (>24 µmol l^{-1}) from that of the measured profile, with most falling within <0.5 ml l^{-1} (<16 µmol l^{-1}) from that of the measured value.

The rate of oxygen production per unit area of seafloor as a function of ambient PAR estimated from the ambient oxygen models ranged between ~0–20 µmol O_2 m^{-2} s^{-1} (Model 1) and ~0–8 µmol O_2 m^{-2} s^{-1} (Model 2; Fig. 3). For Model 1, maximum oxygen production increased with PAR, but there was large variation in oxygen production at low PAR levels. This variation was not evident at high light levels with, for the most part, consistently high oxygen production predicted by the model for PAR over 200 µmol m^{-2} s^{-1}. For Model 2, oxygen production increased rapidly before reaching a plateau at PAR ~20 µmol photons m^{-2} s^{-1}. Total (gross) daily oxygen production was estimated to be 464 ± 28 (SE) and 347 ± 7 mmol O_2 m^{-2} d^{-1} for Model 1 and Model 2, respectively (Table 1).

3.2. Benthic chambers

Ambient photon flux density at 6 m depth on days during which benthic oxygen chambers and PAM fluorometry measurements were undertaken peaked at ~450 µmol photons m^{-2} s^{-1} during midday of 15 February (Day 3 of the diel models), with a comparable, but shorter, peak on 13 February (Day 1) (Fig. 4A). Ambient PAR showed substantial variation between days, reflecting variable cloud cover, with a peak on 21 February <150 µmol photons m^{-2} s^{-1}.

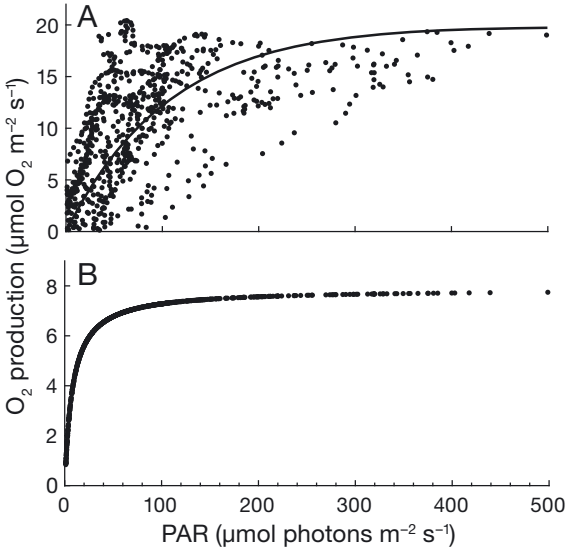

Fig. 3. Photosynthesis vs. irradiance (PAR) obtained from the diel oxygen method from 12 to 23 February 2012 for (A) Model 1, where the model was not constrained by a DO vs. PAR relationship, and (B) Model 2, where the model was constrained by a DO vs. PAR relationship (see Section 2). For Model 1 the curve is fitted according to Platt et al. (1980) where P_s = 20.422, α = 0.187, and β = 0. DO is calculated from 10 min 'blocks' throughout the day-time and PAR is an average of the 10 min period

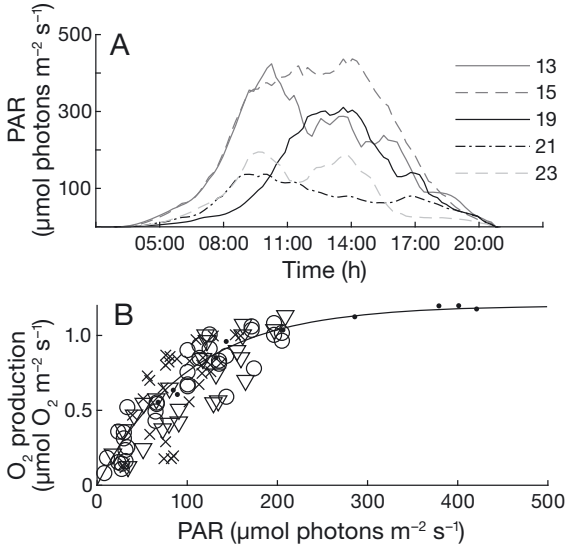

Fig. 4. (A) Diurnal irradiance (PAR) in Canoe Bay (for the days of PAM fluorometry) and oxygen evolution chamber measurements (13, 15, 19, 21 and 23 February 2012). Irradiance was measured at a depth of ~6 m. (B) Photosynthesis vs. irradiance (PAR) obtained from oxygen evolution. Curve is fitted according to Platt et al. (1980) where P_s = 1.2, α = 0.012, and β = 0. Rate of O_2 production is for each m^2 of algal tissue (both sides of thallus). Dot = 15 February; circle = 19 February; cross = 21 February; triangle = 23 February

Table 1. Total gross daily production estimated (mean ±SE) by the benthic chambers and diel oxygen models for 12 to 23 February 2012 (given as d/mo). Units of production are mmol O_2 m^{-2} seafloor d^{-1}. Estimates for each chamber have been scaled to mean biomass density of kelp on the reef. Note that data from the chambers are not available on all days

Source	14/02	15/02	16/02	17/02	18/02	19/02	20/02	21/02	22/02	23/02	Avg GPP
Chamber 1		170				193		218		209	197 ± 11
Chamber 2		202				217		272		149	210 ± 25
Chambers (avg)		186				205		245		179	204 ± 13
Model 1	562	492	420	308	418	479	551	398	542		464 ± 28
Model 2	346	388	378	332	347	339	362	357	353		347 ± 7

Gross photosynthetic rate for each m^2 surface area of tissue increased with increasing irradiance, reaching a maximum rate of 1.1 µmol O_2 m^{-2} s^{-1} on 15 February at an ambient photon flux density of 457 µmol photons m^{-2} s^{-1} (Fig. 4B). After scaling for the density of kelp sporophytes and average sporophyte size at the study site, oxygen net photosynthetic rate reached a maximum of 9.6 µmol O_2 m^{-2} s^{-1}. The rate of oxygen production with PAR increased gradually until ~200 µmol photons m^{-2} s^{-1}, then tended towards an asymptote. The relationship between oxygen production and ambient light intensity was consistent regardless of the day of measurement. Daily O_2 production (mean ± SE) averaged 25 ± 2 mmol O_2 m^{-2} d^{-1} of algal tissue and 204 ± 13 mmol O_2 m^{-2} d^{-1} of benthos.

3.3. PAM fluorometry

rETRmax and *Ek* derived from RLCs measured by PAM fluorometry showed a rapid increase with ambient photon flux density before tending towards an asymptote at PAR of 200 µmol photons m^{-2} s^{-1} (Fig. 5A,C). The peak value for rETRmax was 49 µmol e^- m^{-2} s^{-1} at PAR of 208 µmol photons m^{-2} s^{-1} with a peak in *Ek* of 98 µmol m^{-2} s^{-1} at the same PAR. α declined until PAR of 200 µmol m^{-2} s^{-1} after which values again levelled out (Fig. 5B). Values ranged between 0.9 and 1.2 µmol m^{-2} s^{-1}. There were no differences in the relationship between any of the photosynthetic parameters and ambient light intensity for each of the days. The shape of the curve of rETRmax as a function of PAR was similar to the oxygen production/PAR curve obtained from the chambers (Fig. 6). In both cases rETRmax and oxygen production increased with PAR to reach an asymptote. We note that, given similarities in the curves, it is relatively straightforward to calibrate one against the other.

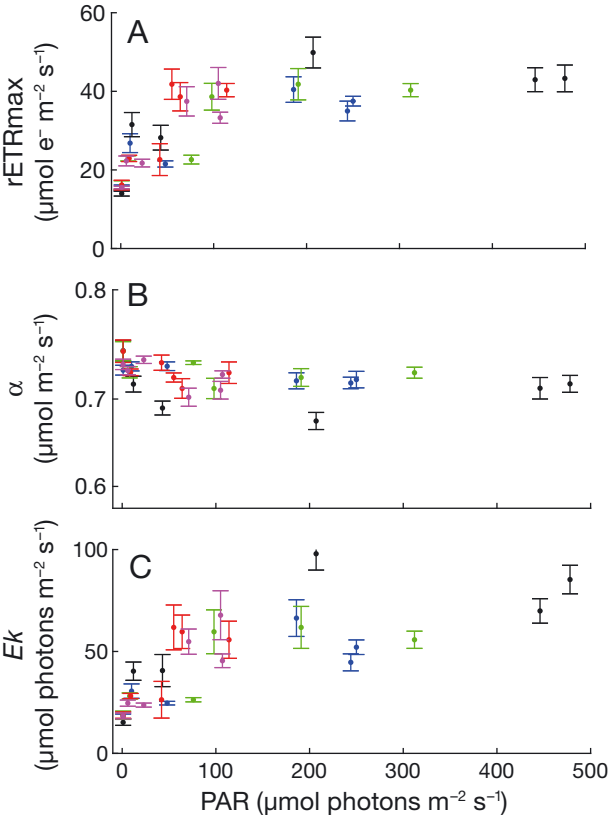

Fig. 5. Photosynthetic characteristics of *Ecklonia radiata* in Canoe Bay during February 2012 as a function of ambient PAR at the time of measurement. Plots show (A) maximum relative electron transport rate (rETRmax); (B) light harvesting efficiency of photosynthesis (α), and (C) saturating light intensity (*Ek*), all derived from RLCs measured by PAM fluorometry. Days are indicated as: blue = 13 February; black = 15 February; green = 19 February; red = 21 February; pink = 23 February

4. DISCUSSION

Measurement of photosynthesis in marine communities *in situ* presents many challenges and uncertainties. This study details an attempt to quantify productivity in *Ecklonia radiata*, the dominant habitat-forming kelp species in southern Australian temperate marine communities. Modelling of 'free water' diel oxygen, change in oxygen concentration in benthic respiration chambers, and PAM fluorometry are all established methods for estimating macroalgal productivity or potential productivity in marine environments; however, each method is subject to limitations. Conducting the 3 methods simultaneously at the same field site permits assessment of their utility and practicality to measure photosynthesis, or proxies thereof, of seaweed or seaweed beds *in situ*.

4.1. Modelling ambient dissolved oxygen

Despite the simplifying assumptions, both models provided a good fit to the observed water column DO data. The fits suggest that the assumptions are largely valid for the study environment and reflect our choice of site (shallow extensive kelp beds in the distal sheltered part of the bay to minimise influence of horizontal transport) and time of year (low tidal range and benign weather conditions). The underestimation/overestimation of DO at the surface/benthos at night may indicate some inaccuracy in the estimate

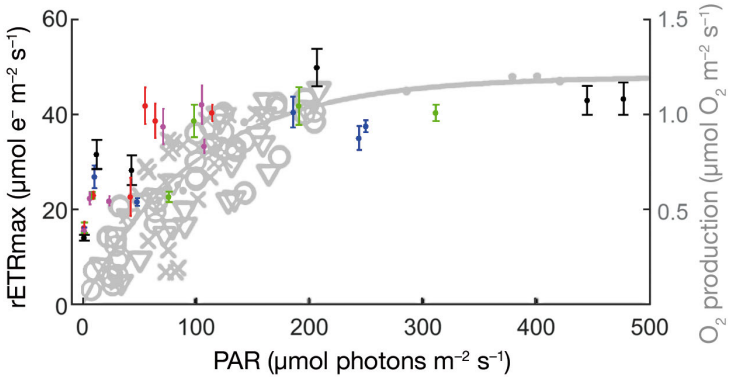

Fig. 6. Photosynthetic characteristics of *Ecklonia radiata* in Canoe Bay during February 2012 as a function of ambient PAR at the time of measurement. Plot shows rETRmax (coloured points) derived from RLCs measured by PAM fluorometry. Days are indicated as: blue = 13 February; black = 15 February; green = 19 February; red = 21 February; pink = 23 February. Overlayed in grey is photosynthesis vs. irradiance (PAR) obtained from oxygen evolution. Curve is fitted according to Platt et al. (1980) where P_s = 1.2, α = 0.012, and β = 0. Rate of O_2 production is for each m^2 of algal tissue (both sides of thallus). Dot = 15 February; circle = 19 February; cross = 21 February; triangle = 23 February

of vertical diffusion of DO when respiration is the key driver of change in water column DO. The fit was less accurate at the surface, possibly indicative of variation in the air–surface diffusivity dependent in part on wind. The models also showed, for the most part, good correlation with the vertical DO profile data (Randall 2018). Our results may indicate small-scale spatial variation in DO concentrations in the environment or, more likely, reflect inaccuracies in estimating vertical diffusion at some times in the diurnal cycle, particularly at the surface. Further information on local water column dynamics may help to better establish recurrent diurnal patterns and improve the accuracy of the models. Nonetheless, as a whole, both models provide a good fit with the observed environmental DO.

The large variability in DO at low irradiances for the first model may reflect that rates of change in DO are different at the beginning and end of the day when PAR is equally low. As irradiance increases in the morning, DO rises in the water column from the minimums reached overnight. This can result in high rates of DO change corresponding to relatively low PAR. DO builds up in the water column over the daytime, and in the afternoon—when irradiance again decreases—DO levels show only minimal increase (or may decrease) from the peak reached in the middle of the day. For the second model, the maximum production rate was less than half of that of the first model, although total daily production was only 25% lower. The sharp increase in production at relatively low PAR indicates that the model is estimating productivity close to maximum levels for a large portion of the day, in contrast to the first model where maximum productivity occurs only during short periods. Hence, although peak productivity rates are much lower, total daily production is reasonably close to that of Model 1.

Overall, both models indicate estimates of DO production much greater (Model 1 >100% and Model 2 >75%) than values produced by incubating individual kelps in benthic chambers *in situ* and correcting for average biomass density of kelp on the reef. This result is in contrast to previous research in stream and coral reef systems where these different methods have been found to be comparable (Klumpp & McKinnon 1989, Hoegh-Guldberg & Jones 1999). However, the nature of the study systems in these previous studies allowed sections of the entire benthic photosynthetic community to be enclosed in the chambers, whereas in the present study DO estimates from the oxygen exchange method are solely the product of individual *E. radiata* sporophytes. Although this rocky reef environment is dominated by the *E. radiata* canopy, it also contains a diverse understory with a myriad of red, green, and other brown seaweeds, including coralline species, of a range of sizes, as well as microbenthic species in the sediment or as biofilms. These species are generally well adapted to a low-light environment beneath the *E. radiata* canopy and can contribute greatly to overall system productivity (Lobban & Harrison 2000, Larkum et al. 2006). Our results indicating that the kelp canopy accounts for about half of the total production of benthic algae are remarkably similar to those from respirometery studies of intertidal communities in New Zealand where the fucoid canopy provided approximately half of the total production (Tait & Schiel 2011, 2018). Interestingly, in their work it was shown that assemblages with more speciose sub-canopies were more productive than when the sub-canopy comprised fewer species (Tait et al. 2014). Given that our benthic chambers recorded oxygen productivity solely by *E. radiata*, it is to be expected that estimates of productivity from the FOM model will be substantially larger as the DO probes integrate the total oxygen output from the entire community. Our results are also consistent with more recent findings on nearby artificial reefs at a similar depth, which showed a clear positive relationship between the diversity of the whole benthic macroalga assemblages and net primary production per

unit biomass of macroalgae (C. R. Johnson unpubl.).

Fairhead & Cheshire (2004) report net daily production of *E. radiata* as measured by oxygen exchange chambers at a depth of 10 m (South Australia) as 382 µmol O_2 g^{-1} dry weight, which when scaled for average algae weight and biomass at our site in Canoe Bay and using a ratio of wet weight:dry weight of 7.1 (Shepherd 2013) would result in a total daily production estimate of ~200 mmol O_2 m^{-2} seafloor d^{-1}. This rate is virtually identical to that which we measured (daily production of 204 mmol O_2 m^{-2} seafloor d^{-1}) with the benthic chamber method, indicating that productivity in this Tasmanian kelp forest is on par with other regions.

Given that the kelp beds are dominated by large kelps or fucoids, it has previously been assumed that scaling up estimates of productivity from small-scale measurements (e.g. oxygen exchange chambers) of individual kelps will give reliable estimates of whole assemblage production. However, the results of our diel models suggest that this will underestimate community production, and that production of the whole assemblage is about double that based on measurement of *E. radiata* alone, as has also been found for southern hemisphere intertidal systems (Tait & Schiel 2011, 2018). Estimates of total kelp bed production might possibly be achieved through the use of large chambers fixed to the benthos that incorporate the understory and substratum, although this would be very difficult on the kind of boulder substratum that characterised our study site. Overall, our results suggest that the diel oxygen method potentially addresses a need for better measurements of whole assemblage production integrated over all species and at more ecologically meaningful scales of space (10^0 to 10^3 m^2) and time (10^0 to 10^1 d).

To the authors' knowledge, no research has utilised measurements of ambient DO to estimate community production in *E. radiata* kelp forests, thus making the accuracy of Models 1 and 2 difficult to ascertain. The method has been widely used in kelp beds dominated by *Macrocystis pyrifera*, with values of 1 mol m^{-2} s^{-1} reported by Jackson (1977), and similar results given by Towle & Pearse (1973). Although this value is ~2 times that estimated in the present study for *E. radiata*, it is important to consider that *M. pyrifera* is a much larger and faster-growing species that spans the entire water column, so in many cases total biomass m^{-2} seafloor of *M. pyrifera* will be much greater than can be achieved for *E. radiata*, although this is dependent on site and density.

It is clear that large-scale holistic methods are needed for estimates of community-level production, and diel oxygen models can provide this approach for appropriate environments. The 2 models presented here illustrate opposite ends of a spectrum, with Model 1 allowing modelling of O_2 production as a flexible function of time but assuming no relation between O_2 production and PAR, whereas Model 2 assumes O_2 production to be a rigid function of PAR. With further work, it is envisaged that ultimately, the best approach will be a compromise between the two models, in which O_2 production is informed by, but not rigidly determined by, PAR. In addition, it is important to note that the models we present are, deliberately, simplified designs. Future developments could benefit by explicit numerical consideration of additional factors such as wave action, tides, and currents.

4.2. Benthic chambers

Using the benthic chamber method yielded results in line with other studies of macroalga production. For example, daily production of *Ulva lactuca* has been measured at 24 ± 5 mmol O_2 m^{-2} (Longstaff et al. 2002), and Cheshire et al. (1996) measured production in sub-samples of fucalean-dominated macroalgal community with estimates ranging from 73 to 167 µmol O_2 g^{-1} wet weight d^{-1} in summer (which converts to ~36–84 mmol using the mass:surface area relationship discussed earlier in Section 2.2). Other studies report estimates in terms of carbon fixation. If estimates of productivity (in terms of carbon) are to be based on O_2 measurements, they must be corrected for the ratio of CO_2 fixed:O_2 released, i.e. the photosynthetic quotient (PQ) (Hurd et al. 2014b). Few measurements of PQ have been made for seaweeds; however, those that have been done give values ranging from 0.42 to 1.50 (Hatcher 1977, Rosenberg et al. 1995). Generally, a 1:1 ratio is assumed (Hurd et al. 2014); with this ratio and a production value of 1 µmol O_2 m^{-2} s^{-1} at PAR >200 µmol photons m^{-2} s^{-1}, using the chamber method converts to ~115 mg C m^{-2} h^{-1}. Estimates of carbon production vary widely depending on species and even within species according to season, for example production of *Ascophyllum nodosum* is estimated to range between 187 mg C m^{-2} h^{-1} in December and 846 mg C m^{-2} h^{-1} in August (Golléty et al. 2008). However, it is important to note that these values are expressed in terms of seafloor area rather than tissue biomass; scaling our values to the average biomass per unit area of sea floor at our study site would result in values ~900 mg C m^{-2} h^{-1}.

As mentioned earlier, production per unit area of sea floor attributed to kelp (*E. radiata*) alone using this method is about half of the estimated gross production from modelling ambient DO. While other species undoubtedly account for a significant amount of the discrepancy, it is also possible that methods using benthic chambers underestimate DO production in nature. Longstaff et al. (2002) reported concerns with self-shading when using the oxygen exchange technique, and no doubt this is a factor to consider (as it is in nature) when interpreting the results of this method. While it is likely that dynamic self-shading occurs, a 'shading effect' is much more likely in relatively low-volume chambers in which individuals cannot be fully extended so that the projected surface area of algae exposed to light is overestimated. Another issue is the magnitude of water motion over the surface of the thallus, which affects boundary layer properties and thus gas diffusion and nutrient uptake rates (Patterson et al. 1991). Although the benthic chambers used in this method were adequate for the size of the *E. radiata* individuals used in the experiment and included mechanical stirrers to effect water motion, the algae were sheltered from the water movement they typically encounter (i.e. surge) in their natural environment. Algae in the natural habitat are semi-erect and move constantly in all directions; therefore, the chambers may artificially reduce gas diffusion and nutrient uptake, thus reducing photosynthetic rate.

Oxygen production in the benthic chambers rose gradually with PAR before tending towards an asymptote ≥200 µmol photons m^{-2} s^{-1}, again, similar to that found in other studies (Cheshire et al. 1996, Longstaff et al. 2002). Although Model 1 also showed production at these levels to taper off, the estimates at medium light intensities were highly variable (Fig. 3). On 21 and 23 February (Days 8 and 10 of the experiment), there were substantially lower maximum PAR levels (Fig. 4A), but this is not reflected in the ambient DO (Fig. 1). Understorey species, particularly red algae, are known for high photosynthetic efficiency at low light levels (Brouwer 1996, Weykam & Wiencke 1996, Eggert & Wiencke 2000) and it is possible that these species contributed to the relatively high oxygen we measured in the water column during days of low light when a lower productivity in the *E. radiata* canopy might be expected.

4.3. PAM fluorometry

The PAM fluorescence method showed estimates of photosynthetic capacity in line with previous research for *E. radiata* (Flukes 2015, Flukes et al. 2015, J. Randall et al. unpubl.). Estimates of rETRmax derived from RLCs determined using the PAM instrument showed a similar pattern to the oxygen evolution as measured in the respirometry, with both rETRs and O_2 evolution rates increasing until ~200 µmol photons m^{-2} s^{-1}, then tending to an asymptote. However, aligning the curves assuming equivalent production at the asymptote, at irradiances <200 µmol photons m^{-2} s^{-1}, the rate of increase was greater for rETRs. The similar asymptotic trend for rETRmax and oxygen evolution at irradiances >200 µmol photons m^{-2} s^{-1} indicates that both methods show an inhibitory response, or, more likely, saturation at high light levels.

Previous studies have found that at saturating light intensities, ETR values tend to overestimate O_2 evolution rates (Franklin & Badger 2001, Gelda & Effler 2002). Although the relationship between ETR and O_2 evolution can be expected to be tightly coupled as both fluorescence and O_2 evolution are tied to PSII, the relationship is not always linear (e.g. Longstaff et al. 2002). Fluorescence measurements yield estimates of photosynthetic potential, but these do not factor alternative electron sinks which may consume O_2 (e.g. Mehler reaction and chlororespiration) (Consalvey et al. 2005). It is important to consider that PAM fluorometry measurements are an indication of maximum potential photosynthesis, but that actual photosynthesis may be substantially lower.

Another factor contributing to overestimating potential photsynthesis using ETRmax can be error in the estimation of light available to photosynthesis in the tissue. Generally, an absorption factor is used to calculate ETR, based on the ability of the tissue to absorb light. Two methods can be used to estimate this absorbance, although both are complicated and are associated with methodological errors (see Enríquez & Borowitzka 2010). In addition, aquatic macrophytes show great variation in tissue light absorption within individuals and communities (Enríquez et al. 1994), and changes also occur diurnally due to chloroplast movement (Sharon & Beer 2008).

There can also be significant differences in photosynthetic rates between different tissues on the same individual (Gerard 1986, Sakanishi et al. 1991, J. Randall et al. unpubl.). Photosynthetic capacity and efficiency as indicated by PAM measurements reflects only the health of photosystems at the immediate location of the measurement and can be strongly influenced by tissue age, condition, and light history (including self-shading) (Enríquez & Borowitzka 2010, Oláh et al. 2010). We have noticed in our own

previous work that it is possible to obtain 'normal' RLCs and quantum efficiency estimates values from small areas of healthy tissue when >90% of an individual alga appears necrotic and senescing. It is thus important that single measurements should not be used to predict organism-scale physiology, and applying one absorption factor to a multitude of situations is likely to result in over-/underestimation of ETRmax. rETRmax was used in this study as it was considered that the errors inherent in applying absorption factors would negate any benefits. Regardless, the use of rETRmax still assumes consistency in light absorption across measurements (just without the multiplication factor), so the risk of over-/underestimation of ETR remains.

5. CONCLUSIONS

The ambient oxygen models provided a good fit to measurements of daily fluctuations in DO throughout the water column. Importantly, this approach provided estimates of DO production rates substantially higher than those estimated from incubation of intact *Ecklonia radiata* sporophytes in benthic respirometry chambers, as might be expected given that the approach with the chambers ignores contributions from all other species of macroalgae growing on the highly convoluted (i.e. boulder-dominated) reef surface. It is envisaged that, ultimately, the best method for modelling the kelp bed system may be a (more complicated) hybrid of both approaches that will both define the relationship between O_2 production and PAR and fit Fourier components. The present 'bookend' approach either rigidly constrains DO to PAR (at one extreme) or considers DO unconstrained by PAR (at the other extreme), but neither scenario is likely to be true to the environment.

The similarity of patterns between O_2 flux and ETR in this study also highlights the effectiveness of both oxygen exchange and PAM fluorescence methods in measuring photosynthetic rates of marine plants, but these measurements are valid only for individuals or parts of individual algae.

For estimating production of entire assemblages of benthic algae (or other photosynthetic organisms), particularly when questions address larger spatial and temporal scales than can be addressed by other techniques, the approach by modelling ambient oxygen levels holds great potential. Equipment and labour requirements are modest and, once sensors are deployed, data can be collected over extended periods. This method provides an estimate of total assemblage production, and not surprisingly, is likely to provide greater estimates of production than methods focussed on single canopy-forming species only. However, the approach is not suitable to estimate production rates of single species, and is yet to be tested in more exposed (turbulent) environments where detailed and difficult hydrodynamic modelling may be required.

Benthic oxygen exchange chambers can be particularly useful for estimating the contribution of particular algal species to overall community production, although care should be taken when considering self-shading in nature and in the chamber and disparities between water movement in the chamber and under natural field conditions.

Both of the oxygen flux methods are superior in providing assemblage or whole algae estimates of production compared to PAM fluorescence which, even as a proxy for potential photosynthesis, gives results that relate only to the small local area of tissue under analysis. We have shown considerable intra-individual variation in parameters measured from application of PAM fluorescence (J. Randall et al. unpubl.) and obtained readings indicating healthy tissue (e.g. an appropriate F_v/F_m ratio) and highly active PSII from particular locations on individuals that are clearly at an advanced stage of senescence. The main advantage of PAM fluorometry is ease of use and ability to provide instantaneous measurements. It can also provide other photosynthetic information relating to photochemical and non-photochemical quenching (Westphalen & Cheshire 1997, Schreiber 2004).

Overall, it is clear that each method of estimating macroalgal production has distinct advantages and disadvantages. When planning future research or comparing to other studies, it will be important to consider that each method provides different kinds of estimates of production or proxies of actual or potential production, and that there needs to be considerable clarity in the question being tackled before selecting a suitable technique for research. It is, however, clear from this research that for accurate and efficient estimates of kelp community production there is a clear advantage in developing open-water techniques.

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