Differential response of forest-forming seaweeds to elevated turbidity may facilitate ecosystem shifts on temperate reefs

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ABSTRACT: Underwater light is essential for fuelling coastal productivity. However, elevated turbidity, resulting from land-based activities and climate change, is often overlooked as a threat to coastal ecosystems. Understanding how low light, and specifically the temporal delivery of light, affects the productivity of forest-forming species is necessary to predict how ecosystems and species will respond to future increases in turbidity. Outdoor mesocosm experiments were used to compare the low-light tolerance of 2 forest-forming macrophytes that vary in their distribution in relation to turbidity, and investigate how the temporal delivery of light, i.e. press vs. pulse low-light disturbance, affects net primary productivity (NPP). We showed that the kelp *Ecklonia radiata*, which dominates reefs with low turbidity, is more productive per unit biomass under high-light conditions than the fucoid *Carpophyllum flexuosum*, which typifies more turbid waters. Under low light, *E. radiata* suffered greater tissue loss and had lower NPP than *C. flexuosum*. Under both press and pulse treatments, *E. radiata* showed significant losses of lamina biomass and reduced NPP, while *C. flexuosum* showed net growth under press disturbance, and only lost tissue and had reduced NPP under pulse disturbance. The greater tolerance of *C. flexuosum* to decreased light, and differential responses of *E. radiata* and *C. flexuosum* to press and pulse low-light conditions, provide mechanistic support for *C. flexuosum* being better suited to turbid low-light environments than *E. radiata*. These results suggest future increases in turbidity may facilitate a shift from kelp-dominated forests to alternate states, resulting in reduced primary productivity.

KEY WORDS: *Ecklonia* · *Carpophyllum* · Underwater forests · Turbidity · Press vs. pulse · Photoacclimation · Primary production · Temperate reef

1. INTRODUCTION

Underwater light is fundamental to maintaining productive coastal ecosystems (Airoldi & Cinelli 1997, Anthony et al. 2004, Aumack et al. 2007, Desmond et al. 2015, Blain et al. 2019, 2020, Pavlov et al. 2019). However in many parts of the world, increased delivery of sediments into the coastal environment due to human land use greatly reduces the amount of light reaching important benthic primary producers (Thrush et al. 2004, Aumack et al. 2007, Cai et al. 2009, Seers & Shears 2015). This reduction in light limits the ability of benthic macroalgae to grow and puts the structure and function of coastal ecosystems at risk (Pehlke & Bartsch 2008, Shepherd et al. 2009, Clark et al. 2013, Derrien-Courtel et al. 2013). Along with continued coastal development, increased coastal erosion due to sea level rise (FitzGerald et al. 2008, Nicholls & Cazenave 2010), increased storm activity (Trenberth 2011, Harley et al. 2017), and coastal flooding (Mousavi et al. 2011, Jongman et al. 2012) suggest

that coastal turbidity will further increase in many coastal regions with climate change (Thrush et al. 2004, Syvitski et al. 2005, Ogston & Field 2010, Klein et al. 2012, Fabricius et al. 2013).

Water clarity, or turbidity, is affected by the scattering of light by fine particles such as suspended sediments, phytoplankton, coloured dissolved organic matter (gelbstoff), and other microscopic organisms (Kirk 1985, Davies-Colley & Smith 2001). In particular, decreased water clarity in coastal environments can be attributed to runoff of sediments from the land due to heavy rainfall (Hickman 1979, Nash 1994, Jing & Ridd 1996), resuspension of sediments in the coastal zone by wind, waves, and currents (Larcombe et al. 1995, Jing & Ridd 1996, Storlazzi et al. 2009, Fabricius et al. 2013), and phytoplankton blooms associated with eutrophication (Smith 2003, Schindler 2006). The interactions between natural and anthropogenic drivers of turbidity can result in short-term pulses of extreme low light, such as those caused by rapid influxes of terrigenous matter following heavy rain or resuspension of sediments during storms, and/or a steady-state reduction in benthic irradiance caused by gradual coastal erosion and accumulation of fine sediments in the coastal environment (Thrush et al. 2004, Oberle et al. 2014, Seers & Shears 2015). Though both may ultimately result in the limitation of light to benthic primary producers, differences in temporal light delivery may have differential effects on macroalgal communities. Despite this, relatively little is known about how the frequency and magnitude of low-light limitation affects macroalgal populations.

The amount of light available to benthic primary producers is naturally variable due to a combination of biological, oceanographic, meteorological, and anthropogenic processes (Kirk 1985, Davies-Colley & Smith 2001, Seers & Shears 2015). High variability in underwater light elicits the need for macroalgae to employ acclimation strategies in order to cope with changes in light availability (Falkowski & LaRoche 1991, Henley 1993, Kirk 2011). Such strategies include cellular and morphological adjustments that enhance the capture and utilization of photons while limiting damage from over-saturation (Falkowski & LaRoche 1991, Kirk 2011). Despite this incredible plasticity, macroalgae are inevitably limited by the minimum light levels required to meet the metabolic requirements of that macroalga (Hanelt & Figueroa 2012).

As natural variations in the light environment are ubiquitous, there is extensive knowledge of the response of macroalgae to changes in light availability (Falkowski & Raven 2007, Kirk 2011). These studies have typically involved investigation of the response of algae to steady-state light environments (such as between different depths) or the effect of total quantum dose, which do not incorporate the temporal variability of light (Chapman & Burrows 1970, Aumack et al. 2007, Desmond et al. 2015, Smale et al. 2016, Blain & Shears 2019). However, dynamic light supply can influence the physiological performance and productivity of macroalgal species (e.g. Dromgoole 1987, 1988, Kübler & Raven 1996, Desmond et al. 2017). Previous studies investigating the effects of dynamic light environments on macroalgae have focused almost exclusively on the influence of light flecks and/or wave-induced light variation at or near saturating irradiances on macroalgal photoinduction and photoinhibition (but see Desmond et al. 2017). Less explored is how the temporal delivery of light under light-limiting conditions affects photoacclimation and productivity of macroalgae. Understanding the effects of acute vs. chronic low-light disturbances on benthic primary producers will be important for accurately assessing the impacts of increased turbidity on macroalgal communities, now and in the future.

In many areas of New Zealand, increased sediment runoff has been recognized as a fundamental threat to coastal ecosystems (Goff 1997, Hayward et al. 2006, Seers & Shears 2015). Turbidity has been shown to be a major determinant of benthic community structure on shallow coastal reefs (Grace 1983, Shears & Babcock 2007). In northeastern New Zealand, monospecific stands of the stipitate kelp *Ecklonia radiata* typically dominate subtidal reefs at depths greater than ca. 5 m (Choat & Schiel 1982, Shears & Babcock 2004). However, at sheltered and or turbid locations in northeastern New Zealand the large fucoid *Carpophyllum flexuosum* can become dominant and form extensive forests (Grace 1983, Shears & Babcock 2004). These distinct distributional patterns suggest that *C. flexuosum* is more tolerant of low-light environments and perhaps has a competitive advantage over kelp at turbid locations. Currently, there is a lack of knowledge on how productivity compares between these 2 important forest-forming species, and whether differential responses to reduced light facilitate the dominance of one species over another.

The aim of this study was 2-fold: (1) to compare the response of *E. radiata* and *C. flexuosum* to low-light conditions and (2) to investigate whether differences in the temporal distribution of low-light disturbances affect the physiological performance and produc-

tivity of these 2 forest-forming brown algae differentially. Firstly, a light intensity mesocosm experiment was used to compare the tolerance of *E. radiata* and *C. flexuosum* to steady-state low-light conditions. Secondly, a press (i.e. moderate, steady-state reduction in light) vs. pulse (i.e. short and intermittent periods of extreme low light) mesocosm experiment was used to assess the effects of low-light disturbances applied at different frequencies and magnitudes on the performance of *E. radiata* and *C. flexuosum*. In both experiments, changes in biomass and photosynthetic–irradiance (*P–E*) response were monitored to assess the effect of different light regimes on the 2 species. These measurements were incorporated into a physiological model of net primary production (NPP) in order to understand the ecological implications of relative changes in biomass and photoacclimation response. Due to the dominance of *C. flexuosum* in turbid environments, it was hypothesized that *C. flexuosum* would show greater acclimation and higher productivity under low-light conditions than *E. radiata*.

2. MATERIALS AND METHODS

2.1. Study species and collection site

This study was carried out with *Ecklonia radiata* and *Carpophyllum flexuosum* sporophytes collected at depths of 5–7 m from Leigh, northeastern New Zealand (36° 41.371′ S, 174° 58.048′ E). The collection site has relatively clear water with an average daily photon flux density (PFD) in summer of ca. 6.5 mol photons m^{-2} or 18% of surface irradiance (Blain & Shears 2019, Blain et al. 2020). At this site, *E. radiata* and *C. flexuosum* co-occur at 5–7 m depth, allowing both species to be collected from the same light environment. *E. radiata* at this depth are characterized by short stipes (~15–20 cm) and long primary laminae (~20–25 cm). Adult *C. flexuosum* at the collection site reach total lengths of up to 50 cm. Note that monospecific stands of *E. radiata* with longer stipes (~1 m in length) dominate the reef at deeper depths.

2.2. Light intensity experiment

Both mesocosm experiments were carried out in large outdoor tanks under natural light conditions, and light was regulated using shade cloth to avoid problems associated with artificial light and mini-mize the effects of differing light spectra (e.g. Forster & Dring 1992, Rodgers et al. 2015). The first mesocosm experiment was used to investigate the relative effects of decreasing light availability on the growth, photosynthetic performance, and productivity of *E. radiata* and *C. flexuosum.* Adult sporophytes were exposed to 4 different light treatments from 19 September to 19 October 2016. A total of 8 experimental tanks (1500 l) with flow-through seawater and a tip-bucket system were used for the experiment. Each tank was randomly assigned 1 of 4 experimental light treatments (ambient, low, critical, or blackout), and 5 individuals of each species were randomly assigned to each tank. Light treatments were created by covering tanks in either 1, 2, or 3 layers of shade cloth or black, opaque plastic sheets ('blackout'). It should be noted that covers were placed on frames built around tanks and not directly on tanks (see Supplement 1 at www.int-res.com/articles/suppl/m641p063_supp.pdf). Incident irradiance (*E*; μmol photons m^{-2} s^{-1}, as photosynthetically active radiation [PAR], 400–700 nm) within each tank was monitored for the duration of the experiment using data loggers with cosine-corrected sensors (Odyssey photosynthetic irradiance recording system, Dataflow Systems) mounted in the center and bottom of each tank. Calibration curves for each logger were produced prior to the experiment by fitting a linear regression between raw data from loggers (mV) and PFD values from a calibrated LI-192 underwater quantum sensor (LI-COR Biosciences). Ambient light treatments were ca. 15% of surface irradiance, similar to that at 5–7 m at the collection site. The 'low' light treatment, ca. 6% of surface irradiance, is typical of moderately turbid sites of the inner Hauraki Gulf (Blain & Shears 2019), and was chosen to give irradiance less than ambient but above the critical light threshold of ca. 0.6–1.2% for kelps (Lüning 1981, 1990). The 'critical' light treatment was chosen to fall within the 0.6–1.2% range and resulted in an average of 0.9% surface irradiance, while the 'blackout' light treatment was chosen to represent extreme light limitation at 0.03% of surface irradiance (Supplement 1). Both the critical and blackout light levels are frequently observed along urbanized coastlines of the Hauraki Gulf, especially after large storm events and heavy precipitation (C. O. Blain unpubl. data).

E. radiata and *C. flexuosum* sporophytes were collected from Leigh on 16 September 2016. Individuals were selected from areas of mixed algal stands (*E. radiata* and *C. flexuosum*) and only adults of <60 cm total length (stipe + laminae) were selected. Care was taken to select healthy individuals free of dis-

colouration or any major abrasions and grazed tissue. Sporophytes were transported to the Leigh Marine Laboratory and held in shaded outdoor tanks with flow-through ambient seawater from the adjacent coast in Leigh. Irradiance in holding tanks was reduced by ~80% using shade cloth. Thalli were attached to the bottom of tanks via the holdfast to ensure upright orientation. Frond movement and water circulation were maintained by a tip-bucket system that dumped ca. 15 l of seawater every 45–50 s (~1200 l h^{-1}) into each holding tank. Temperature was recorded every 30 min in each tank for the duration of the experiment using HOBO Pendent temperature loggers (±0.5°C; Onset Computer Corporation). Mean temperature was 16.5 ± 0.1°C and did not differ significantly among tanks.

Morphological measurements were taken for each individual (5 tank^{-1}) and P–E curves were measured in the laboratory (details below) for 3 randomly selected individuals from each tank of each species at the beginning and end of the experiment. For each *E. radiata*, stipe and primary lamina length were measured. *C. flexuosum* can have multiple fronds originating from the same holdfast; therefore, each primary lamina was counted and the length measured to determine total thallus length (total length; the sum of all laminae from an individual holdfast). For both species, initial and final wet weights and lamina volume were also measured and tissue samples were taken for pigment analyses (details below). Final morphological and photosynthetic measurements were taken between 19 and 21 October.

2.3. Press vs. pulse experiment

To investigate the differential effects of 'press' vs. 'pulse' low-light limitation on *E. radiata* and *C. flexuosum*, a second mesocosm experiment was used in which adult sporophytes were exposed to 3 different lighting regimes from 19 November to 18 December 2016. A total of 12 experimental tanks (200 l) were used for the experiment, and 2 individuals of each species were randomly assigned to each tank. Each tank was randomly assigned 1 of the 3 experimental light regimes including (1) control: ambient light of ca. 6 m depth created by covering tanks with one layer of 80% shade cloth; (2) press: constant low light created by covering tanks with 2 layers of 80% shade cloth and 1 layer of 40% shade cloth; and (3) pulse: blackout created by covering tanks with opaque, black plastic for 2 d and slowly raising irradiance using decreasing layers of shade cloth over 3 d to

ambient light conditions which were maintained for 2 d. The 7 d lighting regime for pulse treatments was repeated 4 times over the duration of the experiment. Ambient, press, and pulse lighting regimes were chosen based on results from the light intensity experiment. Furthermore, press and pulse tanks were chosen to provide comparable total weekly PFD between treatments (see Supplement 2 for details). PFD was measured in each tank using the loggers and methodologies described above. Mean temperature was 17.6 ± 0.1°C and did not differ significantly among tanks throughout the experiment.

E. radiata and *C. flexuosum* sporophytes were collected from Leigh on 15 November 2016 and transported and held at the Leigh Marine Laboratory. Morphological measurements were taken, and P–E curves were measured for each individual (2 tank^{-1}) of each species at the beginning and end of the experiment as in the light intensity experiment. Final morphological and photosynthetic measurements and tissue samples were taken between 19 and 22 December.

2.4. P–E parameters

P–E curves were obtained for *E. radiata* and *C. flexuosum* at the beginning and end of each experiment using photorespirometry chambers and methods described in detail by Rodgers et al. (2015). In short, photorespirometry chambers were composed of a clear polyethylene plastic bag covering a buoyant cylindrical frame (30 cm diameter × 41 cm height) that enclosed the lamina of *E. radiata* or *C. flexuosum* along with a dissolved oxygen logger and PAR logger. Chamber bags were sealed with a closed-cell foam stopper. In the case of *E. radiata*, the foam stopper was fitted around the stipe. An inline pump (Rule Submersible and Inline Pump iL200^{Plus}) with in- and outflow tubes passing through the foam stopper and valve system was used to continually mix the chamber and periodically flush the chamber with fresh seawater (see Rodgers et al. 2015).

Photosynthetic measurements were conducted using 2 replicate photorespirometry chambers in two 200 l indoor tanks under artificial lighting (LED; 6300 lumen, Cree XM-L). For each thallus, P–E curves were determined by measuring dark respiration (R_d) and net photosynthesis at 5 irradiances of 10 min duration each. For each individual, a P–E curve was fitted and P–E parameters derived using R v.3.5.3 (R Core Team 2019) following Webb et al. (1974):

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

where P is net photosynthetic rate at any PFD, P_{max} is the maximum photosynthetic rate at saturating irradiance, and α is photosynthetic efficiency (i.e. the slope of the linear light-limited part of the curve). Saturation irradiance (E_k; the onset of light saturation) was estimated as P_{max} / α) and compensation irradiance (E_c; irradiance at which photosynthesis balances respiration) was calculated as R_d / α.

2.5. NPP modelling

To provide a more ecologically relevant measure of the effect of different light intensities and light regimes on *E. radiata* and *C. flexuosum*, estimates of primary productivity were made using a physiologically based model (Webb et al. 1974, Rodgers & Shears 2016). This model incorporates changes in photosynthetic parameters and lamina biomass under different light conditions to give an overall estimate of NPP (g C m^{-2} h^{-1}) following the equation of (Webb et al. 1974):

$$NPP = [P_{max} \times (1 - e^{-\alpha E/P max}) - R_d] \times b \qquad (2)$$

where P_{max} is calculated from P–E curves (g C g^{-1} dry weight [DW] h^{-1}), α is calculated as the slope of the initial linear part of the curve describing the relationship between mass-specific gross primary productivity (GPP) and irradiance at non-saturating irradiances, E is the value on the seafloor averaged over 1 h (µmol photons m^{-2} s^{-1}), and b is the macroalgal standing crop (g DW lamina m^{-2}). GPP was converted to NPP using mass-specific R_d rates (g C g^{-1} DW h^{-1}) measured in the dark during incubations. Oxygen evolution rates were converted to carbon using photosynthetic quotient of 1 (Rosenberg et al. 1995). For both experiments, we used the average final P_{max}, α, and R_d values of each species with the assumption that after ~30 d the individuals were fully acclimated to their respective lighting regimes. It is important to note that changes in thallus morphology and structure, which enhance acclimation to environmental conditions, occur relatively slowly (months to years) and is, therefore, outside the scope of the present study.

2.6. Photosynthetic pigment analysis

Dimethyl sulphoxide (DMSO) extraction methods (Seely et al. 1972) were used to determine photosynthetic pigment contents in *E. radiata* and *C. flexuosum*. Two 2.5 cm diameter disks were cut from the basal secondary laminae of each *E. radiata* or from a leaf in the case of *C. flexuosum*. One pair of each disk was submerged in 4 ml DMSO for 3–5 min in darkness and then 4 ml 90% acetone for 1 h in darkness to extract chlorophyll (chl) a, chl c and fucoxanthin. The absorbance of each extract was determined spectrophotometrically (Shimadzu UV-2450) using 4 wavelengths (480, 582, 631, and 660 nm for DMSO and 470, 580, 628, and 661 nm for 90% acetone) and standardized by deducting absorbances at 750 nm. Overall pigment content (mg g^{-1} DW) for each sample was determined combining the pigment content from the 2 extractions (DMSO and 90% acetone). Values were standardized using the wet to dry (dried at weight ratios 60°C for 24 h) ratios obtained from the second disk of each thalli.

2.7. Statistical analyses

For both experiments, 3-way mixed model permutational multivariate analysis of variance (PERMANOVA) were applied to normalized data using Type I SS on 9999 permutations (Anderson et al. 2008) with the factors species (fixed effect: *E. radiata* and *C. flexuosum*), light treatment (fixed effect), and tank (random effect: tanks nested within each treatment) were used to investigate differences in the change in lamina biomass, photosynthetic parameters (R_d, P_{max}, α, E_k, and E_c), and pigment content. Differences among levels within a factor were investigated using pairwise comparisons.

To investigate differences in modelled NPP among treatments in each experiment, 2-way ANOVAs with the factors species and treatment were used. For the light intensity experiment, the difference in average daily NPP (mg C g^{-1} DW d^{-1}) was examined whereas for the press vs. pulse experiment, the daily average NPP for each 7 d light cycle was summed and weekly averages (mg C g^{-1} DW wk^{-1}) were used to investigate overall differences between treatments. Both analyses were applied to the raw data. Homogeneity of the variance was and normality were verified by Levene's test and Shapiro-Wilk's statistics (Snedecor & Cochran 1989), respectively. To detect difference among levels within a factor, we used Tukey's HSD multiple comparison tests (comparisons based on least-square [LS] means) (Sokal & Rohlf 2012). A significance threshold of p ≤ 0.05 was used for all statistical tests. All analyses were conducted with JMP v.13.0.0 (SAS Institute), or PRIMER v.7.0.12 (Anderson et al. 2008) in the case of PERMANOVAs.

3. RESULTS

3.1. Light intensity experiment

Changes in lamina biomass showed variable responses to light treatments that differed between species (Table 1). Under the 2 highest light conditions, both *Ecklonia radiata* and *Carpophyllum flexuosum* displayed similar net gains in lamina biomass (Fig. 1a). *E. radiata* began to lose lamina biomass under critical light conditions while *C. flexuosum* gained biomass. Both species showed net declines of lamina biomass in the lowest light treatment (blackout), but declines were ca. 15 times greater in *E. radiata* than *C. flexuosum*. Individuals from blackout treatments showed severe signs of tissue deteriora-

Table 1. Summary of ANOVAs (applied to normalized data using Type III SS and 9999 permutations) examining differences in changes in lamina biomass (proportion of initial biomass) and photosynthetic parameters between species (fixed effect: *Ecklonia radiata* and *Carpophyllum flexuosum*) and among light treatments (fixed effect: ambient, low, critical, blackout [Expt 1] or ambient, press, pulse [Expt 2]) in the light intensity and press vs. pulse experiments. Tank (random effect: nested in treatment) was included in the models as a random effect. P_{max}: maximum photosynthetic rate; R_d: dark respiration rate; α: photosynthetic efficiency; E_k: saturation irradiance; E_c: compensation irradiance. **Bold** values indicate significance (p < 0.05). Detailed results are available in Supplement 3

Source of variation	Light intensity		Press vs. pulse	
	Pseudo-*F*	p-value	Pseudo-*F*	p-value
Change in lamina biomass				
Species	33.67	**0.0001**	18.52	**0.0002**
Treatment	439.27	**0.0078**	11.06	**0.0108**
Species × treatment	17.49	**0.0001**	13.07	**0.0001**
P_{max}				
Species	3.99	0.0527	41.60	**0.0002**
Treatment	10.93	**0.0105**	5.09	**0.0274**
Species × treatment	2.59	0.0723	4.33	**0.0491**
R_d				
Species	9.22	**0.0045**	3.08	0.1142
Treatment	4.05	0.1331	0.88	0.4549
Species × treatment	3.80	**0.0178**	51.41	**0.0001**
α				
Species	1.91	0.1412	8.34	**0.0191**
Treatment	0.06	0.9892	0.24	0.7540
Species × treatment	3.35	0.0730	0.16	0.8454
E_k				
Species	0.20	0.6646	0.02	0.9069
Treatment	0.99	0.5071	0.01	0.9837
Species × treatment	2.36	0.0943	0.11	0.8910
E_c				
Species	1.10	0.2994	5.76	**0.0397**
Treatment	1.31	0.3477	0.79	0.4747
Species × treatment	0.20	0.9007	2.84	0.1149

tion (Fig. 1d). The primary and secondary laminae of *E. radiata* were greatly decreased in length, whereas *C. flexuosum* showed a substantial reduction in photosynthetically active fronds (or leaves) (Fig. 1c). Furthermore, *E. radiata* in blackout tanks became slippery to the touch, suggesting the stress-related release of protective secondary metabolites, while the apices of *C. flexuosum* became darkened and discoloured.

Initial values of P_{max} for *E. radiata* were typically higher than those of *C. flexuosum* (Fig. 2, Supplement 3). At the end of the light intensity experiment, P_{max} tended to decline with decreasing light for both species (Table 1, Fig. 2a). P_{max} of *E. radiata* in ambient treatments was significantly greater than *C. flexuosum* and all other treatments. There was no significant difference in P_{max} among *E. radiata* in the low and critical treatments and *C. flexuosum* in the 3 highest light treatments, but P_{max} was significantly lower in blackout treatments (all pair-wise tests, p < 0.05). The effect of light treatments on R_d differed be-
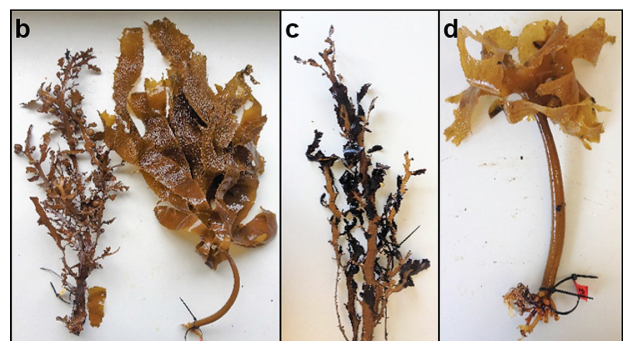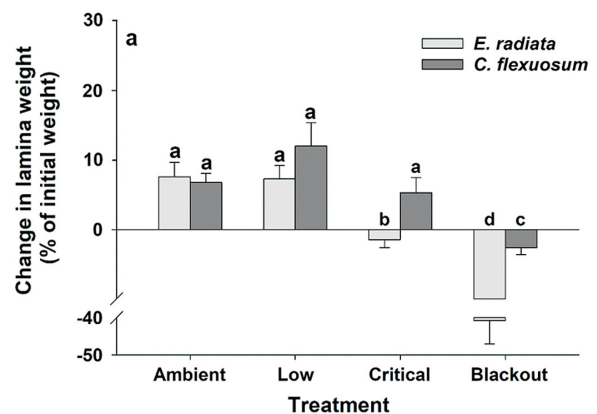

Fig. 1. (a) Mean (±SE) percent change in lamina biomass for *Ecklonia radiata* and *Carpophyllum flexuosum* in each light treatment (ambient, low, critical, and blackout) of the light intensity experiment and images of *C. flexuosum* (left) and *E. radiata* (right) at the end of the experiment from (b) ambient and (c,d) blackout treatments. Bars not sharing the same letter in (a) are significantly different (pair-wise tests, p < 0.05; n = 10 for each bar)

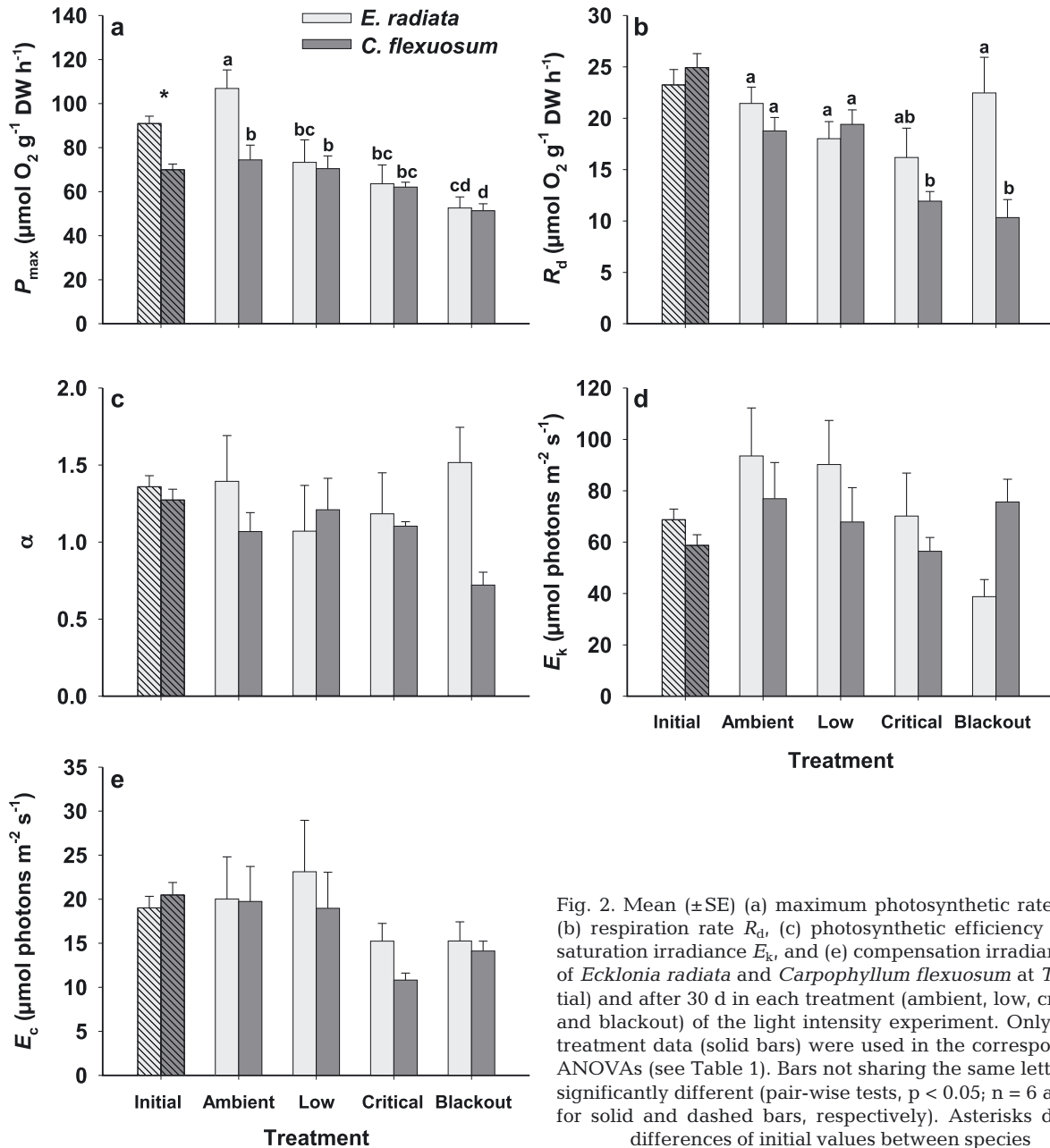Fig. 2. Mean (±SE) (a) maximum photosynthetic rate P_{max}, (b) respiration rate R_d, (c) photosynthetic efficiency α, (d) saturation irradiance E_k, and (e) compensation irradiance E_c of *Ecklonia radiata* and *Carpophyllum flexuosum* at T_0 (initial) and after 30 d in each treatment (ambient, low, critical, and blackout) of the light intensity experiment. Only post-treatment data (solid bars) were used in the corresponding ANOVAs (see Table 1). Bars not sharing the same letter are significantly different (pair-wise tests, p < 0.05; n = 6 and 24 for solid and dashed bars, respectively). Asterisks denote differences of initial values between species

tween the 2 species (Table 1). The rate of respiration for *C. flexuosum* generally declined with decreasing light, whereas R_d for *E. radiata* did not vary significantly among the treatments (Fig. 2b). Values of α were similar among treatment levels for *E. radiata* and *C. flexuosum* (Table 1), though there was a notable (but non-significant) decrease in α for *C. flexuosum* under blackout conditions (Fig. 2c). E_k showed no obvious trend among treatments for *C. flexuosum*, but appeared to decrease consistently with decreasing light for *E. radiata*, though this rela-

tionship was not significant (Table 1, Fig. 2d). E_c did not show any definite differences among treatments or between species, though tended to be lowest in critical and blackout treatments for both species (Table 1, Fig. 2e).

Photosynthetic pigment concentrations of *E. radiata* were generally higher than *C. flexuosum* (Fig. S4.1 in Supplement 4). Differences in chl *a* were not significantly impacted by treatment (Table S3.2 in Supplement 3, Fig. S4.1a). In contrast, chl *c* content varied among treatments (Table S3.1). Chl *c* levels in *E. radi-*
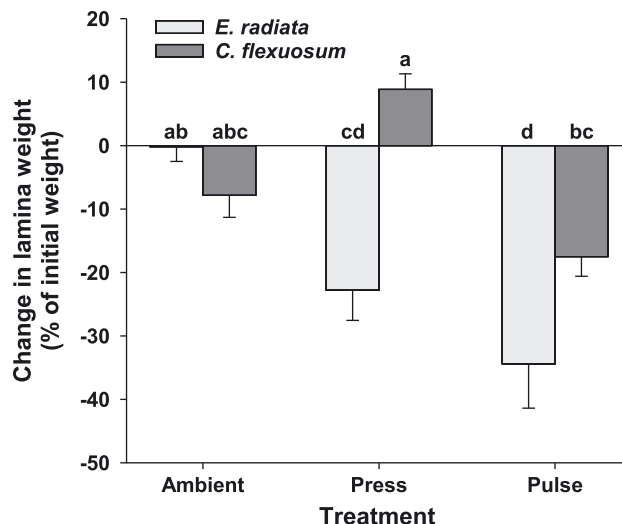
Fig. 3. Mean (±SE) percent change in lamina biomass for *Ecklonia radiata* and *Carpophyllum flexuosum* in each light treatment (ambient, press, and pulse) of the press vs. pulse experiment. Bars not sharing the same letter are significantly different (pair-wise tests, p < 0.05; n = 8 for each bar)

ata were lower in ambient treatments than all other treatments, whereas in *C. flexuosum*, chl *c* levels were lower in ambient, low, and critical treatments than blackout treatments (Fig. S4.1b). Fucoxanthin levels showed variable responses to treatment for each species (Table S3.2). For *E. radiata*, fucoxanthin levels were lowest in ambient treatments, whereas *C. flexuosum* had low fucoxanthin levels in both ambient and low-light conditions (Fig. S4.1c).

3.2. Press vs. pulse experiment

Changes in lamina biomass showed variable responses to light treatments that differed between species (Table 1). Under ambient conditions, *E. radiata* maintained a constant biomass but underwent significant net lamina biomass loss in both the press and pulse treatments (Fig. 3). In contrast, *C. flexuosum* appeared to have greatest tissue loss in the pulse treatment, though this loss was not significantly greater than in the ambient treatment (pairwise test, p = 0.061). *C. flexuosum* showed marginal gains in lamina biomass in the press treatment, which was also evident in the appearance of new fronds and leaves. Losses in lamina biomass were ca. 2 times greater in *E. radiata* than *C. flexuosum* under pulse conditions (pair-wise test, p = 0.0037).

At the end of the press vs. pulse experiment, differences in P_{max} among treatments were evident for *E.*

radiata but not *C. flexuosum* (Table 1, Fig. 4a). P_{max} of *E. radiata* in press and pulse treatments were similar (pair-wise test, p = 0.171) yet significantly lower than ambient treatments (pair-wise test, p = 0.029) (Fig. 4a). The influence of treatment on R_d differed between species (Table 1). The rate of respiration for *E. radiata* from press treatments was higher than ambient and pulse conditions (pair-wise tests, p = 0.028 and 0.027, respectively), while *C. flexuosum* had lower respiration rates in the press treatment (pairwise tests, p = 0.031 and 0.030 for ambient and pulse treatments, respectively). The value of α did not differ among treatments but was higher for *E. radiata* than *C. flexuosum* (Table 1, Fig. 4c). E_k did not differ among treatments or between species (Table 1, Fig. 4d), whereas E_c showed a small difference between *E. radiata* and *C. flexuosum* but not among treatments (Table 1, Fig. 4e).

As in the first experiment, photosynthetic pigment content was higher in *E. radiata* than *C. flexuosum* (Table S3.2, Fig. S4.2). Differences in chl *a* were also significantly impacted by treatment, yet there was no interaction between factors (Table S3.2). For both species, chl *a* content was highest in press treatments (pair-wise test, p < 0.0001) and lowest in pulse treatments (pair-wise test, p < 0.0001) (Fig. S4.2a). Chl *c* content showed variation among treatments that differed for each species (Table S3.2). For *E. radiata*, chl *c* levels were lower in press and pulse treatments than ambient treatments, whereas for *C. flexuosum* a decline was only evident in pulse treatments (Fig. S4.2b). Fucoxanthin content differed between species and among treatments (Table S3.2). For *E. radiata*, fucoxanthin content was lowest in pulse treatments, whereas *C. flexuosum* appeared to have comparably low levels in both ambient and pulse treatments (Fig. S4.2c).

3.3. Modelled NPP

For each experiment, the response of NPP to the different treatments varied between species (Table 2). In the light intensity experiment, NPP of *E. radiata* declined significantly across each light treatment, whereas *C. flexuosum* only had significantly reduced NPP under critical and blackout light levels (Fig. 5a). *E. radiata* had significantly higher (1.9 times) daily NPP than *C. flexuosum* under ambient conditions (least square [LS] means, p < 0.0001), but not in low or critical treatments (LS means, p = 0.96 and 0.087, respectively). For blackout treatments, *E. radiata* had significantly lower
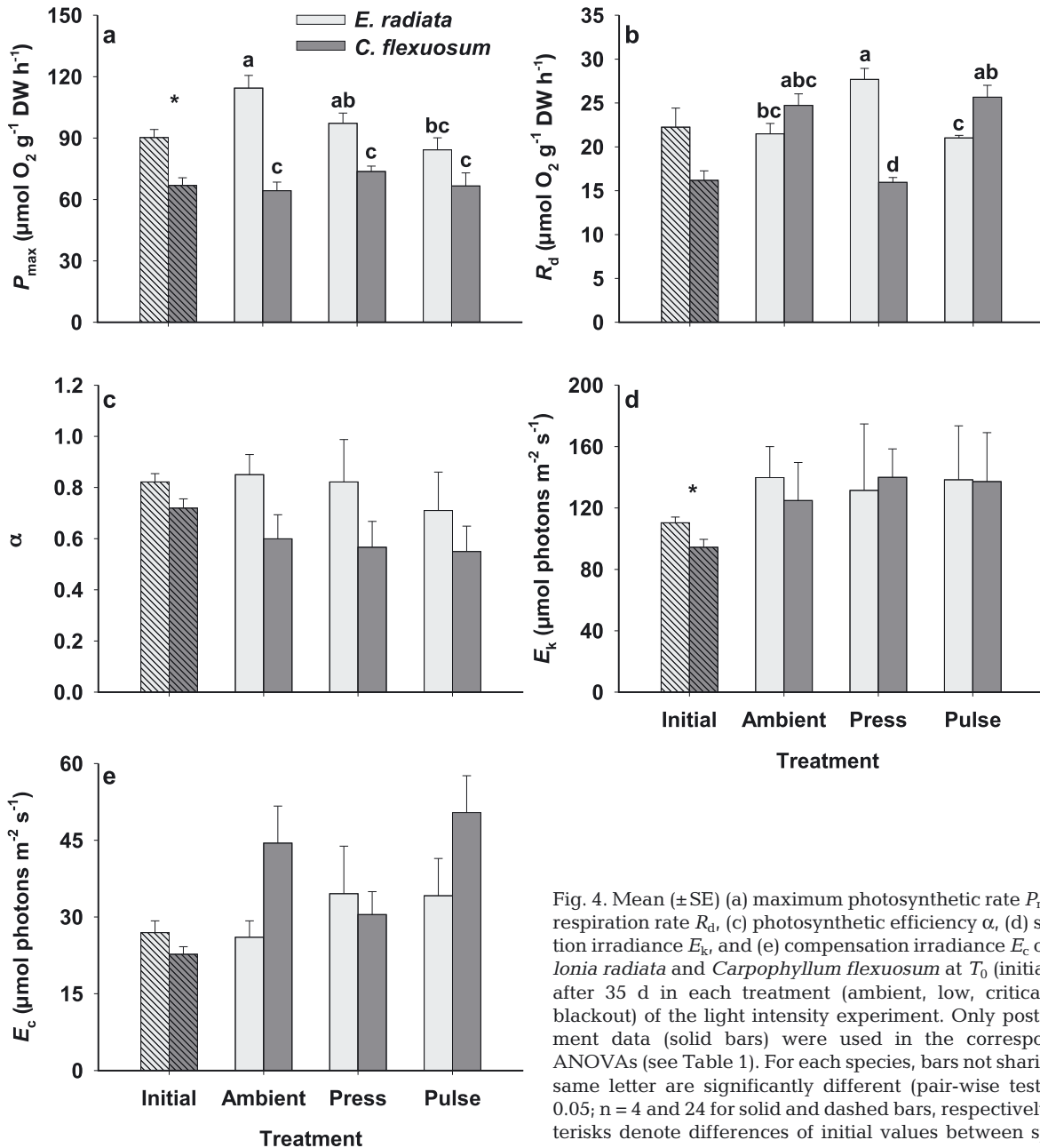
Fig. 4. Mean (±SE) (a) maximum photosynthetic rate P_{max}, (b) respiration rate R_d, (c) photosynthetic efficiency α, (d) saturation irradiance E_k, and (e) compensation irradiance E_c of *Ecklonia radiata* and *Carpophyllum flexuosum* at T_0 (initial) and after 35 d in each treatment (ambient, low, critical, and blackout) of the light intensity experiment. Only post-treatment data (solid bars) were used in the corresponding ANOVAs (see Table 1). For each species, bars not sharing the same letter are significantly different (pair-wise tests, p < 0.05; n = 4 and 24 for solid and dashed bars, respectively). Asterisks denote differences of initial values between species

(2.2 times) daily NPP than *C. flexuosum* (LS means, p < 0.0001). NPP became negative for both species in light treatments <1% of surface irradiance (critical and blackout).

In the press vs. pulse experiment, NPP of *E. radiata* was significantly reduced under both press and pulse treatments, whereas NPP of *C. flexuosum* was only significantly reduced under pulse conditions (Fig. 5b). NPP of *E. radiata* was significantly higher (ca. 13 times) than that of *C. flexuosum* under ambient conditions (LS means, p < 0.0001).

4. DISCUSSION

The results of the current study provide clear evidence that the kelp *Ecklonia radiata,* which dominates reefs with good water clarity (low turbidity), is more productive per unit biomass under high-light conditions than the fucoid *Carpophyllum flexuosum,* which typifies more turbid waters. As light declined, *E. radiata* suffered greater tissue loss and had lower NPP than *C. flexuosum.* Press and pulse disturbances resulted in differential effects on each species. *E. radi-*

Table 2. Summary of 2-way ANOVAs (applied to raw data) examining the effect of species (*Ecklonia radiata* and *Carpophyllum flexuosum*) and treatment on estimated net primary productivity (NPP) for each experiment. DW: dry weight; **bold** values indicate significance (p < 0.05)

Source of variation	df	MS	*F*-value	p-value
Expt 1				
NPP (mg C g⁻¹ DW d⁻¹)				
Species	1	12.76	4.56	**0.0340**
Treatment	3	484.17	172.98	**<0.0001**
Species × treatment	3	54.87	19.60	**<0.0001**
Error	232	2.80		
Corrected total	239			
Expt 2				
NPP (mg C g⁻¹ DW wk⁻¹)				
Species	1	334.42	24.05	**0.0001**
Treatment	2	1539.51	110.70	**<0.0001**
Species × treatment	2	561.33	40.36	**<0.0001**
Error	18	13.91		
Corrected total	23			

ata exhibited significant losses of lamina biomass and reduced NPP under both press and pulse treatments, whereas *C. flexuosum* showed net growth under press disturbance, but lost tissue and had significantly reduced NPP under pulse disturbance. The differential responses of *E. radiata* and *C. flexuosum* to press and pulse low-light conditions provides insight into individual species resilience and potential competitive interactions under the influence of changing coastal light environments. Under degraded light environments, *C. flexuosum* will likely out-perform *E. radiata* and competitive interactions may tend to favour *C. flexuosum*, potentially resulting in lower primary and community production. Our results highlight the capacity of low-light stress to facilitate the reduction of kelp and its possible replacement with more low-light tolerant species. Hence, in a future with more turbid waters we will likely see a reduction in primary production and eventually a shift from kelp forests to alternate states.

4.1. Light intensity experiment

Results of the light intensity experiment showed a general decline in the performance of both *E. radiata* and *C. flexuosum* to decreasing light. However, *E. radiata* underwent significantly higher tissue loss than *C. flexuosum* under the lowest light treatments, indicating that *C. flexuosum* is more tolerant of low light than *E. radiata*. Estimated NPP also declined significantly across each light level for *E. radiata*, yet
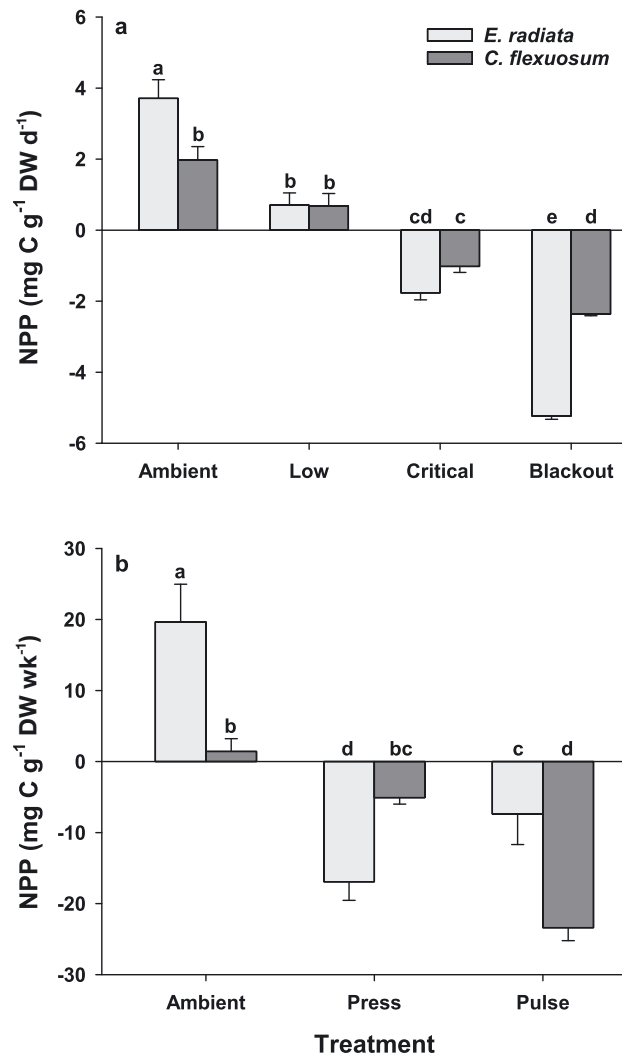

Fig. 5. Mean net primary productivity (NPP) for the (a) light intensity and (b) press vs. pulse experiments. Estimates of productivity are based on the average photosynthetic parameters and light from each treatment in each experiment. Each point in (a) represents the average NPP for each day of the light intensity experiment (n = 30), whereas each bar in (b) represents the average NPP for each week of the press vs. pulse experiment (n = 4). Bars not sharing the same letter are significantly different (least square means tests, p < 0.05)

for *C. flexuosum*, NPP did not differ between ambient and low-light conditions but was significantly lower for the 2 lowest light treatments. This is consistent with the distributional patterns of *E. radiata* and *C. flexuosum* in the Hauraki Gulf, as *C. flexuosum* typically dominates in more turbid environments (Grace 1983). Furthermore, substantial loss of thallus biomass in both species under the lowest level of light (blackout, 0.03% surface irradiance) clearly demonstrates an inability of either species to cope with extremely low light. This was not surprising,

given that most large brown macroalgae are typically restricted to depths where irradiance is greater than ~0.7–1.4 % of surface irradiance (Lüning 1981, 1990). The relatively low biomass loss for *C. flexuosum* compared to *E. radiata* under blackout treatments provides more evidence that, despite similar changes in photosynthetic performance, *C. flexuosum* may be better equipped to withstand chronic low-light environments than *E. radiata*.

Neither of the 2 species examined exhibited clear evidence of photoacclimation to low light based on photosynthetic parameters or photosynthetic pigment contents. Adjustments in photosynthetic parameters, which can occur within hours, typically include down regulation of respiration and increased α in order to decrease metabolic demand and optimize the capture of available light (Falkowski & LaRoche 1991, Kirk 2011). Consequently, low-light acclimation also results in reduced saturation and E_c. Thus, in the current study it was expected that α would increase along with increased photosynthetic pigment levels in low-light treatments. This type of photoacclimation response has been demonstrated in *E. radiata* populations along natural light gradients with increasing depth (Fairhead & Cheshire 2004, Rodgers & Shears 2016), low-salinity surface waters (Miller et al. 2006), and turbidity (Blain & Shears 2019, Blain et al. 2020). In the current study, increases in pigments were only evident in *E. radiata*, which showed a moderate increase of accessory pigments (chl *c* and fucoxanthin) with decreasing light (Supplement 4). This was not reflected in α, which was variable, though E_c did appear to decrease for both species in the 2 lowest light treatments.

R_d did tend to decline with decreasing light for *C. flexuosum*, which may suggest an acclimation response to low light (Falkowski & LaRoche 1991, Kirk 2011). This is similar to the results of Desmond et al. (2017), where *C. flexuosum* from 10 m depth had a lower R_d than those from 2 m. In contrast, R_d was high for *E. radiata* in the lowest light treatment, which may indicate a stress response to low light. For *E. radiata* in the Hauraki Gulf, R_d typically decreases with increasing turbidity as a response to low light (Blain & Shears 2019). However, the positive relationship of R_d with light becomes negative under high sea temperatures, suggesting that the interaction between low light and high temperatures elicits a stress response indicated by an increase in R_d (Blain & Shears 2019). Though temperature was an unlikely stressor in the current study, other stressors associated with being held in tanks (discussed below) cannot be ruled out.

In both species, P_{max} was reduced under low light, but it is unclear whether changes in P_{max} were the result of a stress response or an affiliate of photoacclimation. In Fiordland, New Zealand, *E. radiata* sampled across a light and exposure gradient had similar P_{max}. In this case, increasing α and pigment content with decreasing light (i.e. photoacclimation) was suggested to compensate for low light availability (Miller et al. 2006). Similarly, high P_{max} values in deep *E. radiata* from Goat Island, New Zealand, were coupled with high α and photosynthetic pigment content (Rodgers & Shears 2016). In contrast, P_{max} of *E. radiata* collected across a turbidity gradient in the Hauraki Gulf typically decreased with decreasing light, despite having higher α values and photosynthetic pigment contents (Blain & Shears 2019). However, this relationship was primarily driven by differences in thallus morphology, specifically surface area to volume ratios, across the turbidity gradient (Blain et al. 2020). While morphological acclimation can enhance overall productivity of individuals (Blain et al. 2020), this often occurs over longer periods of months to years, and so was outside the scope of the current study. All specimens in the present study were collected from the same site and depth, thus thallus morphology should not have contributed to differences in photosynthetic parameters among treatments. In this case, the reduction of P_{max} under low light for both species may indeed indicate a stress response. Additionally, the initial decline in P_{max} from ambient to low-light conditions was greater in *E. radiata* than *C. flexuosum*, which indicates that low-light conditions had more pervasive effects on *E. radiata*.

4.2. Press vs. pulse experiment

This is the first study to examine the impacts of press vs. pulse low-light disturbance on the primary production of whole thalli. The results revealed different responses of the 2 species to the temporal delivery of light. Under ambient conditions, the NPP of *E. radiata* was ca. 14 times higher than that of *C. flexuosum*. This difference was higher than that observed in the light gradient experiment and was driven by the lower performance (low P_{max} and α, and high R_d) and higher tissue loss of *C. flexuosum* under ambient conditions of the press vs. pulse experiment compared with that in the light intensity experiment. The higher NPP of *E. radiata* under ambient conditions in both experiments attests to the exceptionally high productivity and growth of kelp

species. Fucoid species, on the other hand, are characterized as slower growing with lower rates of production (Mann 1973, Vadas et al. 2004). Under treatments of light limitation (press and pulse), both species showed negative NPP, which suggests that neither species were able to fully acclimate to the experimental conditions in the given time frame. Despite this, the differential effects of press vs. pulse treatments on NPP estimates of the 2 species suggests that the temporal delivery of light has an important influence on their physiology. Indeed, *E. radiata* showed significantly lower NPP under both press and pulse disturbance compared to ambient light, whereas *C. flexuosum* only had a significant reduction in NPP when exposed to the pulse disturbance. Not only that, *C. flexuosum* showed a net increase in lamina biomass and visible frond production in press treatments, which provides further evidence of higher tolerance of this species to persistent, low-light environments.

Despite the observed differences in lamina production between species, limited change in photosynthetic parameters in response to the low-light treatments was observed. As in the light intensity experiment, it was expected that low-light disturbance would result in an increase in α. However, there were no observed differences in α among treatments for either species, and photosynthetic pigment content tended to decrease in both the press and pulse disturbances (Supplement 4). This may be another indication that neither species was able to fully acclimate to the light conditions under the given time frame. Interestingly, in the press treatment *E. radiata* showed increased R_d while *C. flexuosum* showed decreased R_d. This finding is consistent with the light intensity experiment and indicates a differential response of the 2 species to chronic low-light environments. Specifically, higher rates of R_d for *E. radiata* in the press treatment suggest greater levels of stress under these conditions, whereas lower R_d in the pulse treatment may suggest that *E. radiata* is able to recover to pulse disturbances more quickly. Hence, the opposite may be true for *C. flexuosum*, where low R_d under press conditions indicates enhanced acclimation to low light. This was also reflected in estimates of NPP for each species.

4.3. Study limitations

Like most mesocosm experiments, the experiments described above are not without limitations. Adult *E. radiata* sporophytes are particularly sensitive to labo-

ratory conditions, especially in summer when seawater temperatures are high (C. O. Blain pers. obs.). We chose to work with adult sporophytes to provide results that are ecologically relevant and directly comparable to those of concurrent studies investigating the effects of light on the photosynthetic capacity and growth of *E. radiata* in the Hauraki Gulf (Blain & Shears 2019, Blain et al. 2020). In order to minimize stress on thalli, we took special care during the collection and transportation of individuals to the laboratory, avoiding the emersion of thalli. Once in experimental tanks, the flow of fresh seawater was maximized in order to minimize the build-up of diffusive boundary layers and to maintain water temperature similar to that of the adjacent coast.

While experiments were carried out under natural light, the light spectra within experimental tanks likely differed to some extent from that at the collection site due to differences in attenuation of the light spectra with depth and also differing water column properties. Though we expect that these differences had negligible impacts on our overall conclusions, spectral composition may have important impacts on algal physiology, especially in early life stages (Lüning & Dring 1972, Dring 1986, Forster & Dring 1992, Schmid & Dring 1996, Cuijuan et al. 2005, Wang et al. 2010, 2013), and therefore should be considered in future studies. It is also important to note here that *P–E* curves from both experiments were determined under laboratory conditions using artificial light, which often results in low estimates of P_{max} and thus likely underestimates NPP (Rodgers et al. 2015, Blain & Shears 2019). This is largely the result of the unidirectional nature of lighting in tanks and self-shading among fronds, which can be exacerbated by overly bushy lamina (Blain et al. 2020). Care was taken to select thalli of an appropriate size for photorespirometry chambers in order to minimize these impacts. Consequently, estimates of NPP are strictly for comparisons among treatment within the confines of these experiments, and we caution the reader on comparing the values of NPP to different systems and study species.

Though this study focused on the impacts of reduced light on mature sporophytes, turbidity and decreased light can have differential effects on the different life history stages of each species. Furthermore, increases in coastal erosion and elevated turbidity are often coupled with increased sediment deposition and nutrient inputs, which may also impact species differentially, facilitating shifts in community states and exacerbating reductions in ecosystem functioning (Airoldi 2003). For example, (Blain &

Shears 2020) showed that nutrient enrichment associated with elevated turbidity does not impact the photosynthetic response of *E. radiata* to light but may enhance its ability to allocate a higher proportion of the carbon assimilated through photosynthesis to growth compared to those in high-light (low turbidity) conditions. This suggests that estimates of NPP in the current study should not differ under varying nutrient regimes. However, minor changes in growth associated with the interaction between high nutrients and low light in highly turbid conditions may be expected.

For some species, even a thin layer of settled sediment on their fronds can inhibit photosynthesis by impeding the transfer of vital nutrients and light energy from the seawater to the macroalgae, ultimately resulting in decreased productivity (Airoldi & Cinelli 1997, Airoldi 2003, Eriksson & Johansson 2005, Roleda & Dethleff 2011). This may compound the effects of low light availability on subtidal macroalgae. High levels of suspended and deposited sediments can also negatively impact the diversity and abundance of macroalgae by excluding intolerant species (Daly & Mathieson 1977), inhibiting settlement of reproductive phases (Dayton 1975, Devinny & Volse 1978), or reducing performance and survival (Seapy & Littler 1982, Branch et al. 1990, Chapman et al. 2002). These are factors that may also contribute to the establishment of *C. flexuosum* forests in place of *E. radiata* forests in the inner Hauraki Gulf, as *C. flexuosum* appears to be more tolerant of sedimentation.

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