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WHOLE COMMUNITY ESTIMATES OF MACROALGAL PIGMENT CONCENTRATION WITHIN TWO SOUTHERN NEW ZEALAND KELP FORESTS[1]

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Light availability is a fundamental factor that controls the productivity and distribution of macroalgae and is highly variable, both spatially and temporally, in subtidal coastal systems. Our comprehension of how macroalgae respond to such variability is a significant knowledge gap that limits our understanding of how light influences the structure and productivity of these environments. Here, we examined the pigment characteristics of individual species, and for the first time the whole community, within one low-light, and one high-light kelp-forest system in southern New Zealand. The aim was to quantify the range of pigmentation seen within the two kelp-forests, which differed in irradiance regime. Light availability was 33% and 64% greater at the high-light compared to the low-light site at 2 and 10 m depth, respectively. Results suggested Phaeophyceaen species at deeper depths in the low-light site may be living at the edge of their photosynthetic ability and pigment synthesis appeared significantly restricted. Even with greater investment in the pigment fucoxanthin, biomass of Phaeophyceaen species was significantly lower in the low-light site. Highly pigmented Rhodophyceaen species made a greater proportional contribution to community biomass within the low-light site where they likely possessed a photosynthetic advantage. This work helps explain discrepancies in community structure between the two study sites and explores the complex relationship between irradiance and photoacclimation. The comparison of community pigment concentration holds potential as a tool for assessing the relative degree of photoacclimation occurring between sites and provides a proxy of photosynthetic cost under a specific light regime.

Key index words: **chlorophyll; fucoxanthin; kelp-forest; light; macroalgae; pigment**

***Abbreviation*: LHCP, light-harvesting chlorophyll protein complexes**

Light profiles in coastal waters are typically variable in quantity and quality. This variability can be attributed to day length (Gomez et al. 1997), wave action (Fairhead and Cheshire 2004), cloud cover (Anthony et al. 2004), light flecking (Wing and Patterson 1993, Kubler and Raven 1996), tidal fluctuation (Anthony et al. 2004), and turbidity (Airoldi 2003, Aumack et al. 2007). Also typical is variation in the structure of macroalgal communities between locations that vary in irradiance (Connell 2005, Gattuso et al. 2006, Aumack et al. 2007, Desmond et al. 2015, Rattray et al. 2016, Smale et al. 2016). Similar to terrestrial plants, macroalgae have evolved the ability to acclimate their photosynthetic apparatus to variable irradiance (Falkowski and LaRoche 1991, Raven and Geider 2003, Fairhead and Cheshire 2004, Dubinsky and Schofield 2009). This allows for niche partitioning and the utilization of a wide range of light regimes (Markager and Sand-Jensen 1992, Gomez et al. 1997, Dubinsky and Schofield 2009).

The availability of light controls macroalgal primary productivity in two ways. First, the intensity of light determines the rate of macroalgal carbon fixation under ideal environmental conditions (Dubinsky and Schofield 2009). Second, the quantity and quality of light received often defines the maximum depth at which macroalgae can recruit and grow, as well as the distribution of species within a reef (see Toohey et al. 2004, Gattuso et al. 2006). Therefore, light governs the structure, productivity, and

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function of macroalgal assemblages (Kuppers and Kremer 1978, Dayton 1985, Gomez et al. 1997, Koch 2001, Dubinsky and Schofield 2009).

The process of photoacclimation describes the cellular response of algae to a shift in the local irradiance regime (see Falkowski and LaRoche 1991 for a full description). When irradiance shifts from saturating to subsaturating, macroalgae may lack sufficient energy to maintain high growth. They subsequently respond by investing in the synthesis of light-harvesting chlorophyll protein complexes (LHCP), which leads to a change in the concentration and ratio of chlorophyll *a* (Chl *a*) to accessory light-harvesting pigments held within the LHCP (Henley and Ramus 1989, Raven and Geider 2003, Fairhead and Cheshire 2004, Mansilla et al. 2016). At a physiological level, the outcome of this response is a change in the minimum quantum requirement for photosynthesis (Dubinsky et al. 1986, Falkowski and LaRoche 1991), respiration (Langdon 1988, Falkowski and LaRoche 1991), and growth (Falkowski et al. 1985, Falkowski and LaRoche 1991).

While photoacclimation allows for photosynthetic plasticity in a highly variable environment (Dubinsky and Schofield 2009), there are species-dependent limits to acclimation that are determined by metabolic requirements (Dubinsky and Schofield 2009). In situations where light limitation occurs, energy is diverted from lipid and carbohydrate production and prioritized for the synthesis of LHCPs (Falkowski and LaRoche 1991). This process is reversed when the light climate shifts from limiting to saturating (Falkowski and LaRoche 1991). As a result of light limitation, a decline in growth rate and investment in reproductive structures and tissue maintenance occurs (Falkowski and LaRoche 1991, Kubler and Raven 1994, Raven and Hurd 2012). In chronic cases, when the cost of acclimation is greater than the benefit, a reduction in growth or a total loss of a species may occur (Kubler and Raven 1994, Dubinsky and Schofield 2009). By quantifying pigment concentrations and the ratio of accessory pigments to Chl *a*, an understanding of species response to changing irradiance (interchangeably referred to as light) can be gained.

In order to comprehend regional drivers of macroalgal community structure, productivity and how these may change under varying light regimes, significantly more information regarding the photophysiological attributes of whole communities at a site by site basis is required (see Gomez et al. 1997, Middelboe et al. 2006, Hallerud 2014). By doing so, it will allow an understanding of the range of conditions a particular species may function under and provide predictive power regarding the response of macroalgal communities to changes in local light climates. Two regions in southern New Zealand, East Otago, and Stewart Island were selected based on their disparate subtidal light climates (Desmond et al. 2015). The concentration of dominant pigments in all fleshy macroalgal species from a kelp-forest community in each region was quantified in order to provide an understanding of the photophysiological characteristics under two differing irradiance regimes. Here, we propose a unique approach to examining kelp-forest pigment characteristics by quantifying the average concentration of dominant pigments at a whole community level. By doing so, we aim to establish an approach which can provide meaningful insight into the photosynthetic functioning and ecology of an entire macroalgal community. We predicted that macroalgae within the low-light region of East Otago would show greater investment in pigmentation (i.e., increased pigment concentrations) and that in both regions greater pigment concentrations would be found at the deep extent of the reef compared to shallower communities. We also predicted that trends seen at the species level would be reflected when pigment concentration was considered from the viewpoint of the entire macroalgal community.

MATERIALS AND METHODS

Study sites. Community surveys and specimen collection was carried out at two reefs in southern New Zealand. Huriawa Peninsula (45°38.398 S, 170°40.197 E) is located in the East Otago region of New Zealand's South Island, while Horseshoe Bay (46°52.623 S, 168°08.028 E) is located on Stewart Island, off the south coast of the South Island. The specific reefs were chosen as their subtidal light conditions were known to differ significantly (see Desmond et al. 2015, note: Huriawa is referred to as Karitāne), with Huriawa Peninsula (hereafter low-light) receiving substantially less light than Horseshoe Bay (hereafter high-light). Both reefs had a northerly aspect and a substrate of bedrock and boulders that sloped gently downward to a maximum depth of 10–12 m before reaching sand. The co-occurrence of *Durvillaea* spp. and *Macrocystis pyrifera* indicated that each site was subject to similar levels of wave exposure (Hepburn et al. 2007). Mean annual sea temperature, measured at 2 and 10 m depth, is shown to be similar between the East Otago and Stewart Island regions (Desmond et al. 2015).

Community surveys. Macroalgal community composition was quantified at the high-light site during late January 2014 and at the low-light site during early February 2014. Using SCUBA, all fleshy macroalgae were collected from six, one-square meter quadrats placed randomly along a 20 m transect line at 2 and 10 m below low tide at each site. Randomization was achieved by random number generation with no replacement. Macroalgae were transported back to the laboratory following collection, taxonomically classified to the species level, counted, and then weighed to give an estimate of species-specific density and biomass per square meter. Five replicate individuals of each species were dried in an oven at 60°C until a constant weight was reached to determine the wet to dry weight ratio for later conversion. The following day, five replicate individuals of each macroalgal species present at 2 and 10 m were collected, transported to the laboratory, and frozen at −80°C until pigment analysis was conducted.

Irradiance regime. Light intensity was measured at the surface, 2 and 10 m at each of the two sites using HOBO Pendant Temperature/Light Data Logger 64k, Onset. Loggers were calibrated with a LI-COR underwater quantum sensor (LI-192SA coupled with a LI-250A light meter, LI-COR) and

values converted to photosynthetically active radiation (PAR), see Desmond et al. (2015) for methods.

Finfish and grazer surveys. Herbivorous finfish abundance was quantified at 2 and 10 m at each site by divers using SCUBA. On three consecutive days, the same horizontal 30 m transect of reef was swum at each depth by the same diver following the methods of Samoilys and Carlos (2000). Finfish species abundance was recorded 2 m either side of the transect line, creating a swath of 4 m. Herbivorous species encountered were *Latridopsis ciliaris* (blue moki), *Odax pullus* (greenbone), *Notolabras fucicola* (banded wrasse), and *Aplodactylus arctidens* (marblefish).

The abundance of the main grazer species, *Haliotis iris* (blackfoot pāua), *Haliotis australis* (yellowfoot pāua), and *Evichinus chloroticus* (kina/sea urchin), was quantified along the same 20 m transect at 2 and 10 m at each site using 10 randomly placed one-square meter quadrats.

Pigment extraction and analysis. 0.5 ± 0.05 g of blade tissue was cut from the five replicate individuals of each species and then freeze dried before pigment extraction (Hagerthey et al. 2006). For Phaeophyceaen species, samples were ground in a mortar and pestle. Chl *a*, Chl *c* and fucoxanthin were extracted, first in dimethyl sulfoxide for 15 min at 4°C in the dark, and then in 90% acetone for 3 h at 4°C in the dark (Seely et al. 1972). After each extraction, samples were centrifuged at 3,000*g* for 10 min, the supernatant decanted, and absorbance measured. The tissue pellet was colorless following extraction. For Rhodophyceaen species, samples were ground in a mortar and pestle with the addition of 0.001 g of organic-free sand to assist with the grinding process. A 0.01 ± 0.001 g subsample was taken and phycoerythrin extracted using ice-cold 0.1 M phosphate buffer (pH 6.8) for 24 h in the dark at 4°C (Beer and Eshel 1985). Samples were centrifuged at 10,000 *g* for 20 min, the supernatant decanted and absorbance measured (Beer and Eshel 1985). Chl *a* was then extracted using 90% acetone for 3 h in the dark at 4°C before re-centrifugation and measurement of absorbance of the supernatant (Ritchie 2008). The complete extraction of phycoerythrin is notoriously hard to achieve; therefore, peak absorbance values were used to determine relative values (Ramus et al. 1976).

5 mL quartz cuvettes were used (Ritchie 2008) and to ensure that absorbance remained within range of the spectrophotometer each sample extract was diluted by a factor of four before analysis. Wavelength-specific absorbance was measured using a Shimadzu UV-1700 UV-Visible spectrophotometer. For Phaeophyceaen species, pigment concentrations were determined using the equations of Seely et al (1972), while for Rhodophyceaen species, phycoerythrin and Chl *a* concentrations were determined using the equations of Beer and Eshel (1985) and Ritchie (2008), respectively. All concentrations were standardized to mg · g dry weight^{-1} (DW).

Statistical analysis. For comparison of species pigment concentrations, mean values standardized to mg · g DW^{-1} were used. Phaeophyceaen and Rhodophyceaen community pigment concentration was calculated by multiplying the dry

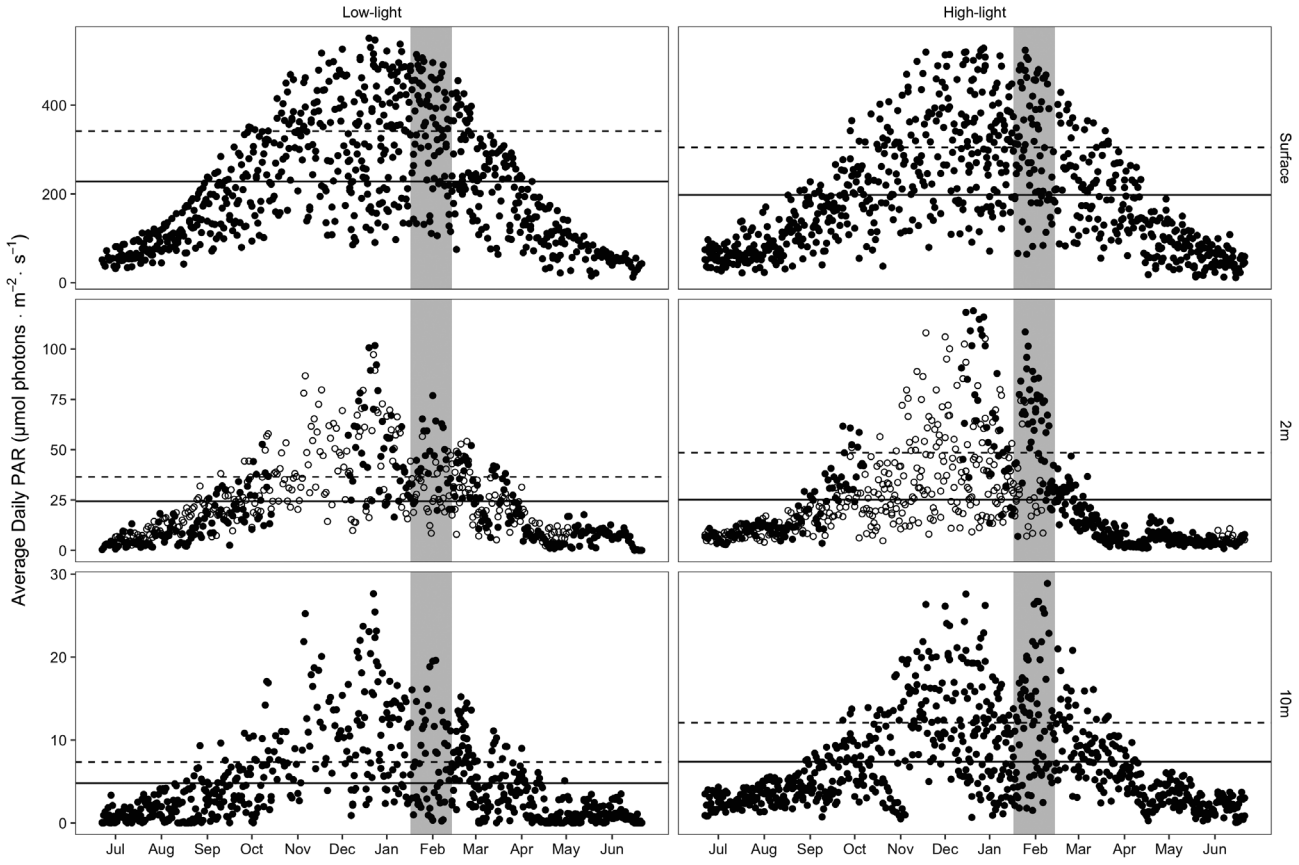

FIG. 1. Average daily PAR against Julian day at the surface (top), 2 m depth (middle) and 10 m depth (bottom) at the low-light (left) and high-light site (right). Data collected during 2013–2015. Black circles indicate measured data, white circles indicate imputed data based on values from the surface and 10 m at that site. Gray area highlights collection period. Dashed line is average daily PAR during collection period, solid line is average daily PAR over the entire year.

weight of each species in each replicate quadrat by their respective pigment concentration. Pigment values were then summed within each quadrat, and then divided by the dry biomass of the entire community in the quadrat to standardize to mg · g DW^{-1}. The mean concentration of each pigment was then calculated from the six replicate quadrats. A two-way analysis of variance (ANOVA) was used to test for differences in community mean pigment concentration and mean Chl *a* to accessory pigment ratio between sites and depths. Differences between means were determined using a Tukey's honestly significant difference (HSD) post hoc test. In all cases, data met the assumptions of an ANOVA comparison (i.e., normality, Shapiro–Wilk test and equal variance, Levene median test). Student's *t*-tests were used to test for differences in mean pigment concentration and mean Chl *a* to accessory pigment ratio for shared species between sites, and for species shared between depths within sites. To avoid the inflation of type one error rates, due to multiple hypotheses being tested, the false discovery rate correction was applied to all *P*-values (Benjamini and Hochberg 1995). Significance was set at the 5% level ($\alpha = 0.05$) for all tests.

To visualize the light environment over a typical year, average daily PAR was plotted against Julian day. To fill gaps in the data at the 2 m depth strata where some periods were missing, light data at the surface and 10 m were used as predictors in a simple linear model to impute missing data. A 4-week period spanning from mid-January to mid-February around the time of sample collection was extracted, and mean light levels at 2 and 10 m were compared using Student's *t*-tests. All statistical analyses were performed using the R statistical software package (V.3.0.1, R Development Core Team 2013).

TABLE 1. Mean dry weight biomass of Phaeophyceaen species, Rhodophyceaen species, and the whole community per square meter of substrate at 2 and 10 m depth in the low-light and high-light site ($n = 6$).

	Biomass (g DW · m^{-2})		Contribution to community (%)	
	Low-light	High-light	Low-light	High-light
2 m				
Phaeophyceae				
Cystophora platylobium		129.39		39.33
Desmarestia ligulata	10.13	9.32	0.59	2.83
Dictyota kunthii	0.40	13.80	0.02	4.19
Landsburgia quercifolia	2.53	70.03	0.15	21.29
Macrocystis pyrifera	11.77	70.79	0.68	21.52
Marginariella boryana	1552.03	0.77	89.88	0.23
Marginariella urvilliana		4.61		1.40
Sargassum sinclairii	5.12		0.30	
Spatoglossum chapmanii	0.99	29.11	0.06	8.85
Xiphophora gladiate	143.78	1.17	8.33	0.35
% total community	100	99		
Rhodophyceae				
Hymenena durvillaei		0.40		100
% total community	0	1		
Total biomass	1,726.75	329.39		
10 m				
Phaeophyceae				
Carpomitra costata		5.27		1.59
Carpophyllum flexuosum	2.87	58.92	6.87	17.76
Desmarestia ligulata	7.43	3.94	17.77	1.19
Dictyota kunthii	0.11		0.25	
Ecklonia radiata	23.04	239.15	55.10	72.10
Halopteris sp.		0.88		0.27
Landsbergia quercifolia	2.65		6.33	
Macrocystis pyrifera	2.46	16.12	5.88	4.86
Marginariella boryana	2.47		5.90	0.00
Marginariella urvilliana	0.79	7.43	1.90	2.24
% total community	65	62		
Rhodophyceae				
Anotrichium crinitum	12.97	0.28	58.25	0.13
Asparagopsis armata		4.04		1.96
Callophyllis sp.		0.88		0.43
Champia chathamensis		2.07		1.00
Cladhymenia oblongifolia	0.07	1.19	0.30	0.58
Craspedocarpus erosus		53.80		26.06
Delisea elegans		87.63		42.46
Delisea plumosa		8.64		4.18
Euptilota formossisima	7.00	0.23	31.43	0.11
Hymenena durvillaei	1.76		7.88	
Laingia hookeri		0.88		0.43
Plocamium sp.		33.64		16.30
Rhodophyllis sp.	0.48	13.15	2.14	6.37
% total community	35	38		
Total	64.08	538.12		

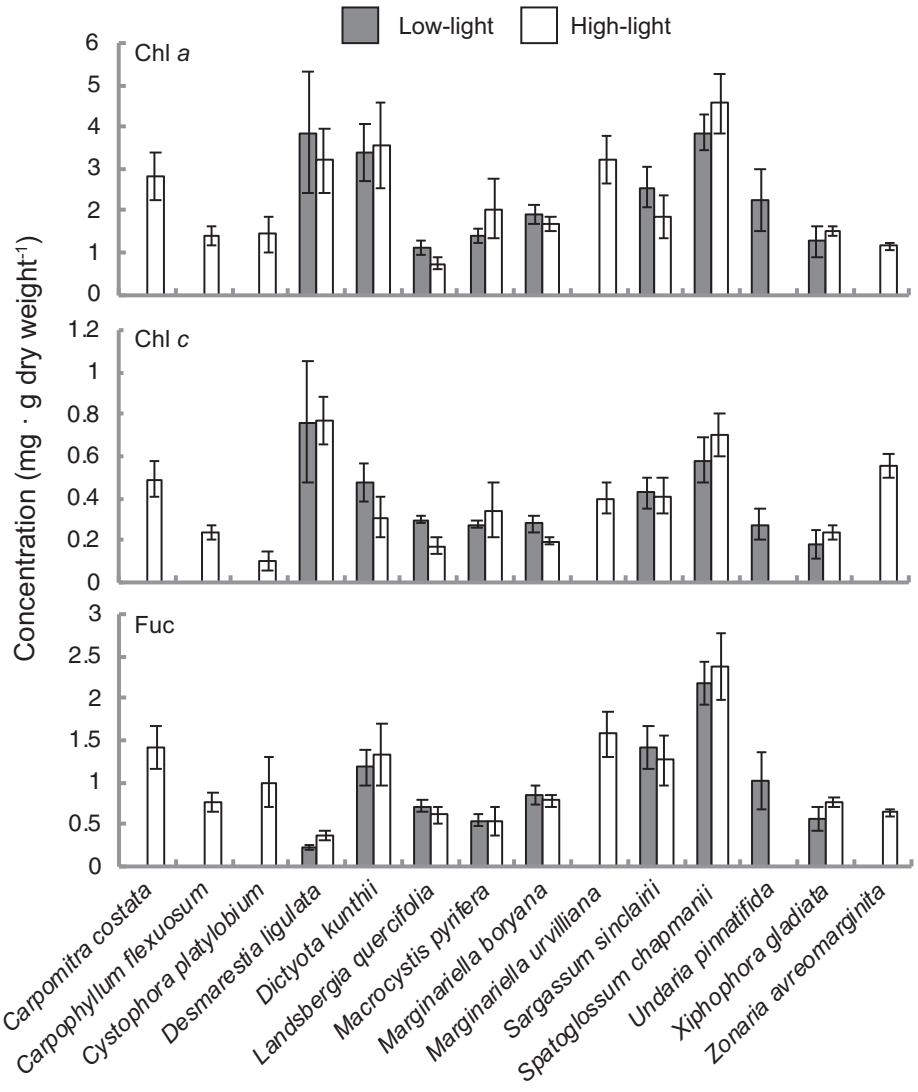

FIG. 2. Pigment concentration of Phaeophyceaen species at 2 m at the low-light (gray bars) and high-light site (white bars). Values represent mean (±SE, $n = 5$) for the pigments Chl *a* (top), Chl *c* (middle), and fucoxanthin (bottom). A missing value means the species was absent.

RESULTS

Irradiance regime. Light availability differed significantly between sites at both 2 (Student's $t_{126.5} = -3.41$, $P = <0.001$) and 10 m (Student's $t_{133.92} = -4.48$, $P = <0.001$) during a 4-week period around the time of sample collection (mid-January to mid-February). At 2 m, the low-light site had an average daily delivery of 36.42 ± 1.95 μmol photons · m^{-2} · s^{-1} while the high-light had an average of 48.49 ± 2.95 μmol photons · m^{-2} · s^{-1}. At 10 m, the low-light site had an average daily delivery of 7.35 ± 0.69 μmol photons · m^{-2} · s^{-1} while the high-light site had an average of 12.06 ± 0.79 μmol photons · m^{-2} · s^{-1} (Fig. 1).

Community structure. Phaeophyceaen species made up the majority of macroalgal biomass at 2 and 10 m in both sites (Table 1). At 2 m in the low-light site, the majority of biomass was represented by *Marginariella boryana*, while in the high-light site, biomass was more evenly spread across multiple species. *Marginariella boryana* was, however, present in great abundance above 2 m depth in the high-light site (M.J. Desmond, pers. obs.) and this difference between regions is likely the result of competitive forces shaping the algal community. *Hymenena durvillaei* was the only Rhodophyceaen species found at 2 m in the high-light site while none were present in the low-light site. A total of 10 Phaeophyceaen species were present across the two kelp-forest communities at 2 m, of which seven were common to both sites (Table 1). At 10 m, community biomass was more than eight times greater in the high-light site (Table 1). The high-light site also had a greater richness of Rhodophyceaen species, but the proportional contribution of both Phaeophyceaen and Rhodophyceaen species to the community biomass was approximately similar at both sites (Table 1). A total of 10 Phaeophyceaen species were present across the two kelp-forest communities at 10 m, of which five were common to both sites, while 13 Rhodophyceaen species were present and four were shared (Table 1).

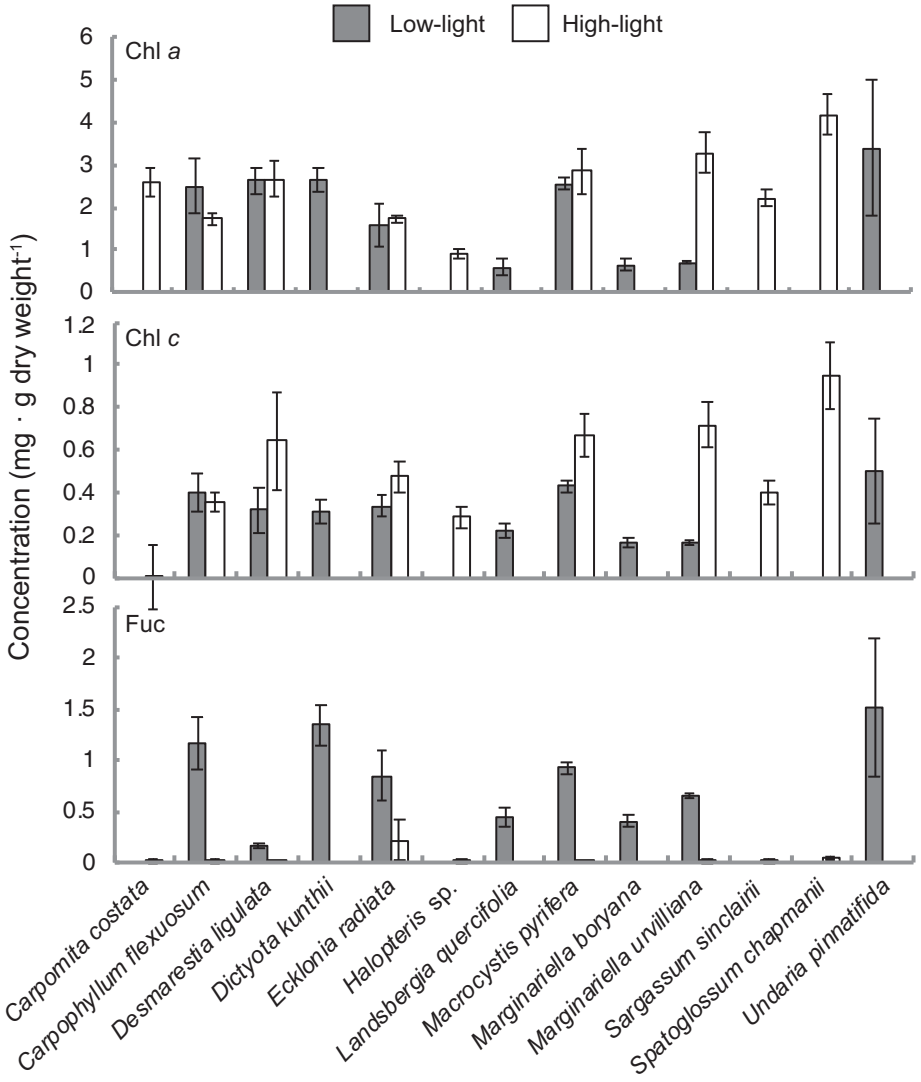

FIG. 3. Pigment concentration of Phaeophyceaen species at 10 m at the low-light (gray bars) and high-light site (white bars). Values represent mean (±SE, $n = 5$) for the pigments Chl *a* (top), Chl *c* (middle), and fucoxanthin (bottom). A missing value means the species was absent.

Finfish and grazer abundance. Four species dominated the herbivorous finfish population at both sites, these were *Latridopsis ciliaris*, *Odax pullus*, *Notolabras fucicola* and *Aplodactylus arctidens*. There was a general trend of greater fish abundance at the high-light site at both 2 and 10 m; however, the only significant difference seen was for the species *O. pullus* (Student's $t_4 = -4.28$, $P = 0.012$) which were 4 times more abundant and *N. fucicola* (Student's $t_4 = -4.25$, $P = 0.013$) which were 3 times more abundant at the highlight site at 2 m (Table S1 in the Supporting Information). Low abundances (0–0.3 m^2) of the dominant grazing invertebrates *Haliotis iris*, *Haliotis australis* (abalone), and *Evichinus chloroticus* (sea urchin) were recorded at both sites and at both depths. No significant differences in the abundance of these species were evident between sites (Table S2 in the Supporting Information).

Phaeophyceaen species. Of the seven species shared between the two kelp-forests at 2 m, pigment concentrations did not differ significantly between sites (Fig. 2).

Of the five species shared at 10 m, *Carpophyllum flexuosum* (Student's $t_8 = -4.4$, $P = 0.002$), *Desmarestia ligulata* (Student's $t_6 = -7.93$, $P = <0.001$), *Macrocystis pyrifera* (Student's $t_8 = -17.71$, $P = <0.001$), and *Marginariella urvilliana* (Student's $t_6 = -37.47$, $P = <0.001$) all had greater fucoxanthin concentrations in the low-light site (Fig. 3), with magnitudes that ranged between 24 and 93 times. *Marginariella urvilliana* exhibited significantly greater concentrations of both Chl *a* and Chl *c* in the high-light site compared to the low-light site (Student's $t_6 = 4.15$, 3.9, $P = 0.006$, 0.008 respectively; Fig. 3).

In the low-light site, five species were shared between 2 and 10 m: *Desmarestia ligulata*, *Dictyota kunthii*, *Landsburgia quercifolia*, *Macrocystis pyrifera*, and *Marginariella boryana*. A trend of higher Chl *a* and Chl *c* concentration at 2 m was observed for all species with the exception of *M. pyrifera*, which

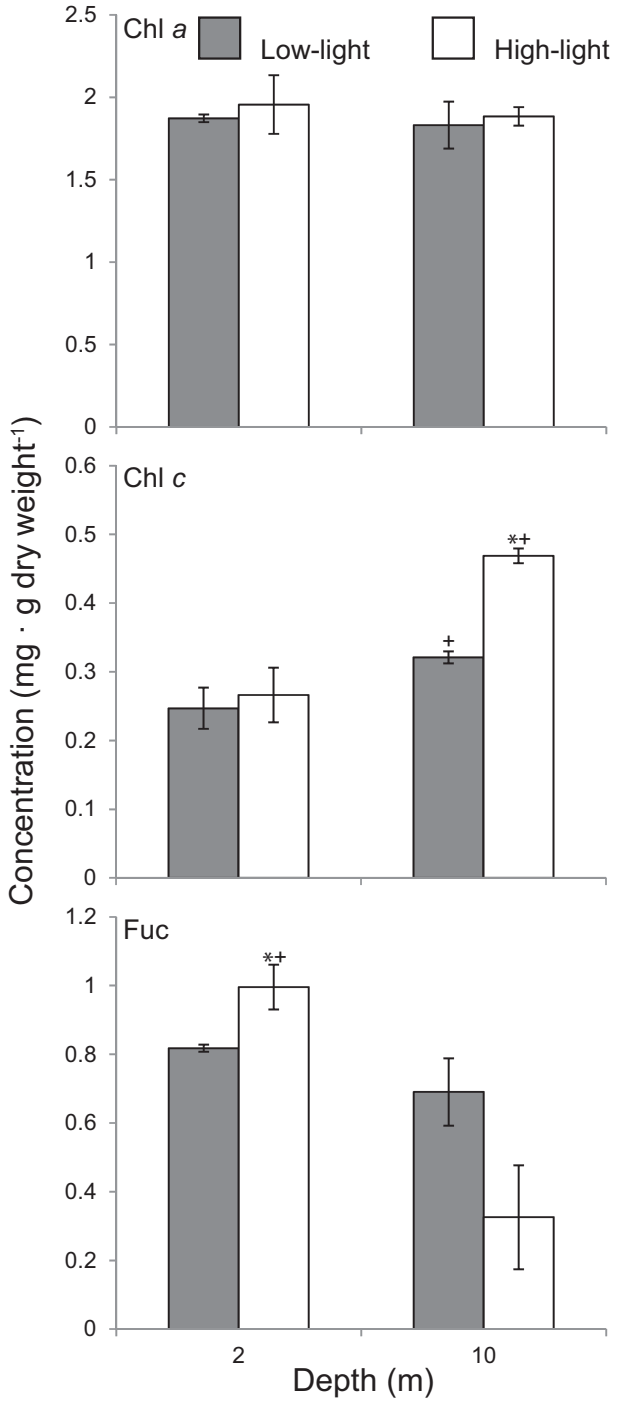

FIG. 4. Phaeophyceaen community pigment concentrations based on the average community assemblage per square meter of substrate ($n = 6$) at the low-light (gray bars) and high-light (white bars) site. Means (±SE) were calculated using biomass weighted species means ($n = 5$ replicate tissue samples per species) for the pigments Chl *a* (top), Chl *c* (middle), and fucoxanthin (bottom). Significant difference between sites is indicated by * and between depths within a site by + ($\alpha = 0.05$).

showed significantly greater concentration of Chl *a* (Student's $t_8 = -4.77$, $P = 0.001$), *c* (Student's $t_8 = -4.29$, $P = 0.003$) and fucoxanthin (Student's $t_8 = -4.07$, $P = 0.004$) at 10 m compared to at 2 m (Figs. 2 and 3).

In the high-light site, three species were shared between 2 and 10 m: *Desmarestia ligulata*, *Macrocystis pyrifera,* and *Marginariella urvilliana*. Fucoxanthin concentrations were 50–170 times greater at 2 m compared to 10 m for all three species (Student's $t_{6,8,6} = 4.57$, 3.06, 5.95, $P = 0.003$, 0.015, <0.001 respectively; Figs. 2 and 3). No significant difference in the concentration of Chl *a* or Chl *c* was present between depths.

Phaeophyceaen community. At 2 m, the community concentration of fucoxanthin was significantly greater in the high-light site (Fig. 4, Table 2, Tukey's HSD, $P < 0.05$). At 10 m, the community concentration of Chl *c* was significantly greater in the high-light site (Fig. 4, Table 2, Tukey's HSD, $P < 0.05$), as was the Chl *c*: Chl *a* ratio (Tables 2 and 3, Tukey's HSD, $P < 0.05$). Although not statistically significant, the concentration of fucoxanthin was more than twice as great in the low-light site (Fig. 4). The fucoxanthin: Chl *a* ratio showed the same difference and was statistically significant (Tables 2 and 3, Tukey's HSD, $P < 0.05$).

Within both sites, Chl *c* concentration was significantly greater at deeper depth (Fig. 4, Table 3, Tukey's HSD, $P < 0.05$), while the opposite was true for fucoxanthin at the high-light site (Fig. 4, Table 2, Tukey's HSD, $P < 0.05$).

Rhodophyceaen species. Only one Rhodophyceae species was found at 2 m depth, this was *Hymenena durvillaei* in the high-light site (Table 1). Mean Chl *a* for this species was 1.65 ± 0.15 mg $\cdot$ g^{-1} and mean phycoerythrin 0.55 ± 0.13 mg $\cdot$ g^{-1}.

Chl *a* concentration was significantly greater in *Anotrichium crinitum* and *Rhodophyllis* sp. at the high-light site (Student's $t_8 = 5.44$, 8.33, $P = <0.001$, <0.001 respectively; Fig. 5). The same trend was observed for phycoerythrin in the species *Euptilota formosissima* and *Rhodophyllis* sp. (Student's $t_8 = 4.35$, 5.53, $P = 0.002$, <0.001 respectively), while phycoerythrin was significantly greater in the low-light site for *Cladhymenia oblongifolia* (Student's $t_8 = -7.9$, $P = <0.001$; Fig. 5). For *A. crinitum* and *C. oblongifolia,* the phycoerythrin:Chl *a* ratio was significantly greater at the low-light site (Student's $t_8 = -4.79$, -13.86, $P = 0.001$, <0.001 respectively) while the opposite was true for *E. formosissima* (Student's $t_8 = 2.96$, $P = 0.018$; Table 4).

Rhodophyceaen community. At 10 m, phycoerythrin concentration was significantly greater in the low-light site by a factor of 3.5 (Fig. 6, Table 2, Tukey's HSD, $P < 0.05$). The phycoerythrin: Chl *a* ratio followed the same trend and was significantly greater by a factor of 18 (Table 2, Tukey's HSD, $P < 0.05$).

DISCUSSION

Although the theory of photoacclimation, and the role of pigmentation, is fairly well established

TABLE 2. Results of two-way ANOVA comparing Phaeophyceaen and Rhodophyceaen community pigment concentration and accessory pigment to Chl *a* ratio between the low-light and high-light site at 2 and 10 m depth. Significant differences are **Bold** ($\alpha = 0.05$).

Class	Pigment	Depth (m)	*F*	df	*P*
Phaeophyceae	Chl *a*	Site	0.334	1	0.57
		Depth	0.228	1	0.638
		Site × depth	0.016	1	0.9
	Chl *c*	Site	10.523	1	**0.004**
		Depth	28.864	1	**<0.001**
		Site × depth	6.209	1	**0.021**
	Fucoxanthin	Site	0.949	1	0.341
		Depth	17.218	1	**<0.001**
		Site × depth	8.005	1	**0.01**
	Chl *c*: Chl *a*	Site	7.608	1	**0.012**
		Depth	41.355	1	**<0.001**
		Site × depth	6.871	1	**0.016**
	Fucoxanthin: Chl *a*	Site	1.46	1	0.241
		Depth	12.248	1	**0.002**
		Site × depth	7.859	1	**0.011**
Rhodophyceae	Chl *a*	Site	0.086	1	0.772
		Depth	10.761	1	**0.004**
		Site × depth	2.351	1	0.141
	Phycoerythrin	Site	11.12	1	**0.003**
		Depth	36.23	1	**<0.001**
		Site × depth	12.3	1	**0.002**
	Phycoerythrin: Chl *a*	Site	14.68	1	**0.001**
		Depth	18.35	1	**<0.001**
		Site × depth	15.09	1	**<0.001**

TABLE 3. Mean (±SE) accessory pigment to Chl *a* ratios for Phaeophyceaen species and the whole Phaeophyceaen community at 2 and 10 m depth in the low-light and high-light site ($n = 5$).

		Chl *c*: Chl *a*		Fucoxanthin: Chl *a*	
Depth (m)	Species	Low-light	High-light	Low-light	High-light
2	*Cystophora platylobium*		0.06 ± 0.01		0.71 ± 0.02
	Desmarestia ligulata	0.2 ± 0.01	0.27 ± 0.06	0.08 ± 0.01	0.12 ± 0.02
	Dictyota kunthii	0.14 ± 0.01	0.12 ± 0.03	0.35 ± 0.01	0.4 ± 0.05
	Landsburgia quercifolia	0.27 ± 0.03	0.25 ± 0.04	0.64 ± 0.04	0.89 ± 0.07
	Macrocystis pyrifera	0.2 ± 0.01	0.17 ± 0.01	0.38 ± 0.01	0.27 ± 0.01
	Marginariella boryana	0.15 ± 0.01	0.12 ± 0.01	0.44 ± 0.01	0.47 ± 0.01
	Marginariella urvilliana		0.12 ± 0.01		0.49 ± 0.02
	Sargassum sinclairii	0.19 ± 0.03		0.56 ± 0.01	
	Spatoglossum chapmanii	0.15 ± 0.01	0.16 ± 0.01	0.56 ± 0.01	0.52 ± 0.01
	Xiphophora gladiata	0.14 ± 0.03	0.16 ± 0.02	0.46 ± 0.02	0.5 ± 0.01
	Community	0.13 ± 0.02	0.13 ± 0.01	0.44 ± <0.01	0.53 ± 0.05
10	*Carpomitra costata*		0.19 ± 0.06		0.01 ± <0.01
	Carpophyllum flexuosum	0.16 ± <0.01	0.20 ± 0.01	0.48 ± 0.02	0.01 ± <0.01
	Desmarestia ligulata	0.12 ± 0.04	0.24 ± 0.03	0.06 ± <0.01	<0.01 ± <0.01
	Dictyota kunthii	0.12 ± 0.02		0.51 ± 0.05	
	Ecklonia radiata	0.36 ± 0.13	0.28 ± 0.05	0.57 ± 0.04	0.12 ± 0.11
	Halopteris sp.		0.31 ± 0.03		0.01 ± <0.01
	Landsburgia quercifolia	0.41 ± 0.06		0.8 ± 0.11	
	Macrocystis pyrifera	0.17 ± <0.01	0..24 ± 0.02	0.36 ± 0.01	<0.01 ± <0.01
	Marginariella boryana	0.28 ± 0.03		0.66 ± 0.04	
	Marginariella urvilliana	0.24 ± 0.02	0.22 ± 0.01	0.94 ± 0.06	0.01 ± <0.01
	Community	0.18 ± 0.02	0.25 ± 0.01	0.4 ± 0.07	0.17 ± 0.08

(Ramus et al. 1976, 1977, Henley and Ramus 1989, Falkowski and LaRoche 1991, Raven and Geider 2003), this study presented a number of findings that demonstrate that relationships between light availability and pigment synthesis are not as straight forward as often presumed. These complexities were particularly evident at the extremities of light availability. Phaeophyceaen species shared across depths at the low-light site exhibited few significant differences in both total pigment concentration and pigment ratios. There was, however, a tendency for species to have slightly greater concentrations of all three pigments at 2 m compared to 10 m. This finding contradicts the well-established relationship of

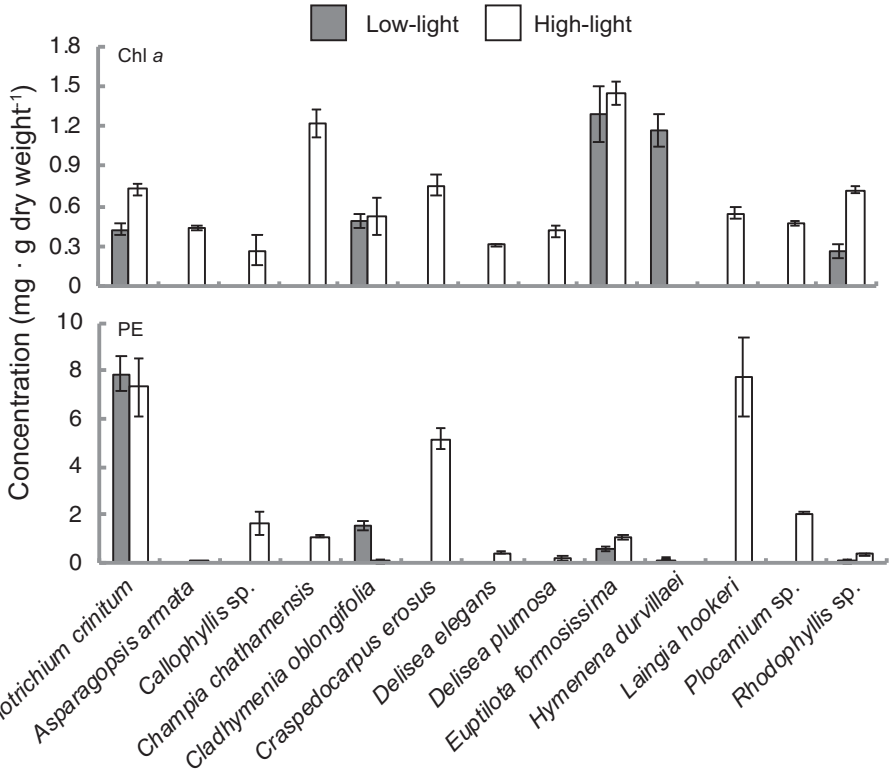

FIG. 5. Pigment concentration of Rhodophyceaen species at 10 m at the low-light (gray bars) and high-light site (white bars). Values represent mean (±SE, $n = 5$) for the pigments Chl *a* (top) and phycoerythrin (bottom). A missing value means the species was absent.

TABLE 4. Mean (±SE) accessory pigment to Chl *a* ratio for Rhodophyceaen species and the whole Rhodophyceaen community at 2 and 10 m depth in the low-light and high-light site ($n = 5$).

Depth (m)	Species	Phycoerythrin: Chl *a*	
		Low-light	High-light
2	*Hymenena durvillei*		3.57 ± 0.65
	Community		0.06 ± 0.06
10	*Anotrichium crinitum*	18.51 ± 0.96	10.03 ± 1.49
	Asparagopsis armata		0.1 ± 0.02
	Callophyllis sp.		2.8 ± 1.2
	Champia chathamensis		0.93 ± 0.06
	Cladhymenia oblongifolia	3.21 ± 0.2	0.04 ± 0.01
	Craspedocarpus erosus		6.98 ± 0.69
	Delisea elegans		1.37 ± 0.14
	Delisea plumosa		0.51 ± 0.2
	Euptilota formosisima	0.42 ± 0.06	0.75 ± 0.08
	Hymenena durvillii	0.1 ± 0.03	
	Laingia hookeri		13.98 ± 2.74
	Plocamium sp.		4.46 ± 0.07
	Rhodophyllis sp.	0.41 ± 0.1	0.57 ± 0.06
	Community	8.7 ± 2.13	0.48 ± 0.12

increasing pigment concentration with depth (Ramus et al. 1976, 1977, Wheeler 1980; Lopez-Figueroa 1992, Talarico and Maranzana 2000). This may suggest that light availability at 10 m could be low enough to limit the synthesis of pigments, indicating that these species may be living on the edge of their photosynthetic capabilities (see Pritchard et al. 2013). Further work is required to assess whether this is the case. The finding of significantly greater fucoxanthin concentration and fucoxanthin: Chl *a* ratio at 2 m compared to 10 m at the high-light site also contradicts this theory (Ramus et al. 1977, Stengel and Dring 1998, Fairhead and Cheshire 2004). Dring (1982) first suggested that fucoxanthin may perform two functions after observing decreasing fucoxanthin:Chl *a* ratios with decreasing irradiance. It was proposed that fucoxanthin may play a light-harvesting role in low irradiance and a photoprotective role in high irradiance. This theory may explain the observation in this study but further exploration of this topic is needed before any conclusions can be drawn.

Consistent with previous observations, variation in pigment concentration and ratio to Chl *a* occurred at the species level between sites (Ramus et al. 1976, 1977, Dring 1986, Henley and Ramus 1989, Falkowski and LaRoche 1991, Mansilla et al. 2016). A significantly greater concentration and ratio of fucoxanthin was observed for multiple Phaeophyceae species within the low-light site at 10 m compared to the high-light site. Even with this additional investment in important light-harvesting pigments, the biomass of these species per m^2 was still significantly less in the low-light site. This suggests that the physiological cost of increasing the synthesis of pigments is likely substantial (see Raven 1984, Henley and Ramus 1989, Dubinsky and Schofield 2009, Raven and Hurd 2012), and the energy, otherwise used for lipid and carbohydrate synthesis and ultimately growth, may no longer be available. This may, in part, explain the

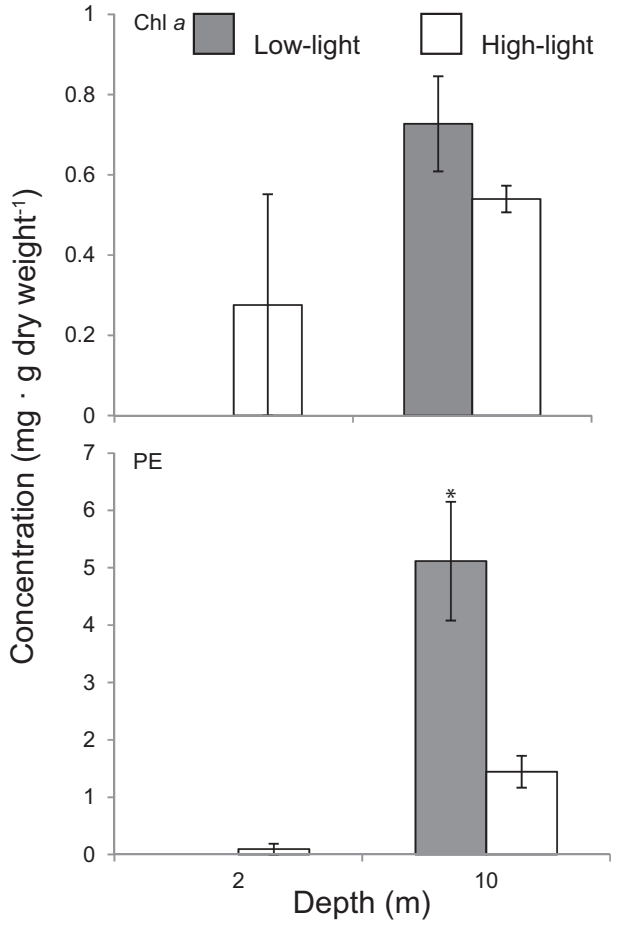

Fig. 6. Rhodophyceae community pigment concentrations based on the average community assemblage per square meter of substrate (n = 6) at the low-light (gray bars) and high-light (white bars) site. Means (±SE) were calculated using biomass weighted species means (n = 5 replicate tissue samples per species) for the pigments Chl *a* (top) and phycoerythrin (bottom). Significant difference between sites is indicated by * and between depths within a site by + (α = 0.05).

large difference in macroalgal biomass observed in this study, and in previous work by Desmond et al. (2015). Also observed was a greater proportional contribution of highly pigmented Rhodophyceae species to the Rhodophyceae community biomass at the low-light site. *Anotrichium crinitum* and *Euptilota formosissima* composed 58% and 31% of the community biomass respectively in the low-light site, while their combined contribution to the Rhodophyceae community biomass in the high-light site was <0.5%. At the low-light site, these highly pigmented species may hold a competitive advantage which is not the case in the high-light site Ramus 1988, Pritchard et al. 2013). These findings indicate potential costs and advantages that come from pigment investment and this, among other factors, may help to explain certain differences observed in community structure between sites. The relationship between cost versus benefit of pigment synthesis, however, is highly complex and requires further investigation in order to determine its role in structuring these, and other, communities.

In addition to the light environment, the availability of nutrients (specifically nitrogen) has the potential to alter macroalgal pigment concentration (Shivji 1985, Mcglathery 1992, Mcglathery and Pedersen 1999, Gordillo et al. 2006), and must therefore be considered in the trends observed in this study. Although seawater nitrogen was not measured in this study, Stephens (2015) quantified total seawater nitrogen within the regions of East Otago (low-light) and Stewart Island (high-light) during summer 2012. The percent nitrogen within *Macrocystis pyrifera* tissues was also quantified, providing a time-integrated perspective of nitrogen availability. In both cases, nitrogen concentrations were significantly greater in the high-light region and, in fact, in the low-light region tissue nitrogen was below 1% dry weight, which is an indication that nitrogen availability was limited (Gerard 1982). This suggests that increased pigmentation among species from the low-light site is not attributed to nutrient availability (Shivji 1985, Stephens and Hepburn 2014, 2016). Additionally, even with potential nutrient limitation species in the low-light site in this study maintained high pigment concentrations compared to those in the high-light site. This information, coupled with the fact that grazing pressure by invertebrates and finfish was similar between Horseshoe Bay and Huriawa, supports the idea that light availability is likely limiting macroalgal growth at this site, even with the additional investment in pigment synthesis.

For the first time, pigment concentrations were examined from the whole community perspective. Three main drivers, occurring at the species level, likely resulted in differences in the community pigment characteristics, these were (i) dissimilar concentrations within species shared between kelp-forests (e.g., greater fucoxanthin concentration in species from the low-light site at 10 m), (ii) a greater presence of a particular species (e.g., greater biomass of highly pigmented *Anotrichium crinitum* in the low-light site, and (iii) the presence, or absence, of a particular species (e.g., the low-light site supported five unique species and the high-light site 12). This approach shows potential as a tool for assessing the relative response of an entire community to changes in the subtidal light environment. At a species level, algal photophysiological responses may be varied and complex as light availability changes. By standardizing this information to reflect the community as a whole a broader understanding can be gained, from this information it is possible to then investigate the specific, that is, species level, changes that result in whole community differences. This information would be of value when assessing the impact of changing irradiance, for example, as a result of events that may increase turbidity such as land derived sedimentation, dredging activity or natural storm events.

CONCLUSIONS

These results provide a valuable snapshot in time of species-specific pigment characteristics which adds to our general understanding of the physiological flexibility of macroalgae. More data, over a seasonal range and from multiple environments, are needed to construct a comprehensive picture of how macroalgae acclimate and respond to changing light environments and to determine the thresholds beyond which they can no longer do so. Whole community estimates of pigment concentrations hold potential as a tool to examine differences and/or changes in community structure that result from changing light availability. This approach, however, needs to be refined in order to inform the specific changes at a species level that drive community changes. This knowledge is fundamental for accurately predicting the productivity and future resilience of macroalgal communities in a changing subtidal light climate.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Table S1. Density of dominant herbivorous fish species at 2 and 10 m depth in the low-light and high-light site ($n = 3$). Each transect survey was a 30 m $\times$ 4 m swath of reef.

Table S2. Density of dominant grazing invertebrate species at 2 and 10 m depth in the low-light and high-light site ($n = 6$).