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A novel system for measuring *in situ* rates of photosynthesis and respiration of kelp

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ABSTRACT: Macroalgae are important primary producers on temperate reefs worldwide, yet obtaining accurate measurements of *in situ* rates of photosynthesis and respiration for large seaweeds, particularly kelp, is challenging. Here we describe a novel and inexpensive photorespirometry system that can be used to generate photosynthetic–irradiance (*P–E*) curves for an entire adult kelp *in situ*. To demonstrate the application of this system, we (1) measured and compared *P–E* curves of the stipitate kelp *Ecklonia radiata* at 2 depths in northeastern New Zealand, and (2) compared laboratory-derived *P–E* curves to those obtained *in situ*. The system enclosed the lamina of the kelp and was sealed around the stipe, and oxygen evolution was recorded by an enclosed logger. By varying the irradiance in the chamber with shade cloth, and utilizing the variation in light associated with depth, the photosynthetic rates of an individual were measured over a range of irradiances *in situ*. Photosynthetic parameters of *Ecklonia* from field measurements varied with depth. *P–E* curves from individuals measured *in situ* differed from those measured in the laboratory, with maximum photosynthetic rates in the laboratory being 42 and 55% lower under natural and artificial light respectively. This system provides, for the first time, a method for generating *P–E* curves and estimating photosynthetic parameters for entire adult *E. radiata* individuals *in situ*. It can be adapted for use on other kelp and large seaweeds, and in tank-based experiments. Importantly, our findings also indicate that estimates of productivity based on laboratory-derived photosynthesis measurements likely underestimate kelp forest productivity.

KEY WORDS: Primary productivity · Macroalgae · Photosynthesis · Respiration · Photosynthesis–irradiance curves · *In situ* · Laminarian · *Ecklonia radiata*

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INTRODUCTION

Macroalgae-dominated reefs in shallow coastal waters are among the most productive ecosystems in the world (Mann 1973). Kelp (Laminariales) make up the majority of macroalgal biomass on exposed or semi-exposed coastlines in temperate latitudes and provide food and habitat for many associated organisms (Dayton 1985, Steneck et al. 2002). These large macroalgae contribute organic matter to local food webs, and also to adjacent intertidal, deep water and terrestrial habitats (Krumhansl & Scheibling 2012). Accurately quantifying the primary production of macroalgae is therefore fundamental to increasing our understanding of ecosystem functioning, energetics and tropho-dynamics in coastal marine ecosystems. Increasingly, information is also needed about spatial and temporal patterns of productivity from which to assess and compare the consequences of global and regional climate change.

Kelp productivity is typically estimated using methods that measure either long-term yield or biomass accumulation (Mann 1973, Mann & Kirkman 1981, Kirkman 1984, Dunton 1990, Reed et al. 2008, 2009)

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or short-term rates of photosynthesis (Hatcher et al. 1977, Dunton & Jodwalis 1988, Cheshire et al. 1996, Fairhead & Cheshire 2004a). While biomass has been used to provide good estimates of net primary production (NPP) in some kelp systems, particularly the well-studied southern Californian giant kelp *Macrocystis pyrifera* forests (Reed et al. 2008, 2009), estimates based on biomass measurements are typically complicated by the need to account for tissue loss from grazing or erosion, or loss of entire individuals if estimating at the population level. Another approach to estimating productivity is to incorporate information on the photosynthetic responses of seaweeds into physiological models (Brinkhuis 1977, Jackson 1987, Miller et al. 2012). Rates of net oxygen evolution provide a rapid measure of photosynthesis under a given set of environmental conditions. Photosynthetic rates can either be measured at ambient light levels *in situ* (as in Miller et al. 2009), or alternatively, at a range of different irradiances in order to generate a photosynthesis–irradiance (*P–E*) curve that quantifies the relationship between photosynthesis and irradiance (Kirk 2011). The photosynthetic parameters obtained from the *P–E* curve can then be combined with light and biomass information in physiological models to estimate productivity (Brinkhuis 1977, Jackson 1987, Burd & Dunton 2001, Binzer & Sand-Jensen 2002a, Elkalay et al. 2003, Miller et al. 2012, Harrer et al. 2013). The parameters from *P–E* curves are also useful for within or between species comparisons over temporal or spatial scales, even when measurements are made in differing light intensities (Gomez & Wiencke 1996, Fairhead & Cheshire 2004b, Miller et al. 2012).

Photosynthesis and respiration rates of seaweeds have traditionally been measured in photorespirometry chambers in the laboratory. This method, whereby oxygen evolution and uptake are measured in chambers to quantify photosynthetic and respiration rates, has been widely used to study the physiology and production of macroalgae (Binzer & Sand-Jensen 2002b, Middelboe et al. 2006, Staehr & Wernberg 2009, Richards et al. 2011). However, most studies have typically focused on turf and foliose algal species, and those that measured kelp photosynthesis and respiration in chambers were limited to juveniles or tissue pieces (Staehr & Wernberg 2009, Richards et al. 2011). Scaling up such measurements to estimate production of entire adult individuals is problematic due to the considerable variation in rates between different tissues within an individual, along a blade or among fronds of varying age (Hatcher 1977, Gerard 1986, Gevaert et al. 2011). Consequently, measuring photosynthetic rates of entire kelp individuals is preferable, in order to remove the effect of variation in photosynthetic and respiration rates within and between blades (Arnold & Manley 1985, Gerard 1986, Dunton & Jodwalis 1988, Gevaert et al. 2011). In some cases, photosynthetic rates have been calculated for kelp in the laboratory, with their stipes removed so they could fit into incubation tanks (Miller et al. 2012), but it remains unknown how transferrable these results are to a field situation.

The development of photorespirometry chambers that enclose an entire macroalgal individual or algal community in the field has provided greater insight into photosynthesis under natural conditions (Chisholm et al. 1990, Cheshire et al. 1996, Westphalen & Cheshire 1997, Fairhead & Cheshire 2004a, Miller et al. 2009, Tait & Schiel 2010, Gevaert et al. 2011). However, due to the large size of kelp and the logistical challenges of measuring photosynthesis in shallow, wave-exposed coastal habitats, there are only a few cases where chambers have been used for kelp or other large seaweeds (Hatcher et al. 1977, Gerard 1986, Fairhead & Cheshire 2004a,b, Miller et al. 2009, Delebecq et al. 2011, Gevaert et al. 2011). Of these, most have required the kelp to be detached from the substrate and placed inside a rigid-walled chamber (Hatcher et al. 1977, Cheshire et al. 1996, Fairhead & Cheshire 2004a,b, Delebecq et al. 2011, Gevaert et al. 2011), thereby removing the kelp from its natural setting and eliminating any wave action or water movement. Furthermore, in most cases, juveniles (Fairhead & Cheshire 2004a,b) or pieces of adult kelp (Gerard 1986) have been enclosed in chambers, making it difficult to extrapolate rates to entire kelp forests. *In situ* photosynthetic measurements have been carried out on adult *Laminaria digitata* using a system that involves detaching entire individuals from the substrate and placing them inside a fully enclosed rigid dome chamber (Gevaert et al. 2011). However, the major impediment to *in situ* photorespirometry measurements on many kelp is their large size in both biomass and vertical extent from the seabed. This makes chambers that seal to the reef impractical, but also unnecessary as the majority of photosynthesis occurs in the canopy blades of stipitate kelp (Arnold & Manley 1985, Gerard 1986, Gevaert et al. 2011). Due to difficulties in measuring *in situ* photosynthetic rates of kelp, few *P–E* curves exist for kelp, particularly adult kelp, in nature. Those that have been constructed from field measurements of photosynthetic rates utilized changes in irradiance over the course of the day (Dunton & Jod-

walis 1988, Fairhead & Cheshire 2004b), or changes in irradiance with varying water depth associated with tides (Delebecq et al. 2011, 2013), or moved blades of kelp to different depths (Gerard 1986). To date, no simple, robust and easily deployed chamber systems have been developed that not only allow replicate measurements of respiratory and photosynthetic rates *in situ* at a range of light levels, but also allow the generation of *P–E* curves for whole adult kelp. Given the importance of kelp forests to ecosystem functioning on temperate reefs worldwide, there is a clear need to further develop methods for measuring photosynthetic rates and deriving *P–E* curves of these species to generate more robust estimates of kelp forest primary production.

In this paper, we describe a photorespirometry chamber system that measures oxygen production of the stipitate kelp *Ecklonia radiata* in the field. The system is relatively inexpensive, simple to construct and deploy, and the method developed allows *P–E* curves to be generated for multiple replicate kelp in 1 d. The chamber system is novel in that it is large enough to enclose whole adult canopy-forming kelp in their natural setting within the kelp forest, and novel procedures have been developed for manipulating irradiance levels inside the chambers using shade cloth and depth-related variation in irradiance to allow for the generation of *in situ P–E* curves of individual kelp. We used this method to generate, for the first time, *P–E* curves and photosynthetic parameters for entire adult *E. radiata* individuals *in situ*. To examine the applicability of using this system to improve our understanding of kelp productivity, we measured and compared *P–E* curves of adult *E. radiata* at 2 depths in northeastern New Zealand. Furthermore, to better understand the relative importance of conducting photosynthetic measurements *in situ*, we compared the *P–E* curves from kelp measured in the field, and under both natural and artificial light conditions in the laboratory.

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. Photosynthetic measurements took place at 2 sites ~300 m apart on the west side of Goat Island, at 6 m depth (Alphabet Bay) and at 14 m depth (North Reef). 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 >6 m depth. *Ecklonia radiata* (C. Agardh) J. Agardh is a perennial species that is frequently the dominant canopy-forming kelp on temperate rocky coasts in Australasia (Wernberg et al. 2003b, Goodsell et al. 2004, Shears & Babcock 2007). The morphology of *E. radiata* exhibits a high degree of plasticity, with variations at local and regional scales (Wernberg et al. 2003a, Fowler-Walker et al. 2005, 2006, Miller et al. 2011, Mabin et al. 2013). At Goat Island, it has a long stipe (up to ~150 cm) and comparatively shorter primary lamina (range ~10–50 cm), and can live for up to 10 yr (Novaczek 1980).

Description of the chamber and components

The photorespirometry chamber consisted of a cylindrical frame (30 cm diameter × 41 cm height) constructed of flexible plastic pipe (Buteline) that was covered with a clear polyethylene plastic bag (45 × 90 cm, 100 µm thick) (Fig. 1A). The chamber and plastic bag enclosed the blades (lamina) of the kelp, as well as a dissolved oxygen logger and a PAR (photosynthetically active radiation) logger, and the bag was tightly sealed and secured around a closed-cell foam stopper fitted around the stipe of the kelp (Fig. 1A). The chamber enclosed only the lamina of the kelp, and excluded the stipe and holdfast, as the vast majority of photosynthesis (>99%) and respiration (95%) occurs in the blades of stipitate kelp (Gevaert et al. 2011). The pump system was comprised of an inline pump (Rule Submersible and Inline Pump iL200^{Plus}), with inflow and outflow tubes passing through the foam stopper into the chamber, and valves to allow water to be exchanged between the surrounding water and the chamber (flushing), and circulated in a closed-circuit flow. The pump had a flow rate of 5 l min^{-1} and was powered by an external submersible battery pack (Fig. 1A). The bag was sealed at a pre-marked position and the pump and valves were used to fill the bag, ensuring that the volume of the chamber was consistent across incubations (32.2 l, SE = 0.27, n = 11). The positively buoyant frame provided attachment for the loggers, and shape to the chamber system, allowing the blades of the kelp to array and move naturally within the chamber. The chamber was large enough to contain adult individuals that dominate the canopy (size range: 10–40 cm primary lamina length).

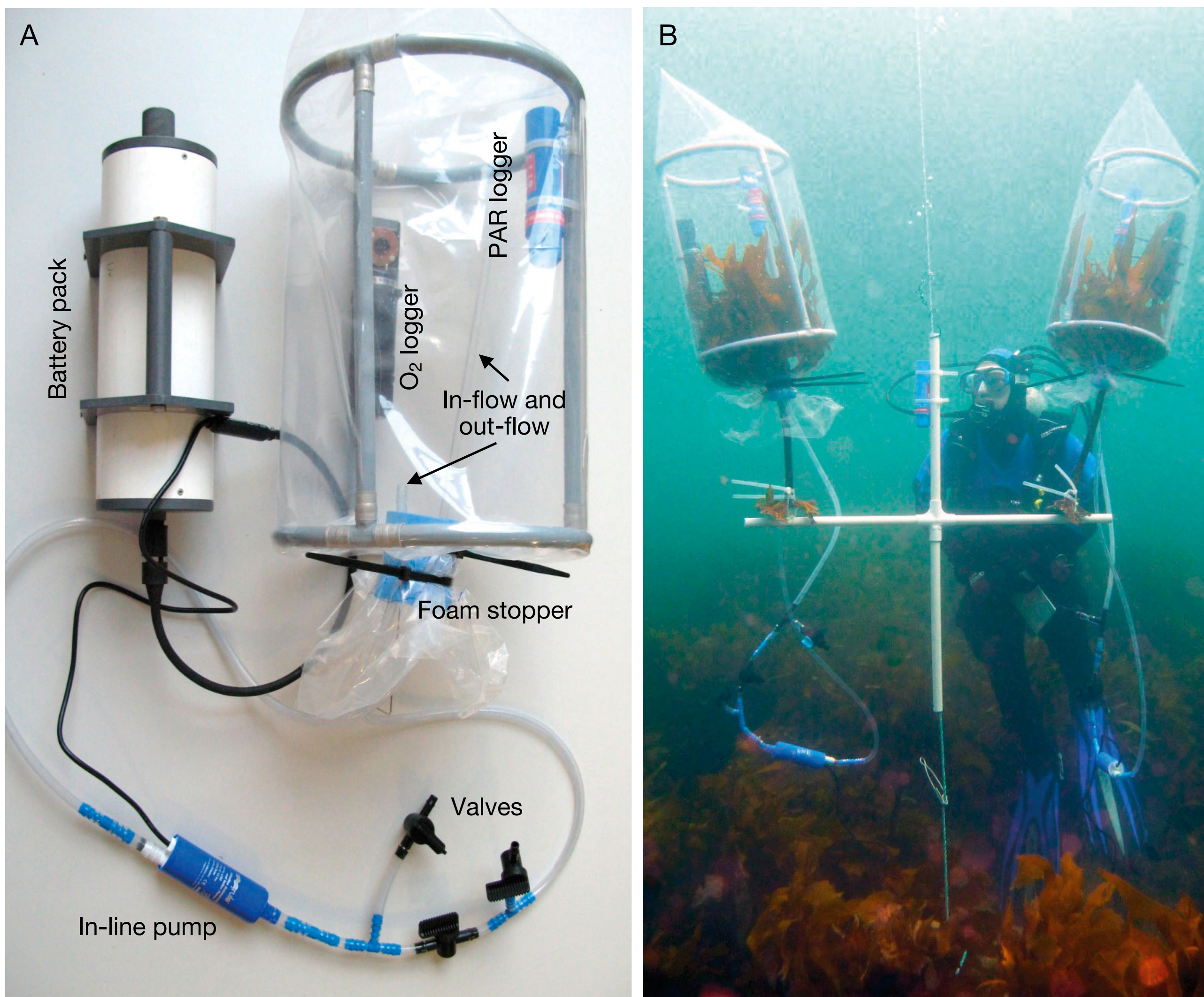

Fig. 1. (A) Photorespirometry chamber system components consisting of a cylindrical frame with attached PAR (photosynthetically active radiation) logger and dissolved oxygen logger enclosed in a polyethylene bag that seals around a foam stopper. A pump system is powered by a battery. (B) The chamber system deployed *in situ* with 2 individual *Ecklonia radiata* attached to a lift frame. Kelp can be incubated while attached to the substratum or while attached to a lift frame, allowing the kelp to be moved up the water column into saturating light conditions near the surface. The battery packs in (B) are obscured by the kelp forest, but are clipped onto the lift frame line as kelp are raised higher into the water column

Dissolved oxygen concentration and temperature inside the chamber were logged at a frequency of once per minute by an optical dissolved oxygen logger (D-OptoLogger, Envco). The D-OptoLogger uses a solid-state optical sensing system that measures dissolved oxygen without consuming oxygen (conventional polarographic dissolved oxygen sensors do), is unaffected by water movement and is highly stable over long periods of time. The D-OptoLogger corrected for temperature effects on dissolved oxygen and the data was post-corrected for salinity. Irradiance (E) (measured as photon flux density, PFD; PAR 400–700 nm) was recorded using loggers with planar cosine-corrected PAR sensors (Odyssey Photosynthetic Irradiance Recording System, Dataflow Systems) mounted at the top inside the chamber, and unimpeded by the frame or kelp lamina. Odyssey PAR loggers were calibrated on land against a LI-190 quantum sensor (LI-COR Biosciences). These loggers are simple to deploy and are small and easy to mount inside the chamber. They have also been shown to have close agreement with LICOR spherical 4π scalar PAR sensors over a range of conditions (Long et al. 2012).

Development and testing of the chamber

The accuracy and limitations of the chamber system were assessed in a series of laboratory tests. An effective seal and impermeable chamber walls are necessary to prevent any transfer of water or gases between the inside of the chamber and the surrounding water. The seal and permeability of the chamber were visually tested by releasing a dye inside the chamber; results indicated a highly effective seal with no evidence of leakage or loss of pressure within the bag. A further, more precise test was made by filling the chamber with distilled water, reducing oxygen concentrations to ~20% with nitrogen gas (N_2), and submerging the sealed chamber (with artificial stipe) in ambient seawater for 2.5 h. Oxygen concentrations remained constant over the 2.5 h duration, indicating an effective seal and impermeability of the chamber walls to oxygen.

Water motion is a key determinant of macroalgal production through its influence on most of the abiotic and biotic factors that control net production (Hurd 2000); thus, interruption of the natural flow rate by the chamber walls could affect photosynthetic rates of the kelp in the chamber. Water motion within photorespirometry chambers is necessary to minimize boundary layers and prevent mass-transfer limitation of photosynthesis (Hurd 2000), and to ensure a well-mixed water body within the chamber for accurate readings of total dissolved oxygen. Previous tests of *in situ* incubation techniques using flexible bags indicated that water motion inside the bags was comparable to that in the surrounding water for a variety of flow and wave conditions (Gust 1977, Gerard 1986, Miller et al. 2009). However, initial tests in the present study revealed inconsistencies in dissolved oxygen concentration during measurements, indicating that a pump was required to provide adequate and uniform mixing of the water within the chamber. Incorporating a pump into the chamber also ensured a constant flow rate (5.0 l min^{-1}) and mixing under all the conditions in which the photorespirometer was used. Variation in flow rate could affect photosynthetic rates, but this was not supported by test measurements in the laboratory under constant light conditions; these measurements found no relationship between photosynthetic rates and flow rates over a range of 4.6 to 7.0 l min^{-1}. This indicated that photosynthetic rates were not limited by water flow of 5 l min^{-1} in the chamber.

A significant challenge to continuous measurements of oxygen production in a chamber system is accurately measuring production while also avoiding oxygen supersaturation and nutrient and carbon dioxide limitation within the chamber that could potentially lead to declines in rates of oxygen production over time. Determining a suitable incubation duration, or duration of time before seawater within the chamber is renewed, is essential to ensure that algae are maintained in natural ambient conditions and photosynthetic rates are not compromised (Gerard 1986, Fairhead & Cheshire 2004b, Tait & Schiel 2010, Gevaert et al. 2011). A laboratory trial found that a maximum incubation time of 40 min was a conservative duration to ensure that the photosynthetic rate of *E. radiata* was not limited, which would be indicated by a decline in rates under constant light (see Supplement at www.int-res.com/articles/suppl/m528p101_supp.pdf for details). Accordingly, chambers were partially flushed (50% of total volume replaced) after 40 min in all field and laboratory incubations.

Using the chamber system to generate *P–E* curves for kelp *in situ*

Individual kelp of a suitable size (primary lamina length ~15–35 cm) and with minimal visible epiphyte cover were randomly selected for incubation, and any visible epifauna (i.e. gastropod molluscs) were removed. The foam stopper was attached around the stipe of the attached kelp, the frame and bag placed over the lamina, and the bag sealed tightly around the stopper with cable ties to ensure a watertight seal (Fig. 1B). The chamber was filled to a consistent volume using the pump and valves that allow water to be drawn into the chamber. When completely filled, the inflow and outflow valves were closed and the in-line valve opened to create a closed-circuit flow-through system whereby changes in oxygen could subsequently be measured. The chamber could also be flushed periodically with fresh seawater.

Dark respiration (R_d) was measured by enclosing the entire chamber in a double layer of black plastic. Photosynthetic rates were measured at 5 light levels in order to generate *P–E* curves for individual kelp. With kelp attached to the reef, light levels were manipulated using layers of shade cloth, and changes in oxygen concentration were measured over a given period for each light level. However, in order to expose kelp to higher and potentially saturating irradiances, the kelp was detached from the substrate, attached to a lift frame by its holdfast, and suspended at shallower depths on a lift frame (Fig. 1B). The lift frame used in this study held 2 individuals, was made of PVC pipe and could easily be

moved up a line secured to the seabed and held taut by a subsurface buoy (Fig. 1B). The positive buoyancy of the chamber and the rigidity of the stipe held the kelp and chamber upright. The utilization of the lift frame and layers of shade cloth allowed rates of photosynthesis to be measured across a sufficient range of light levels to generate a *P–E* curve. The order of light sequence (increasing or decreasing) was assumed not to affect photosynthetic rates based on Duarte et al. (2013). During field incubations, individuals remained completely intact but were carefully detached from the substrate and attached to the lift frame. This did not cause visual indicators of stress, such as exudation of tannins, and testing showed that detaching and moving the plant up through the water column on the lift frame did not adversely affect photosynthetic rates. Paired *t*-tests indicated that there was no significant difference in photosynthetic rates when kelp (n = 4) were detached from the substrate and attached to the lift frame at the same depth (p = 0.196), and when they were returned to the initial depth following measurements at shallower depths on the lift frame (p = 0.190).

Accurately measuring irradiance is essential; thus, to determine whether movement of the chamber with the surrounding water motion had any effect on the irradiance recorded, additional PAR loggers were mounted in a cleared space in the kelp forest nearby for comparison with the logger inside the chamber. Upward- and downward-facing PAR loggers were mounted ~30 cm above the seabed to measure downwelling irradiance (E_d) and to determine if there was significant upward reflected irradiance (E_u) that would not be recorded by our upward-facing logger inside the chamber. Upward reflected irradiance was low (<10 µmol m^{-2} s^{-1}) and downwelling irradiance recorded within the chamber and the nearby fixed logger were very similar after adjusting for the effects of the plastic bag. E_d recorded by the logger within the chamber was used for all further data analyses as it most closely reflected the irradiance received by the algae during the photosynthetic measurements.

Application of the photorespirometry chamber

In situ measurements of *P–E* curves for kelp at multiple depths

Adult *E. radiata* sporophytes were incubated at 6 m (n = 6) and 14 m (n = 6) at Goat Island from June to August 2013. Two replicate photorespirometer chambers were deployed simultaneously between midday and 14:00 h on clear cloudless days to utilize the highest available light levels and ensure that maximum photosynthetic rates were achieved, and to minimize fluctuations in light over the duration of the incubations. In each incubation, photosynthetic rates of an individual kelp were measured at 5 irradiances in order to generate a *P–E* curve for that individual, in addition to a respiration (dark) measurement, with each measurement occurring over a 10 min interval (60 min total). A duration of 10 min for each irradiance was found to be sufficient to show linear changes in oxygen concentration from which to calculate rates of respiration and photosynthesis; these linear changes were not different from those occurring over longer time periods (30–40 min). The short time period minimized fluctuations in light intensity during incubations at each irradiance level. This approach meant that a *P–E* curve could be generated for 2 individuals in a single dive.

The different irradiances were achieved using slightly different procedures between the 2 depths, in order to ensure an appropriate range of irradiances to generate *P–E* curves. At 6 m, following the respiration (dark) phase, kelp were exposed to 45% (2 layers of shade cloth), 67% (1 layer of shade cloth) and 100% (no shade cloth) of ambient PFD. The chamber was then flushed (15 l) for 3 min to partially refresh the water inside the chamber. The sporophyte (including holdfast) was then carefully detached from the substrate, attached to the lift frame by the holdfast, and photosynthetic measurements were taken at depths of 3 and 1 m (both with no shade cloth). At 14 m, light levels included 40% (one layer of shade cloth) and 100% of ambient PFD while attached to the bottom, followed by 3 min flushing and measurements on the lift frame at 10, 5 and 1 m depths. At the end of the photosynthetic measurements, kelp were collected and the volume, wet weight (WW) and dry weight (DW; dried at 60°C for 48 h) of the lamina were measured in the laboratory.

In situ versus laboratory measurements of photosynthesis

To investigate whether field measurements of photosynthetic rates could be replicated under laboratory conditions, individuals of *E. radiata* (n = 10) were initially incubated in the field (at 6 m depth using the methods described in the previous subsection) and then immediately transported in dark-

ness back to the Leigh Marine Laboratory on the shore adjacent to Goat Island, for laboratory-based measurements. Kelp were kept individually in shaded outdoor tanks (200 l, 67 cm diameter × 83 cm depth; shading reduced PFD by 84 %, simulating typical subtidal conditions at 6 m depth) with a continuous flow-through seawater system. The kelp were attached by the holdfast to a base so that they were orientated upright in the tanks. Water motion and turbulence were generated by a tipper bucket (~5 l every 90 s) above the tank, refreshing the entire tank volume every 1 h.

Photosynthetic measurements in the laboratory were carried out both indoors under artificial light, and outdoors under natural sunlight. These measurements were made in a randomized order over the following 2 d, 24 and 48 h after the *in situ* measurements on the same individuals. Incubations in the laboratory occurred at the same time of day as the *in situ* measurements, with 24 h between measurements to minimize stress to the individuals. A single water source supplied the indoor and outdoor tanks and these were identical to the holding tanks. For the indoor measurements, the artificial light source was provided by four 500 W halogen lights above each tank. R_d was measured first by covering the entire tank with 2 layers of black plastic in a darkened room. Photosynthesis was then measured at 5 irradiances by varying the amount of shade cloth covering the tank (4 layers to none). The dark and light phases were 10 min each in duration. The chambers were flushed for 3 min between the third and fourth light phases, matching the field procedure. Light profiles in the indoor tanks were measured with an underwater quantum sensor (LI-192, LI-COR Biosciences), and the extinction curve was used to calculate the irradiance for each incubation based on the depth in the tank where the majority of the lamina tissue of individual kelp was located. For outdoor measurements, dark respiration (R_d) was measured while light was excluded by a double layer of shade cloth and 2 layers of black plastic covering the entire tank. PAR loggers inside the chambers showed that this was sufficient to reduce irradiance to <1 µmol m^{-2} s^{-1}. Photosynthesis was then measured at 5 irradiances by varying the amount of shade cloth covering the tank (4 layers to none). PFD was measured with PAR loggers placed in each tank at the depth where the majority of the lamina tissue was located. The clear polyethylene walls of the chamber resulted in a slight reduction (4 %) of incoming PFD into the chamber (measured in seawater using the LI-192 underwater quantum sensor); thus, PFD data from both the indoor and outdoor tanks were adjusted to account for this. At the end of the photosynthetic measurements, the volume, WW and DW (dried at 60°C for 48 h) of the lamina were measured in the laboratory.

Data analysis

Respiration and photosynthesis rates were calculated from the linear slope of oxygen concentration over the dark and light phases of the incubation period. Linearity of slope within each phase was inspected for any indication of changing rate (nonlinearity), 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 nonlinearity. Ten minutes of data were used for each phase, with the minute spanning the transition being excluded. Irradiance was averaged over the same time period. Rates of respiration and photosynthesis were expressed per unit of dry biomass per hour (µmol O_2 g^{-1} 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) was calculated following Webb et al. (1974):

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

where P is the net photosynthetic rate at any photon flux (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, and E is the incident irradiance. 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).

Linear regression was used to analyze the relationship between photosynthetic parameters and algal weight. For the depth comparison, no relationship with size was evident; thus, differences between the 2 depths were compared using 1-way ANOVA. A larger size range of kelp was used for the *in situ* and laboratory comparison and there was a relationship with size. Therefore, ANCOVA was performed to compare the relative differences in photosynthetic

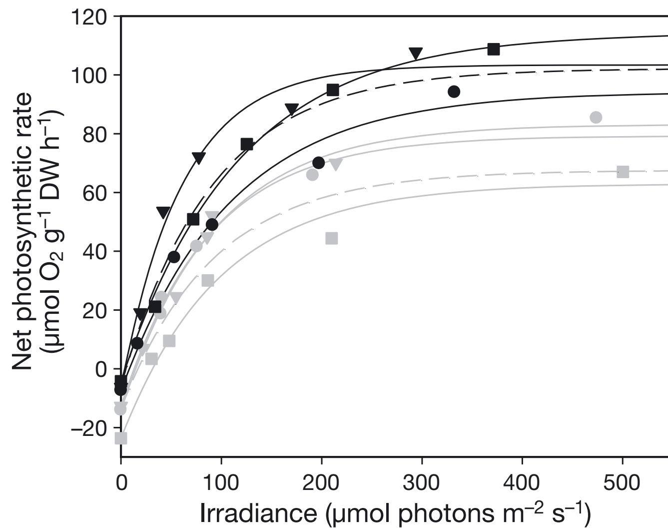

Fig. 2. *Ecklonia radiata*. Examples of *in situ* P–E curves for individuals at 6 m (grey) and 14 m depth (black) at Goat Island. Only 3 randomly chosen individuals (different symbols) from each depth are shown, but dashed line indicates mean P–E curve for each depth (n = 6) based on average parameters (Table 1)

parameters and respiration rates *in situ*, and in the laboratory under natural light and artificial light. Data was log transformed to fulfill the assumption of equal variance. Analysis was performed in SigmaPlot 11.0 and R v.3.0.

RESULTS

P–E curves and photosynthetic parameter comparison between depths

Using the photorespirometry system and the methods described above, we successfully generated accurate P–E curves for entire adult kelp individuals *in situ* (see Fig. 2 for examples from both depths). Photosynthetic rates measured across the range of irradiances in a single incubation meant that saturating irradiance was achieved and P_{max} could be modeled. The resulting P–E curves had r^2 values between 0.91 and 0.99.

Sporophytes were of similar size at both depths, with comparable stipe length (40–78 cm), total length of stipe and primary lamina (53–99 cm), and lamina DW of ~30 g (Table 1). The mean lamina DW of *Ecklonia radiata* at the 2 depths was not significantly different (p = 0.604). P–E curves differed between the 2 depths (Fig. 2, Table 1). P_{max} was significantly higher in kelp at 14 m ($F_{1,10}$ = 24.432, p < 0.001; Table 1). At 6 m, P_{max} ranged from 49.3 to 83.2 μmol O_2 g^{-1} DW h^{-1}, whereas it ranged from 84.9 to 114.4 μmol O_2 g^{-1} DW h^{-1} at 14 m. There was no relationship between P_{max} and size at either 6 m (r^2 = 0.001, p = 0.958) or 14 m (r^2 = 0.060, p = 0.641). The photosynthetic efficiency α did not differ significantly between the 2 depths ($F_{1,10}$ = 3.947, p = 0.075; Table 1), although generally higher α was exhibited by kelp at 14 m (Table 1). α also did not significantly differ with size for individuals from either 6 m (r^2 = 0.180, p = 0.402) or 14 m depths (r^2 = 0.157, p = 0.437). Respiration rates (R_d) were significantly higher in kelp at 6 m ($F_{1,10}$ = 6.167, p = 0.035; Table 1) and did not significantly differ with size at 6 m (r^2 = 0.152, p = 0.445) or 14 m (r^2 = 0.116, p = 0.575). E_k varied from 33.1 to 125.8 μmol photons m^{-2} s^{-1}, and was not significantly different between depths ($F_{1,10}$ = 0.767, p = 0.402; Table 1). E_k did not differ with size at 6 m (r^2 = 0.170, p = 0.416) or 14 m (r^2 = 0.317, p = 0.245). E_c, the irradiance at which photosynthesis balanced respiration, was significantly different between the 2 depths ($F_{1,10}$ = 9.774, p = 0.012), with kelp at 14 m requiring lower irradiance than those at 6 m for photosynthesis to balance respiration (Table 1). E_c did not differ with size at 6 m (r^2 = 0.066, p = 0.624) or 14 m (r^2 = 0.046, p = 0.731).

Table 1. *Ecklonia radiata*. Mean (±SE) dry weight (DW) and wet weight (WW) of lamina (g), stipe length (SL, cm), total length of stipe and primary lamina (TL, cm), photosynthetic parameters and respiration rates at 6 m (n = 6) and 14 m (n = 6) in winter 2013. Significant differences between depths: *p < 0.05, ***p < 0.001, 1-way ANOVA. P_{max}: maximum rate of net photosynthesis (μmol O_2 g^{-1} DW h^{-1}); α: initial slope of the P–E curve at non-saturating irradiance; E_k: saturation irradiance (μmol photons m^{-2} s^{-1}); E_c: compensation irradiance (μmol photons m^{-2} s^{-1}); R_d respiration rate (μmol O_2 g^{-1} DW h^{-1}); r^2: fit of P–E curve

Depth (m)	DW (g)	WW (g)	SL (cm)	TL (cm)	r^2	P_{max} (μmol O_2 g^{-1} DW h^{-1})	α	R_d (μmol O_2 g^{-1} DW h^{-1})	E_k (μmol photons m^{-2} s^{-1})	E_c (μmol photons m^{-2} s^{-1})
6	28.6 ± 4.2	184.6 ± 22.7	54.0 ± 2.6	67.0 ± 2.8	0.98 ± 0.01	67.6 ± 5.4***	0.87 ± 0.08	−13.5 ± 2.8*	80.3 ± 7.8	15.0 ± 2.8*
14	29.7 ± 1.6	199.7 ± 12.2	64.8 ± 5.6	81.7 ± 6.4	0.98 ± 0.01	102.2 ± 4.5***	1.19 ± 0.14	−5.7 ± 0.8*	91.9 ± 10.7	5.1 ± 0.8*

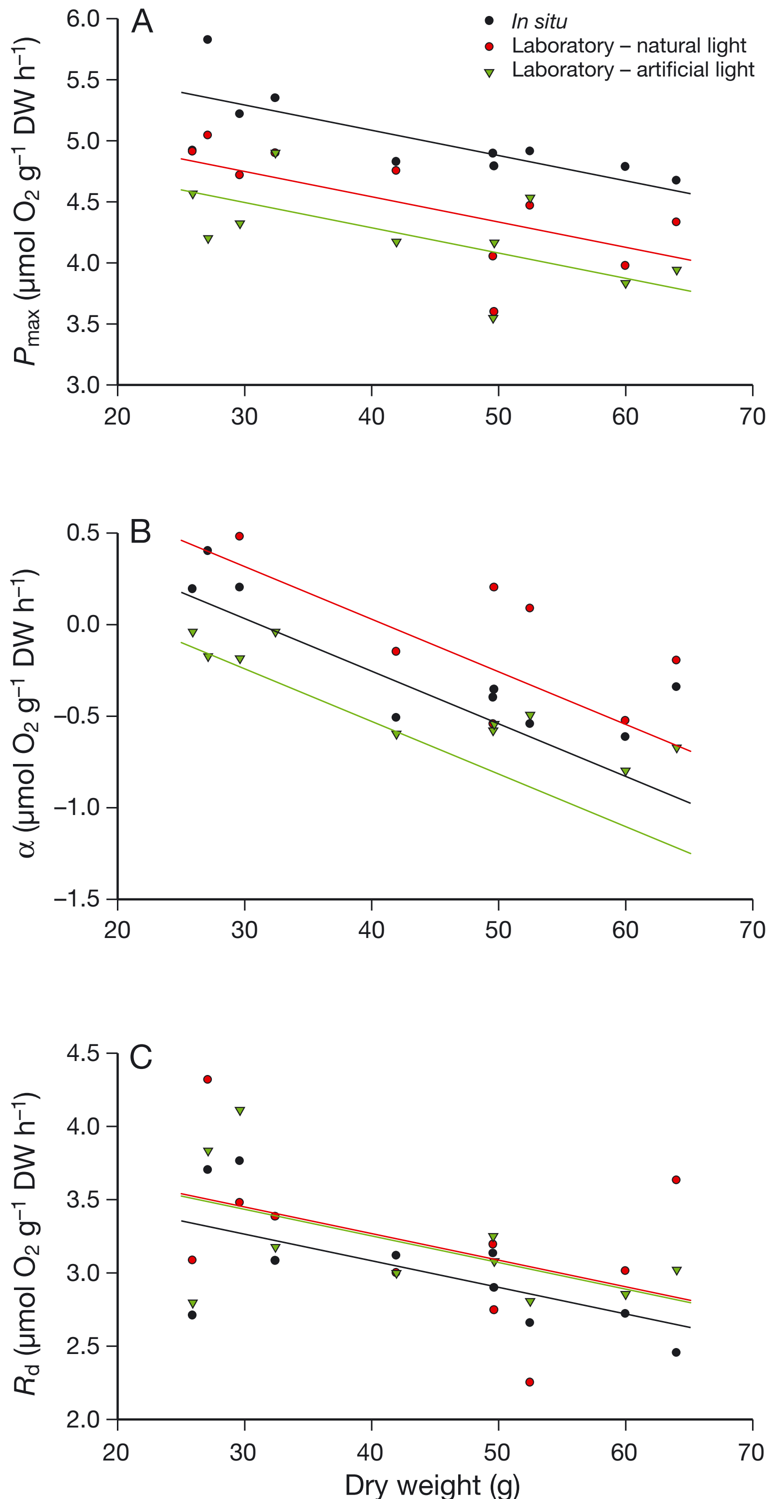

Fig. 3. *Ecklonia radiata*. Relationship between size (dry weight of lamina) and photosynthetic parameters (for definitions see Table 1): P_{max}, alpha (α) and respiration rates (R_d) measured *in situ* and in the laboratory under natural and artificial light sources (n = 10). P_{max}, α, and R_d data were $\log_e$ transformed. Regression lines were fitted with ANCOVA (see 'Results' for significance)

In situ vs. laboratory *P–E* curves and photosynthetic parameters

The average length of kelp used in this experiment was 65.3 ± 1.4 cm (SE) (stipe plus primary lamina) and ranged from 60 to 75 cm. Average lamina DW was 43.2 ± 4.4 g and ranged from 27 to 63 g. In this comparison, photosynthetic parameters were found to vary with kelp size (DW) (Fig. 3). P_{max} varied in relation to size and treatment (ANCOVA, $r^2 = 0.70$, $F_{3,26} = 19.39$, $p < 0.001$). P_{max} in the field differed from that in the laboratory under natural light ($t = -3.83$, $p < 0.001$) and artificial light ($t = -5.85$, $p < 0.001$). For kelp of a given size, the median P_{max} in the laboratory under natural light and under artificial light were 42% (22 to 57%, 95% CI) and 55% (41 to 66%, 95% CI) lower than *in situ* rates. α varied in relation to size and treatment ($r^2 = 0.76$, $F_{3,26} = 27.9$, $p < 0.001$). α in the field differed from that in the laboratory under natural light ($t = 2.285$, $p = 0.03$) and artificial light ($t = -2.57$, $p = 0.02$) (Fig. 3). The median α in the laboratory under natural light was 33% (2 to 72%, 95% CI) greater, and under artificial light it was 24% (5 to 39%, 95% CI) lower, than that *in situ*. R_d varied in relation to size but did not vary with treatment ($r^2 = 0.30$, $F_{3,26} = 3.57$, $p = 0.02$) (Fig. 3). E_k did not differ significantly with size of individual in any of the treatments (*in situ* $r^2 = 0.142$, $p = 0.283$; natural light $r^2 = 0.054$, $p = 0.520$; artificial light $r^2 = 0.002$, $p = 0.914$). One-way ANOVA on E_k found significant differences between treatments ($F_{2,27} = 20.746$, $p < 0.001$), with E_k being higher *in situ* than in laboratory-based treatments (Table 2). E_c did not vary with size (*in situ* $r^2 = 0.008$, $p = 0.809$; natural light $r^2 = 0.228$, $p = 0.163$; artificial light $r^2 = 0.032$, $p = 0.623$), or between treatments ($F_{2,27} = 2.560$, $p = 0.096$) (Table 2).

DISCUSSION

In this study, we describe a photorespirometry system that can be used to measure photosynthesis of intact adult kelp while they are attached to the substrate, as well as to generate *P–E* curves for entire adult kelp *in situ*; to our knowledge, this is a unique design and application of such a system. Furthermore, the results presented from applying this method in the field, and comparing photosynthetic per-

Table 2. *Ecklonia radiata*. Means (±SE) of photosynthetic parameters and respiration rates *in situ*, and in the laboratory under natural and artificial light (n = 10). r^2: fit of *P–E* curve. Heading definitions and units as in Table 1

Treatment	r^2	P_{max}	α	R_d	E_k	E_c
In situ	0.99 ± 0.003	160.6 ± 22.0	0.95 ± 0.14	−22.5 ± 3.4	179.0 ± 14.2	25.3 ± 2.9
Laboratory – natural light	0.97 ± 0.009	96.0 ± 12.6	1.29 ± 0.20	−28.6 ± 5.7	80.6 ± 8.5	24.5 + 4.1
Laboratory – artificial light	0.99 ± 0.006	72.67 ± 9.1	0.69 ± 0.06	−26.9 ± 4.7	105.5 ± 8.4	39.6 ± 5.1

formance of kelp between the field and the laboratory, highlight the importance of carrying out photosynthetic measurements *in situ* and on adult kelp, rather than extrapolating photosynthetic results from laboratory-based studies, typically on small individuals or pieces of adult kelp, to entire kelp forests.

A photorespirometry chamber system for kelp

The chamber described in this study contrasts with those used previously in that it was sealed and attached around the kelp's stipe, and a flexible bag enclosed the entire lamina of an adult alga that was suspended in the water column, while the alga remained attached to the bottom. This means the kelp remained in its natural orientation and position within the kelp bed, thereby allowing rates to be measured in as close to natural conditions as possible. It also allows the enclosed kelp to move freely in the water column, which is not possible if the chamber is fixed to the bottom where it is difficult to maintain a seal and the chamber is more vulnerable to waves (e.g. Miller et al. 2009). A further novel aspect is that the alga can then be detached and the entire system moved up the water column into saturating light necessary to achieve maximum photosynthetic rates and generate a *P-E* curve, with minimal stress on the alga. The fact that rates of photosynthesis did not differ from the original *in situ* measurement when the detached kelp was returned to its original depth after being moved to the surface to obtain data to derive a *P–E* curve, suggests that detaching and moving the kelp on the lift frame do not cause any alteration in rates.

The incorporation of within-individual and within-canopy shading effects in measurements made using the chamber is important for productivity measurements. This is because laboratory studies have suggested that photosynthetic rates of individual thalli cannot be scaled to estimate community production due to shading resulting from canopy architecture effects (Binzer et al. 2006 and references therein). However, by measuring photosynthetic responses of intact whole thalli that are naturally orientated within intact natural canopy architecture, the within- and between-individual shading effects were incorporated into the measured *P–E* curves, thereby accurately reflecting photosynthesis in nature. The latter part of our method involves lifting the kelp out of the canopy and up toward the surface to expose them to higher light levels required to saturate photosynthesis, thereby removing them from within-canopy and between-individual shading. The lack of difference in photosynthetic rates observed at a depth within the canopy and when the kelp was removed from the canopy suggests that removing the kelp from the canopy and attaching them to the lift frame have no short-term effects on photosynthetic rates.

Enclosing an individual inside a chamber to measure photosynthesis, however, has inherent issues, such as potential self-shading, the potential presence of other photosynthesizing or respiring organisms and alterations in water flow that could affect measured rates. The current system has been developed to minimize these limitations and, where possible, these limitations were tested. We avoided the problem of increased self-shading by developing a large cylindrical chamber that did not excessively constrict the laminae of the individuals measured. The contribution of other organisms, apart from the kelp, to changes in oxygen concentration in the chamber was most likely negligible given that coarsely structured species such as *Ecklonia radiata* contain much lower epifaunal densities than finely structured macroalgae (Taylor & Cole 1994), and the contribution of organisms in the water (phytoplankton, zooplankton and bacteria) has been shown to be negligible even during the spring period of high phytoplankton standing crop (Gerard 1986, Cheshire et al. 1996, Fairhead & Cheshire 2004a). A potential limitation of any measurement system that encloses a living organism is that the immediate environment sur-

rounding the organism is likely modified as a result of the enclosure. The pattern of water motion around the kelp was modified by the chamber and it is possible that a chemical property of the polyethylene bag or the tubing associated with the circulation system may have adversely affected photosynthetic rates. However, it is likely that any such effects were minimal, if only because the incubations required were short-lived.

Quantifying photosynthesis–irradiance relationships for kelp *in situ*

Application of this method in northeastern New Zealand provided the first *in situ* *P–E* curves for entire adult individuals of *E. radiata*. The higher P_{max} and greater (albeit not significantly) photosynthetic efficiency (expressed in terms of α) of individuals measured at greater depth are generally consistent with photoacclimation at lower irradiances (Falkowski & LaRoche 1991, Kirk 2011). However, the rates of P_{max} recorded for the adult sporophytes in the current study (ranging from 49 to 114 µmol O_2 g^{-1} DW h^{-1}) were considerably lower than those recorded for juveniles (20–30 cm length, 1–19 g DW of entire individual) at a similar time of year in South Australia (~300 µmol O_2 g^{-1} DW h^{-1}) (Fairhead & Cheshire 2004b). While a relationship between the size of individuals and P_{max} was not found for the range of sizes incubated in this comparison, the P_{max} for kelp incubated in the field vs. laboratory study declined with increasing biomass (size range from ~25 to 65 g lamina DW). The smaller individuals (<30 g) in this experiment had P_{max} values (163–183 µmol O_2 g^{-1} DW h^{-1}) that were approx. half of the values reported by Fairhead & Cheshire (2004b). This indicates that small adult individuals have lower rates than juveniles, and that the lower rates of P_{max} and α recorded in the depth comparison in this study are due to the larger size of the adult kelp incubated. Differences in photosynthetic characteristics between different developmental stages of sporophytes have been reported, with higher pigment concentrations and rates of photosynthesis and respiration in morphologically less complex, younger stages of development (Gomez & Wiencke 1996, Campbell et al. 1999), highlighting the problems associated with scaling photosynthetic results from small younger individuals to large older ones.

The higher P_{max} of *E. radiata* recorded at the deeper site may not necessarily translate into higher net primary productivity compared to the 6 m population as overall irradiance is lower at greater depths and population density may vary. In fact, Novaczek (1984) recorded considerably higher rates of growth in the dense populations of *E. radiata* at 7 m at Goat Island, compared to the more sparse populations at 15 m. Higher rates of growth in algae are frequently supported by increased rates of respiration (Geider & Osborne 1989, Markager & Sand-Jensen 1994). That rates of respiration at 6 m were greater than at 14 m would be consistent with Novaczek's observations of higher growth rates. Combining the photosynthetic parameters obtained using the methods described in this study with biomass (standing stock) and irradiance data in a productivity model (e.g. Miller et al. 2012) would provide opportunities for estimating NPP and reconcile the relative importance of photosynthetic performance, light and biomass in determining kelp forest productivity. These results demonstrate how this system can be used to better understand the productivity of a highly important kelp species. While this method was only used on *E. radiata* here, it can be easily customized for use on other kelp and large macroalgae by modifying the sizes of the chamber frame, the stopper, and the plastic bags.

Measuring photosynthetic rates in the field vs. laboratory

Laboratory-derived *P–E* curves measured under both natural and artificial light did not closely reflect *P–E* curves of the same individuals *in situ*. In particular, P_{max} were lower when plants were incubated in the laboratory under both light conditions compared to *in situ* measurements. These differences could be due to issues arising from transporting the kelp from the field to the laboratory, and/or related to the different light sources. During field incubations, individuals remained intact, and attaching the kelp to the lift frame and lifting it up through the water column did not appear to cause stress, or to affect photosynthetic rates. Removing the kelp from the ocean and transporting them to the laboratory undoubtedly caused short-term stress, but this was done as quickly as possible (~20 min) in darkness, and there was no evidence of permanent tissue damage, discoloration or exudation of tannins. The similarity in respiration rates among the 3 treatments can also be taken as evidence that transporting and holding the kelp in the laboratory did not cause undue stress. Nevertheless, if stress was

partly responsible for the lower rates of photosynthesis in the laboratory, this will likely apply to most laboratory-based measurements of photosynthesis on kelp and large seaweeds.

Differences in light regimes was considered the most likely explanation for the differences observed in the *P–E* curves between the field and the 2 laboratory treatments. A fundamental difference between natural and artificial light is that light in the laboratory is delivered from a beam source and is constant, whereas light from the sun is more spatially diffuse (particularly at low solar elevation) and highly variable over multiple time scales (i.e. seconds to annually). Irradiance is even more variable underwater, where wave-induced light fluctuations vary over very short time scales, creating light flecking or flashes. The dynamic light environment underwater has been shown to enhance algal productivity (Dromgoole 1988, Wing & Patterson 1993). Differences in the spectral distributions of solar vs. artificial irradiance are also likely and would mean that at the same irradiance for overall PFD, photosynthetic rates could differ (Kirk 2011, Cullen et al. 2012). For example, the rate of photosynthesis in phytoplankton from deep water in the central North Pacific gyre is twice as great with blue light as with white light of the same photon flux density (Laws et al. 1990). Differences in light spectra with depth may also influence *in situ* measurements, with greater exposure to white light at the surface. While our data suggests that this is not necessarily important as kelp from both depths photosynthesized most rapidly in the higher PFD near the surface, there are reasons for caution, and further investigation is needed into how variation in spectra associated with depth and also the experiment set-up (e.g. plastic bag and shade cloth) could influence the photosynthetic results.

Artificial light in the laboratory is also highly directional with a fixed angle of incidence, resulting in marked light gradients from the surface to the bottom of the tank. We attempted to account for this by calculating a light extinction curve for the tank and calculating average irradiance during the incubation based on the depth in the tank of the majority of the laminae. This clearly introduces some error, as some of the algal tissue would have been exposed to more irradiance, and some to less, than the amount measured. The same is true for the outdoor treatment in the laboratory, where the light source was solar irradiance; proximity of the walls of the tank would likely have significantly affected the directionality and scattering of light and established much steeper gradients of light over smaller depth changes, compared to underwater conditions at the field sites. Deciding how and where in the tank to take light readings posed quite a challenge, and the position of these measurements likely influenced the parameter values generated from the *P–E* curves. For example, the high photosynthetic efficiency (α) recorded in the outdoor tanks under natural sunlight could be influenced by where light was measured in the tank, i.e. the measured irradiance may have been lower than the value that the majority of the algal tissue was exposed to, thus making the slope of the light-limited part of the curve steeper than it would be if a higher irradiance value was used for those measurements. These findings clearly demonstrate that careful consideration is needed in choosing the type of light source to be used and how the light environment is quantified within a laboratory setting.

The difficulties in producing a light environment in the laboratory that replicates natural settings, and in accurately measuring irradiance in the laboratory, are significant problems for laboratory-based photosynthesis measurements; these highlight the value of carrying out photosynthesis measurements *in situ*. For example, the lower P_{max} recorded in the laboratory than in the field in this study would result in an underestimate of overall kelp productivity. Thus, while there are many valid applications of measuring photosynthetic rates in a controlled laboratory setting (e.g. for comparing photosynthetic response among species, depths and even experimental treatments), we recommend that caution be taken when parameters from laboratory studies are applied to estimates of *in situ* production. Nevertheless, measurements of *in situ* rates of photosynthesis and respiration can act as a robust guide in assessing the reliability of other photosynthesis measurements that are not made *in situ*, as well as other methods used in estimating net primary productivity (e.g. those based on standing stock).

CONCLUSIONS

The method described here provides, for the first time, a robust means of measuring photosynthesis–irradiance relationships (*P–E* curves) of adult kelp, as well as other large seaweeds, *in situ*. The results highlight the potential limitations of carry-

ing out such measurements under laboratory conditions, in particular the use of artificial light sources, and suggest that using laboratory-derived photosynthesis measurements could underestimate kelp forest productivity. While we do not fully understand the effects that varying light spectra may have on rates of photosynthesis in nature, this technique is one important avenue that offers progress towards attaining that understanding. More generally, application of this method in both field and laboratory provides an opportunity to better understand temporal and spatial variation in benthic primary productivity, the drivers of variation in productivity, and how primary productivity will be affected by climate change and other anthropogenic impacts such as sedimentation and eutrophication.

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