

Temperature and light explain spatial variation in growth and productivity of the kelp *Ecklonia radiata*

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ABSTRACT: Understanding the relative importance of environmental variables on growth and productivity of macroalgae is key to understanding how they might be influenced by environmental change. This study evaluates spatial and temporal patterns in growth and productivity of the kelp *Ecklonia radiata* in Marmion Lagoon (Western Australia) and tested how well these patterns could be explained by temperature, light, water movement and nutrient concentrations. Growth rates (thallus extension and productivity, measured as biomass accumulation and mass-standardised biomass accumulation) varied between seasons, with the highest rates observed during spring, followed by summer. Temperature and light best explained spatial patterns in growth and productivity of *E. radiata*. Bottom water velocity and nutrient concentrations typically explained less of the variation, but in some cases they were well-correlated with patterns in productivity. Temperature was the best explanatory variable in summer, when higher water temperatures were associated with lower growth and productivity. Light explained patterns in growth and productivity during winter and spring, when light intensities were lower at some sites, especially at deeper offshore sites, than in summer. The repeated associations between temperature or light and patterns in thallus extension and biomass accumulation suggest that these 2 variables are the most important influences on growth and productivity of *E. radiata* in Marmion Lagoon. This inference is supported by the knowledge that these 2 variables strongly influence rates of photosynthesis. Our findings suggest that a sustained increase in temperature or reduction in light will reduce growth and productivity of *E. radiata*.

KEY WORDS: Macroalgae · Seasonal variation · Water movement · Nutrient · Ocean warming · Climate change

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INTRODUCTION

Macroalgae growing on temperate reefs generate rates of primary productivity that are among the highest of any ecosystem (Cebrian 1999). The main influences on the rates of primary productivity in macroalgae are well known, and include light (Dieckmann 1980, Novaczek 1984), water movement (Jackson 1977, Vanderklift et al. 2009, Mass et al. 2010), temperature (Staeher & Wernberg 2009) and concentrations of limiting nutrients (Hanisak 1983, Pedersen et al. 2010). These variables often co-vary in nature, and it can be difficult to separate their

influence in field studies. However, doing so is key to understanding how species cope with contemporary conditions, and how they might be affected by future changes to those conditions.

Temperature is an important influence on the distribution of species and the growth rates of individuals (Moore et al. 1995, Hughes 2000). In addition, temperature can influence rates of productivity because metabolic rates generally increase with increasing temperature (Hochachanka & Somero 1984, Wernberg et al. 2003, Rinde & Sjtun 2005). However, most species of macroalgae are capable of growing and reproducing over a wide range of tem-

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peratures and most have geographic distributions that span a wide range of temperatures (Bolton & Lüning 1982, Schils & Wilson 2006). Macroalgae accomplish this by changing rates of photosynthesis and respiration. For example, *Ecklonia radiata*—the dominant species of macroalgae across most of southern Australia (Womersley 1981, Kirkman 1989, Connell & Irving 2008)—from lower (warmer) latitudes have been found to have 50% lower photosynthetic rates and 90% lower respiration rates at their optimum temperature than *E. radiata* from higher (cooler) latitudes (Staeher & Wernberg 2009). Water temperature can also influence the morphology of macroalgae, with higher temperatures being associated with greater plant length, lamina length and stipe diameter in *E. radiata* (Fowler-Walker et al. 2005). However, there is a limit to the ability of macroalgae to acclimate to temperature extremes. This is best illustrated by the observation that their biogeographical range extents are frequently determined by their tolerances to temperature extremes (van den Hoek 1982, Lüning 1984, Staeher & Wernberg 2009, Bojorge-Garcia et al. 2010).

While temperature typically determines the extent of a species' biogeographical range, light typically determines the depth at which macroalgae can grow (Brown 1984, Kirk 1994, Wernberg et al. 2010). Differences in the rates of productivity of macroalgae between sites in close proximity, but at different depths, have often been attributed to differences in light penetration, with higher irradiance being linked to higher rates of photosynthesis and growth (Dieckmann 1980, Fairhead & Cheshire 2004a). However, at any given place the amount of light reaching the seafloor can also vary temporally, because light attenuation is influenced by solar angle (which varies seasonally due to the Earth's orbit around the Sun) and water clarity (which is influenced by the amount of particulate matter in the water). The amount of light received during a day will also depend on day length, which also varies seasonally. Growth rates and reproduction of macroalgae vary seasonally in response to variations in temperature and light (Kain 1989). *Ecklonia radiata* can acclimate to changes in light intensity by altering the pigment content and the ratio of photosynthetic pigments relative to photoprotective pigments in their tissues (Staeher & Wernberg 2009). In addition, *E. radiata* growing at depth have been found to have long stipes relative to lamina length (Fowler-Walker et al. 2005), suggesting that productivity is directed differently by plants growing in low light conditions.

Nutrient concentrations can also influence the growth and productivity of macroalgae. Various nutrients are required for metabolic processes such as photosynthesis and growth, including the production of amino acids and chlorophyll, regulation of the rate of photosynthesis and the partitioning of photosynthate (Theodorou et al. 1991, McGlathery et al. 1996). Nitrogen has been considered a primary limiting nutrient for macroalgae in many coastal marine ecosystems (Jackson 1977). However, in some ecosystems, the limiting nutrient is phosphorus (Howarth 1988, Lapointe et al. 1992).

The productivity of macroalgae can also be influenced by water motion. The rate of exchange of dissolved nutrients, oxygen and inorganic carbon between macroalgae and the surrounding water is usually inversely proportional to the thickness of the diffusive boundary layer (DBL) and increasing water velocity makes the DBL thinner (Jackson 1977, Mass et al. 2010). Water motion can also enhance nutrient concentrations by resuspending sediments and associated pore water nutrients (Lourey & Kirkman 2009). Hepburn et al. (2007) found that exposure to waves ameliorated the negative effect of low nitrogen concentrations during summer and autumn at some sites in a nitrogen-limited system.

Temperature, light, water movement and nutrient concentrations can each vary considerably among locations—even places in close proximity. In addition, at any given location, temperature, light, nutrient concentrations and water movement vary over time. Understanding how temporal and spatial variability in these variables influence rates of primary productivity will provide important insights into how macroalgae respond to a changing environment. It is urgent that we achieve this understanding, as the conditions that populations experience are changing as a result of global climate change (Wernberg et al. 2010) and localised changes in water quality from anthropogenic influences (Connell et al. 2008, Gorman & Connell 2009). Kelp might also stabilise species interactions during climate change (Falkenberg et al. 2012), so that changes to their productivity might have profound consequences for the subtidal ecology of rocky coasts.

Our aim was to determine the extent to which spatial variation in light, temperature, wave-induced water velocity and nutrient concentrations explained spatial variation in growth and productivity of *Ecklonia radiata*, and how the relative importance of these influences varied among different times of the year. To do this we investigated the growth and productivity of *E. radiata* at 3 times of year at 19 sites in close

proximity that encompassed different depths and exposures to waves. We used a model selection approach based on multiple regression to identify variables that best explained spatial patterns in growth and productivity.

MATERIALS AND METHODS

Study area

Our study focused on Marmion Lagoon in south-western Australia (31° 49.4' S, 115° 44.0' E). The lagoon is semi-enclosed by a series of limestone reefs at depths of 1 to 30 m that run parallel to the shore; these attenuate and refract wave energy, creating spatial variations in water velocity experienced at the seafloor (Symonds et al. 2011). Mean monthly seawater temperatures in Marmion Lagoon peak at around 23°C between January and April and fall to a minimum of approximately 16°C between July and September (Smale & Wernberg 2009). Nitrate concentrations are consistently low and are typically below 0.5 $\mu\text{mol l}^{-1}$ for nitrate and below 0.2 $\mu\text{mol l}^{-1}$ for phosphate (Lourey et al. 2006, Lourey & Kirkman 2009).

We chose 19 sites to span the range in depth and water velocity experienced by *Ecklonia radiata* in Marmion Lagoon. The sites encompassed a depth range of 2.5–17.3 m and were all within 5 km of each other. At all sites, *E. radiata* forms continuous beds. *Ecklonia radiata* exhibits a seasonal growth pattern with a maximum in the austral spring (October to December) followed by a rapid decline to a minimum during January to March (Kirkman 1984, 1989, Larkum 1986, Wernberg & Goldberg 2008). Consequently, measurements were taken in the austral summer (December 2008–January 2009), late autumn/winter (May–June 2009) and spring (September–October 2009). The density of *E. radiata* at each of the sites was calculated by counting all sporophytes >10 cm tall in three 0.25 m² quadrats, haphazardly placed within a 10 m radius from a stake marking each site.

Measurement of growth and productivity

The growth (thallus extension) and productivity (biomass accumulation) of *Ecklonia radiata* was measured following a method described by Mann & Kirkman (1981) and adapted by Fairhead & Cheshire (2004b). The method takes advantage of the fact that

the primary meristem of kelps, including that of *E. radiata*, is located at the junction of the stipe and thallus, so that movement of a hole punched in the basal area of the thallus over time gives a good measure of thallus extension (Kirkman 1989). Individual *E. radiata* were marked by punching 2 holes into the central lamina, 5 and 10 cm from the junction between the stipe and the lamina. The first hole (at 5 cm) was punched since it was anticipated that the majority of growth would be below this point. The second hole (at 10 cm) was to evaluate this assumption; 95% of individuals recorded all growth between the stipe and the first hole.

Twenty adult individuals were marked at each site during each survey. Only mature plants greater than 100 g wet mass were used to ensure that all measurements were comparable. A total of 1140 individual *E. radiata* were tagged during the study, of which 752 were retrieved (Table S1 in the supplement at www.int-res.com/articles/suppl/m476p059_supp.pdf). The plants were collected 31–54 d later and the distance of each hole from the junction between stipe and lamina was measured in the laboratory. Extension rates were calculated by dividing the thallus extension (cm) by the number of days between punching the hole and collecting the kelp.

The lower (basal) 20 cm of the thallus was then cut into 5 cm strips and weighed (wet weight, in grams). The strip with the maximum biomass was then used to calculate biomass accumulation (BA; g ind.⁻¹ d⁻¹) as $BA = xM/5d$, where x is the thallus extension (cm), M is the mass of the heaviest strip (g wet weight) and d is the number of days between punching the hole and collecting the kelp. The rate of BA per plant was then divided by the mass of the entire thallus to produce an estimate of BA relative to total biomass (Mann & Kirkman 1981, Kirkman 1984, 1989, Hatcher et al. 1987, Fairhead & Cheshire 2004b). This measure is referred to here as the mass-standardised biomass accumulation (MSBA; mg g⁻¹ d⁻¹) but has been variously referred to as relative growth rate, specific growth rate, relative biomass accumulation and productivity (Kirkman 1984, Fairhead & Cheshire 2004b).

Environmental variables

Light (lx) and temperature (°C) measurements were obtained at each site every 10 min with a Hobo™ light and temperature logger (Onset Computer Corporation, part UA-002-64 or UA-002-08) (Table S1). Each logger was attached to the top of a metal stake

30 cm above the substrate. Two loggers were positioned at each of 4 sites to assess inter-logger variation: measurements from the 2 loggers were highly correlated at each site (temperature, $r^2 > 0.90$; light, $r^2 > 0.57$). Seven loggers were lost during winter, and one site was inaccessible during winter and so kelps could not be retrieved; these sites were excluded from analyses. Only light measurements from the first 15 d of logger deployment was used in the analysis because fouling of the sensors typically made light measurements unreliable (a gradual decline in measurements was typically observed after 15 d).

Because the loggers measured illuminance (lx), which is not always a reliable measure of irradiance (which is most relevant to photosynthesis), a comparison of illuminance and irradiance (measured as photosynthetically active radiation; PAR) was also performed on 2 occasions (December 2009 and July 2010) by attaching 3 Hobo loggers to a instrument array equipped with a PAR sensor. Measurements were obtained from depths of 3, 5, 10, 15, 20, 30 and 35 m during a 10 min period. A single lux measurement was obtained from each of the Hobo loggers at each depth and compared with the corresponding PAR measurements; in each case there was a strong positive nonlinear relationship ($r^2 > 0.90$ and exponent 1.6–1.8 in each case).

Light intensity measurements can be summarised by several distinct metrics, and the choice of metric can influence the outcomes of analyses. We compared the average lux (calculated as the average of the 15 daily averages), average lux at solar noon (calculated as the average of the lux measurements for 2 h each side of solar noon) and lux hours (lx h^{-1} ; average lux, multiplied by the number of hours of light). Of the 3 metrics, average lux at solar noon and lx h^{-1} were highly correlated and yielded qualitatively similar results in subsequent analyses (Table S2 in the supplement at www.int-res.com/articles/suppl/m476p059.pdf). We elected to use lx h^{-1} as our preferred metric, because it accounts for patterns in day length as well as patterns in light intensity (Hoyo-Meléndez et al. 2011).

Water velocity at the seafloor was estimated using the SWAN model (simulating waves nearshore; Booij et al. 1999), which simulates wave generation, propagation and dissipation. Wave height and direction were simulated for the period 1 July 2007 to 30 June 2008, over an 18 km (north–south) by 11 km (east–west) grid encompassing Marmion Lagoon, with grid cells of 30×30 m. The model was forced at its western boundary using wave height, period and direction values obtained from the Rottneast wave

buoy (located 20 km southwest of the study area). Daily-averaged fields of wave height throughout Marmion Lagoon were produced.

The orbital water velocity at the bottom (U_{bot}) was calculated from the wave height, period and wavelength (Booij et al. 1999, Holthuijsen 2007). The SWAN-modelled wave heights were positively correlated with daily-averaged wave height measured by an acoustic wave and current meter (AWAC) instrument located in the Marmion lagoon ($r = 0.80$).

Nutrient samples were obtained from water below the kelp lamina by divers (before harvesting kelp) using 50 ml plastic vials. Samples of seawater from the sites were analysed for phosphate, nitrate and nitrite, and ammonia. Phosphate and nitrate/nitrite were analysed using flow injection analysis while ammonia concentration was determined using a flow injection analysis, gas diffusion, derivatisation–fluorescence detection method (Diamond 1998, 1999, Wolters 2003, Watson et al. 2005).

Statistical analyses

To assess the magnitude of variation in productivity among sites, relative to the variation observed among individual kelps, we determined the relative magnitude of effects (ω^2 ; Graham & Edwards 2001) calculated as the variance component of each effect, divided by the sum of all variance components (Winer 1971). Because different numbers of individuals were retrieved from each site, the statistical model was unbalanced, and so we used a formula for unbalanced models obtained from Quinn & Keough (2002).

The main focus of analyses was determining which of the environmental variables (temperature, light, U_{bot} and nutrients) best explained spatial variation in growth (thallus extension) and productivity (BA and MSBA). To do this we used multiple linear regression, using averages for each variable at each of the sites, and searched for the best combination of explanatory variables from all possible combinations of each number of variables (i.e. of linear models of each size). Regression models were compared using 2 metrics: Akaike's information criterion (AIC) and the Schwarz Bayesian information criterion (BIC). These 2 metrics provide different approaches to compare statistical models. They do not always select the same model (they did in 5 of 9 cases in our analyses; Tables S3 to S5 in the supplement at www.int-res.com/articles/suppl/m476p059.pdf), and when they do not they provide complementary information

(Kuha 2004). Analyses were conducted using the leaps package (Lumley 2009) in the statistical software R (R Development Core Team 2010). Candidate models were then assessed for statistical significance in SPSS 17.0 (IBM). Separate regression models were produced for each of the metrics of growth and productivity (i.e. thallus extension, BA and MSBA) in each survey period.

RESULTS

Despite the close proximity of the sites, there was considerable variation in temperature, light intensity and water velocity (Table S1 in the supplement). Average water temperatures were higher inshore than offshore by up to 1.4°C (21.6 to 23.0°C) during summer, but this gradient was reversed in winter, with inshore sites up to 1.2°C (19.2 to 20.4°C) cooler than offshore. There was little difference in spring, with average temperatures differing by 0.5°C (17.3 to 17.8°C).

The amount of light reaching the seafloor each day differed by up to 89 256 lx h⁻¹ (4421 to 93 677 lx h⁻¹) during winter, 102 146 lx h⁻¹ (9940 to 112 086 lx h⁻¹) during spring and 223 574 lx h⁻¹ (1385 to 224 959 lx h⁻¹) during summer. Light intensity was lower in winter than in summer, especially at deeper sites, which received less than 30 % of the light they received during summer. In addition, some sites received consistently less light in all 3 survey periods despite being a similar depth to other nearby sites—probably due to the amount of resuspended particles in the water as well as light attenuation by the overlying water column.

There were no clear spatial patterns in nutrient concentrations. Nitrate and nitrite concentrations were highest during winter and lowest in spring (data not shown). Phosphate concentrations displayed a similar pattern. However, ammonia concentrations tended to be highest in spring and lowest in winter and summer. The nutrient concentrations and temporal patterns observed in this study were consistent with those obtained from previous studies (Keesing et al. 2006, Lourey et al. 2006, Lourey & Kirkman 2009).

Analyses yielded highly significant among-site differences for each of the measures of growth and productivity in each season, but the amount of variance that among-site differences accounted for was typically less than among-

individual variation—the sole exception to this trend was BA in the spring, when productivity was highest (Table 1). The relative amount of variation accounted for by among-site differences ranged from 24.4 to 30.7 % for thallus extension, 17.5 to 60.4 % for BA and 10.1 to 39.3 % for MSBA.

Model selection

Analyses yielded statistically significant (p < 0.05) models for each measurement in each season, but the model selected depended on the metric used to evaluate the models (i.e. AIC or BIC).

Temperature was the first variable to be added to all candidate models in summer. Thallus extension, BA and MSBA each tended to be lower at sites with higher temperature (Fig. 1). For thallus extension, both AIC and BIC suggested that temperature alone

Table 1. Results of ANOVAs testing for differences in thallus extension, biomass accumulation (BA) and mass-standardised biomass accumulation (MSBA) between and within sites

	df	MS	F	p	Variance components	ω ²
Thallus extension						
Summer						
Site	18	18.7	5.37	<0.001	1.12	24.44
Residual	239	3.48			3.48	
Winter						
Site	17	12.63	6.24	<0.001	0.89	30.69
Residual	198	2.03			2.02	
Spring						
Site	18	28.48	6.09	<0.001	1.65	26.14
Residual	257	4.67			4.67	
BA						
Summer						
Site	18	3.32	3.87	<0.001	0.18	17.48
Residual	239	0.86			0.86	
Winter						
Site	17	0.64	3.38	<0.001	0.04	20.77
Residual	198	0.18			0.18	
Spring						
Site	18	12.15	9.69	<0.001	0.76	60.37
Residual	257	1.25			1.25	
MSBA						
Summer						
Site	18	10.13	2.51	<0.001	0.45	10.10
Residual	239	4.02			4.02	
Winter						
Site	17	22.62	8.66	<0.001	1.69	39.26
Residual	198	2.61			2.61	
Spring						
Site	18	23.12	3.75	<0.001	1.18	16.07
Residual	257	6.16			6.16	

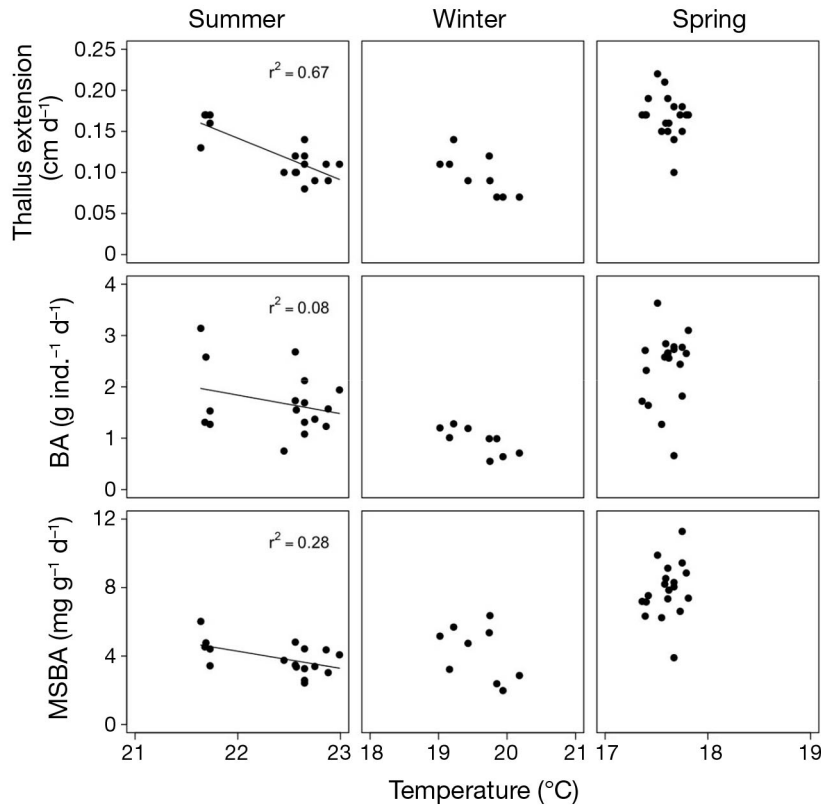


Fig. 1. Comparison of temperature with each of the measures of growth and productivity during summer, winter and spring. Regression lines and adjusted r^2 values are shown for statistically significant relationships yielded by multiple linear regression. BA: biomass accumulation; MSBA: mass-standardised biomass accumulation

was the optimal predictor, and this model also yielded the only statistically significant fit. For biomass accumulation, both AIC and BIC found the most parsimonious model contained temperature and light, but this model was not statistically significant ($p = 0.078$), and only the model containing temperature alone was statistically significant ($p = 0.025$). For MSBA, both AIC and BIC suggested the optimal model consisted of temperature with nitrate/nitrite and U_{bot} . However, this model was not a statistically significant ($p = 0.169$), and, as for thallus extension and BA, the only model to yield a statistically significant fit contained temperature alone ($p < 0.001$; Table 2).

Light was the first variable to be added to all candidate models in winter. Thallus extension, BA and MSBA each tended to be higher at

sites that received the most light (Fig. 2). For thallus extension, AIC suggested that the optimal model contained only light, while BIC suggested that the optimal model contained light with nitrate/nitrite and ammonia. However, this model was not statistically significant ($p = 0.75$), and the only statistically significant model contained light alone ($p = 0.006$; Table 2). For BA, both AIC and BIC suggested that the optimal model contained all variables. However, this model was not statistically significant ($p = 0.940$), and, as for thallus extension, the only statistically significant model contained light alone ($p = 0.04$; Table 2). For MSBA, BIC suggested the optimal model contained light, U_{bot} and nitrate/nitrite (a model that was not statistically significant: $p = 0.132$) while AIC suggested that the optimal model contained light and U_{bot} , a model which was statistically significant ($p = 0.027$; Table 2).

Unlike analyses of summer and winter data, analyses of spring data yielded inconsistent results, with substantially different models selected for thallus extension, BA and MSBA.

For thallus extension, both BIC and AIC suggested that ammonia was the only variable required for the optimal model, a model that was also statistically significant ($p = 0.013$; Table 2). Rates of thallus extension tended to be higher at sites with higher concentrations of ammonia (Fig. 3). For BA, AIC suggested that the optimal model contained

Table 2. Summary of the amount of variation accounted by among-site differences (ω^2), and regression models that fulfilled dual criteria of lowest Schwarz Bayesian information criterion (BIC) and statistical significance at $p < 0.05$. AIC: Akaike's information criterion; U_{bot} : orbital water velocity at the bottom

Season	Growth measure	ω^2 (%)	Model	Adj. r^2	AIC	BIC
Summer	Extension	24.44	Temperature	0.60	-2.09	-12.45
	BA	17.48	Temperature	0.22	1.39	2.16
	MSBA	10.10	Temperature	0.42	8.84	-6.65
Winter	Extension	30.69	Light	0.49	2.14	-4.30
	BA	20.77	Light	0.28	16.65	-0.07
	MSBA	39.26	Light + U_{bot}	0.75	1.32	-11.59
Spring	Extension	26.14	NH_4	0.28	0.36	-1.29
	BA	60.37	Light	0.21	2.04	3.29
	MSBA	16.07	U_{bot} + Light	0.32	8.91	-0.50

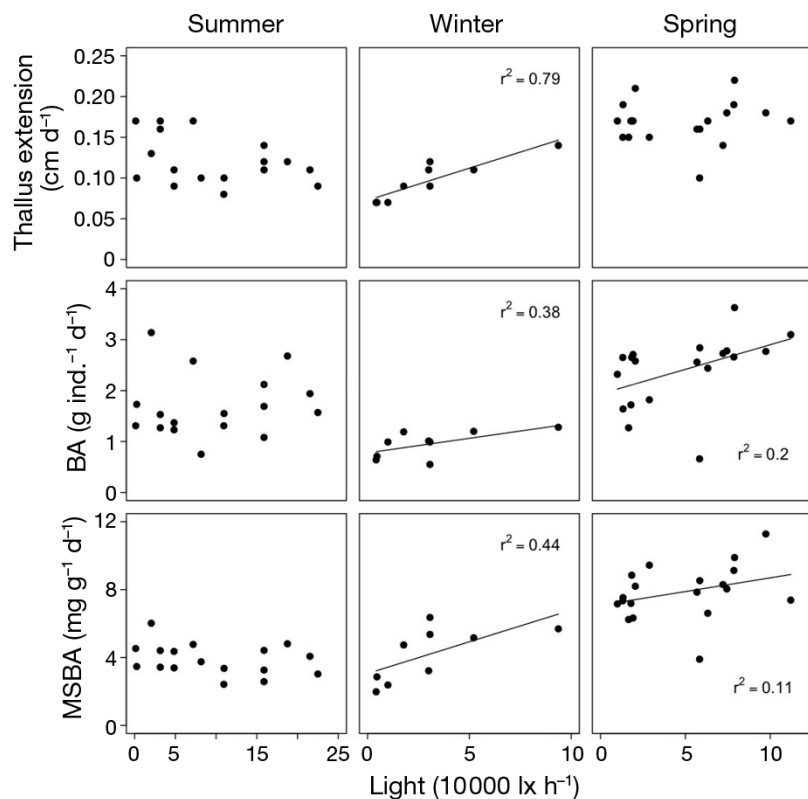


Fig. 2. Comparison of light intensity (illuminance) with each of the measures of growth and productivity during summer, winter and spring. Other details as in Fig. 1

both light and temperature (a model that was not statistically significant: $p = 0.19$). However, BIC suggested that light alone was required for the optimal model, a model that was statistically significant ($p = 0.024$; Table 2). As in winter, BA tended to be higher at sites that received more light (Fig. 2). For MSBA, BIC suggested that the optimal model included U_{bot} , light and phosphate, while AIC suggested that the optimal model contained these factors as well as ammonia and nitrate/nitrite. Neither model was statistically significant. Only models containing U_{bot} alone or in conjunction with light were statistically significant ($p < 0.001$; Table 2). MSBA tended to be higher at sites that had higher water velocity and that received more light (Figs. 2 & 3).

Considering only the models that conformed to the dual criteria of (1) being statistically significant ($p < 0.05$), and (2) yielding the lowest BIC (Table 2), several patterns emerged. Temperature alone was selected for each of the measurements in summer, and these models accounted for 22 to 60% of the variance (adjusted r^2 in Table 2). Light alone was an optimal predictor for measurements of BA, and light in combination with U_{bot} for measurements of MSBA,

in winter and spring (Table 2). Each of these models accounted for 21 to 75% of the variance. Light alone was also selected for thallus extension in winter, a model that accounted for 49% of the variance. Ammonia alone was selected for thallus extension in spring, a model that accounted for 28% of the variance. Overall, temperature or light was selected in 8 of the 9 models.

DISCUSSION

Controlled laboratory investigations of the influence of light intensity, temperature, water velocity and nutrient concentrations have found that each can have an independent effect on the growth and productivity of marine macroalgae (Novacek 1984, Maegawa et al. 1987, Mass et al. 2010, Pedersen et al. 2010). However, in natural conditions, the importance of each of these influences will depend on the magnitude of natural variation relative to other influences. Our results suggest that spatial variation in growth and productivity of *Ecklonia radiata* was

best explained by among-site patterns in temperature and light variations. Bottom water velocity and nutrient concentrations also explained patterns in growth and production, but these patterns were strong only in a few cases. The strength of associations between the environmental variables and the measures of growth and production varied between the different times of the year.

Temperature

Temperature can be an important influence because it affects reaction rates and reaction equilibria (Hochachanka & Somero 1984), and therefore influences physiological processes such as photosynthesis, respiration and development in kelp (Luning 1980, Rinde & Sjutun 2005). Previous studies have inferred that temperature plays an important role in the productivity of *Ecklonia radiata* (Kirkman 1984, Miller et al. 2011), despite it having a distribution range that spans temperature gradients of several degrees Celsius (Staehr & Wernberg 2009). In our study, temperature alone was the best predictor for

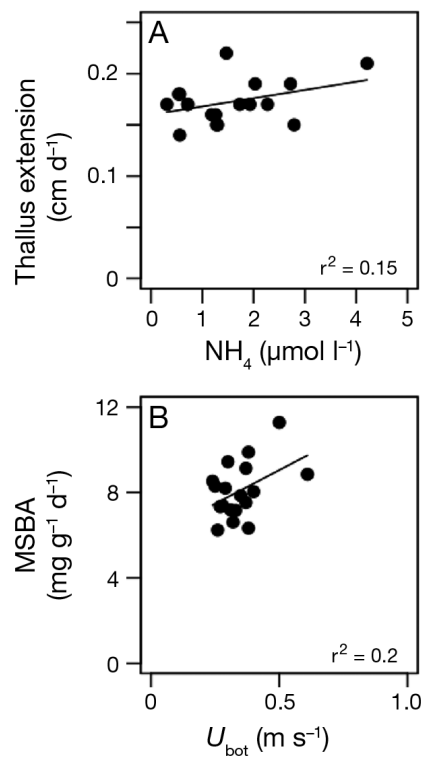


Fig. 3. Comparison of (A) ammonia concentration with thallus extension during spring and (B) water velocity (U_{bot}) with mass-standardised biomass accumulation (MSBA) during spring. Regression lines and adjusted r^2 values are shown

all measures of growth and productivity in summer, when temperatures were highest and the range in temperatures was greatest.

Hatcher et al. (1987) suggested that *Ecklonia radiata* would be precluded from places that have average temperatures above 23°C for more than 6 mo because they observed lower extension rates at places where this occurred. However, the optimum temperature (T_{opt}) for net photosynthesis for *E. radiata* has been estimated to be approximately 25°C (Staehr & Wernberg 2009). In our study, the productivity of *E. radiata* tended to be highest at sites with low temperatures during summer, when the range of water temperatures was greatest. Average temperatures of 22.8 to 23.0°C were recorded at some of the inshore sites during the entire summer survey period. These sites typically had between 22 and 25 d with peak temperatures above 23°C and between 8 and 12 d with temperatures above *E. radiata*'s T_{opt} of 25°C.

The most likely explanation for reduced growth rates of *Ecklonia radiata* at some places during periods of high summer temperatures is that respiration rates are more sensitive to increasing temperatures than photosynthetic rates if temperatures are above

the T_{opt} for net photosynthesis (Staehr & Wernberg 2009). *Ecklonia radiata* can optimise its metabolic balance to the existing temperature conditions by changing rates of light capture and enzymatic processes, and does this by altering its cellular pigment concentration (Staehr & Wernberg 2009, Miller et al. 2011). In our study, lower light intensity at the deeper (cooler) sites during summer might have been compensated for by lower rates of respiration and/or increased efficiency of light utilisation, facilitated by cooler temperatures. Conversely, higher illuminance at shallower sites during summer did not result in higher growth rates, probably because of higher rates of respiration due to warmer temperatures.

Increasing summer temperatures might also be responsible for the seasonal decline in *Ecklonia radiata* productivity from the maximum in the spring to the minimum during late summer (January to March; Kirkman 1989). This inference is supported by the observation that deeper sites, which maintained cooler temperatures in summer, also yielded the highest rates of growth and productivity. In winter and spring, when average temperatures were consistently <21°C, temperature was not selected in any of the models.

Light intensity

The relationship between photosynthesis and irradiance has been extensively studied in macroalgae (Hatcher 1977, Dieckmann 1980, Dunton 1990, Davison 1991). These investigations describe an asymptotic relationship where higher irradiance is linked to higher rates of photosynthesis until saturation is reached. Fairhead & Cheshire (2004b) found evidence of a seasonal acclimation response in *Ecklonia radiata* in which an increase in the efficiency of light utilisation at low irradiance in winter was accompanied by a decrease in both sub-saturating photon irradiance and the irradiance required for photosynthetic compensation. Net maximum photosynthesis also increased during the winter and autumn months and respiratory requirements decreased. Fairhead & Cheshire (2004b) found that these changes enabled *E. radiata* to produce an optimal photosynthetic performance throughout the year despite changes in the surrounding environment. However, Kirkman (1989) used an artificial shading experiment in Marmion Lagoon to show that reduced light intensity reduced *E. radiata* productivity (measured as mg g⁻¹ d⁻¹) during winter and autumn but not during summer or spring.

During winter and spring, light was the variable that best explained patterns in growth and productivity in our study. Light was selected in all models for winter and for BA and MSBA in spring. In each case, the trend followed that expected, with a tendency for higher growth and productivity at sites that received more light.

During winter, sites >11 m deep received less than one-third of the light they received in summer and kelps at these sites had the lowest productivity (as MSBA), despite lower temperatures than summer, which might otherwise have been favourable for growth. In spring, the amount of light reaching the seafloor was higher than in winter (but typically lower than summer), and temperatures were uniformly low. In general, rates of growth of *Ecklonia radiata* tended to be highest at sites with a combination of low temperature and high light intensities, and lowest at sites with a combination of low light and high temperature or high temperature and high light.

Modelled water velocity

Laboratory experiments have shown that productivity of some species of algae increases with water velocity, probably due to 2 separate mechanisms. First, water movement can break down the DBL, or remove waste products from the vicinity of the plant (Hurd 2000, Mass et al. 2010). Second, water velocity may resuspend nutrients locked in the sediments (Lourey & Kirkman 2009). We attempted to (at least partially) separate these 2 possibilities by including nutrient concentrations and modelled bottom water velocity as separate variables.

Hepburn et al. (2007) found evidence of enhanced *Macrocystis pyrifera* growth at wave-exposed sites during times of the year when growth was nitrogen limited. Exposure to waves modified the seasonal pattern of *M. pyrifera* growth by ameliorating the negative effect of low seawater nitrogen concentrations during summer and autumn. Blade and stipe growth had distinct seasonal patterns, with low growth during summer and autumn at lower water velocity sites and more uniform growth at higher water velocity sites.

In our study, during both spring and winter the combination of U_{bot} and light was selected as the best model to explain patterns in MSBA. During these periods, rates of MSBA were higher at sites with high water velocity compared with at sites with lower water velocity. Spring is also the period of maximum

growth when nitrogen uptake is likely to be high and when the breakdown of the DBL is likely to be most crucial for enhanced growth.

Nutrient concentrations

Marmion Lagoon is characterised by consistently low nutrient concentrations (Keesing et al. 2006, Lourey et al. 2006, Lourey & Kirkman 2009) yet it supports a high biomass of *Ecklonia radiata*. Occasional high concentrations of nutrients occur (Lourey & Kirkman 2009), but these tend to be relatively transient.

Hepburn et al. (2007) observed that nutrient concentrations and water movement were found to have a significant seasonal effect on the growth of *Macrocystis pyrifera*. In our study, concentrations of nitrate/nitrite and phosphate were highest during late autumn/winter and lowest in spring. In our study, concentrations of nutrients were not typically among the best predictors of growth or productivity. The sole exception was ammonia, which explained rates of thallus extension in the peak growth period of spring. The higher winter nitrate/nitrite and phosphate concentrations observed in our study are likely to have sustained increased growth in *Ecklonia radiata* during spring such that nutrient concentrations were not limiting.

Nutrient storage (both N and P) has been shown to exist in many different types of macroalgae (Pedersen & Borum 1996, Pedersen et al. 2010). The ability of *Ecklonia radiata* to take up and store nutrients is currently unknown and requires further study (Fairhead & Cheshire 2004b). However, low nutrient concentrations have been implicated in limiting the growth of *E. radiata* in previous studies (e.g. Kirkman 1984). If *E. radiata* has the capacity to store nutrients, then it may be able to take advantage of occasional short-term pulses of nutrients for longer-term growth.

Environmental influences on kelp productivity

The observation that temperature was one of the 2 most frequently selected variables in the models, and the only variable selected for the warmest period surveyed, suggests that temperature is an important influence on spatial variation in growth and productivity of *Ecklonia radiata*, at least at some times of the year. This inference, combined with the observation that the relationship between temperature and pro-

ductivity was negative during summer, suggests that growth and productivity of *E. radiata* is likely to be reduced by sustained temperature increases. *Ecklonia radiata* beds in northern (warmer) latitudes have a lower resilience to external perturbations compared with southern (cooler) kelp beds, and temperature is the most likely cause (Wernberg et al. 2010). The ocean off western Australia has been warming at rates of approximately 0.01 to 0.02°C yr⁻¹ (Pearce & Feng 2007, Thompson et al. 2009) and Poloczanska et al. (2007) predicted that surface waters around Australia will warm further by 1–2°C by the 2030s and 2–3°C by the 2070s. If water temperatures increase by this magnitude, productivity of *E. radiata* will likely be reduced, and this reduction would likely be most pronounced in shallower (<6 m) reef sites towards the northern range limits.

A sustained increase in water temperature is likely to lengthen the duration of the period that warm temperatures reduce *Ecklonia radiata* growth; the lower growth rates we observed in summer might extend into late spring and early autumn. The temperature thresholds beyond which the growth and productivity of *E. radiata* will be compromised remain unknown. The reduction in productivity caused by increasing atmospheric temperatures is likely to be largest at shallow sites, because we recorded the highest summer temperatures at the shallowest sites.

The importance of temperature on growth and productivity of *Ecklonia radiata*, combined with the observations of increasing water temperature, highlight the importance of understanding the effects of likely future temperature changes. However, increases in nutrient concentrations (Thompson et al. 2009), changes in bottom water velocities as storm patterns change (Frederiksen & Frederiksen 2007), and reduced light due to declining water quality (Connell et al. 2008) are important synergistic effects. As a result, the relative importance of each variable could conceivably change in ways that are difficult to predict in advance. Nonetheless, the ability of temperature and light to explain patterns of production in *E. radiata* implies that these 2 variables are the most important influences on growth and productivity (a conclusion that is supported by the knowledge that these 2 variables strongly influence rates of photosynthesis). Our findings suggest that a sustained increase in temperature (for example due to atmospheric warming) or reduction in light (for example by declining water quality) will negatively impact the patterns of growth and productivity of *E. radiata*.

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LITERATURE CITED

- Bojorge-Garcia M, Carmona J, Beltran Y, Cartajena M (2010) Temporal and spatial distribution of macroalgal communities of mountain streams in Valle de Bravo Basin, central Mexico. *Hydrobiologia* 641:159–169
- Bolton J, Lüning K (1982) Optimal growth and maximal survival temperatures of Atlantic *Laminaria* species (Phaeophyta) in culture. *Mar Biol* 66:89–94
- Booij N, Ris RC, Holthuijsen LH (1999) A third-generation wave model for coastal regions—1. Model description and validation. *J Geophys Res Oceans* 104:7649–7666
- Brown JH (1984) On the relationship between abundance and distribution of species. *Am Nat* 124:255–279
- Cebrian J (1999) Patterns in the fate of production in plant communities. *Am Nat* 154:449–468
- Connell SD, Irving AD (2008) Integrating ecology with biogeography using landscape characteristics: a case study of subtidal habitat across continental Australia. *J Biogeogr* 35:1608–1621
- Connell SD, Russell BD, Turner DJ, Shepherd SA and others (2008) Recovering a lost baseline: missing kelp forests from a metropolitan coast. *Mar Ecol Prog Ser* 360:63–72
- Davison IR (1991) Environmental effects on algae photosynthesis and temperature. *J Phycol* 27:2–8
- Diamond D (1998) QuikChem method 31-115-01-1-G. Determination of orthophosphate in brackish or seawater by flow-injection analysis. Zellweger Analytics, Milwaukee, WI
- Diamond D (1999) QuikChem method 31-107-04-1A. Determination of nitrate in brackish or seawater by flow-injection analysis. Zellweger Analytics, Milwaukee, WI
- Dieckmann GS (1980) Aspects of the ecology of *Laminaria pallida* (Grev) J.Ag. off the Cape Peninsula (South Africa). 1. Seasonal growth. *Bot Mar* 23:579–585
- Dunton KH (1990) Growth and production in *Laminaria solidungula*: relation to continuous underwater light levels in the Alaskan High Arctic. *Mar Biol* 106: 297–304
- Fairhead VA, Cheshire AC (2004a) Seasonal and depth related variation in the photosynthesis-irradiance response of *Ecklonia radiata* (Phaeophyta, Laminariales) at West Island, South Australia. *Mar Biol* 145:415–426
- Fairhead VA, Cheshire AC (2004b) Rates of primary productivity and growth in *Ecklonia radiata* measured at different depths, over an annual cycle, at West Island, South Australia. *Mar Biol* 145:41–50
- Falkenberg LJ, Russell BD, Connell SD (2012) Stability of strong species interactions resist the synergistic effects of local and global pollution in kelp forests. *PLoS ONE* 7: e33841
- Fowler-Walker MJ, Connell SD, Gillanders BM (2005) To what extent do geographic and associated environ-

- mental variables correlate with kelp morphology across temperate Australia? *Mar Freshw Res* 56:877–887
- Frederiksen JS, Frederiksen CS (2007) Interdecadal changes in southern hemisphere winter storm track modes. *Tellus* 59A:599–617
- Gorman D, Connell SD (2009) Recovering subtidal forests in human-dominated landscapes. *J Appl Ecol* 46:1258–1265
- Graham MH, Edwards MS (2001) Statistical significance versus fit: estimating the importance of individual factors in ecological analysis of variance. *Oikos* 93:505–513
- Hanisak M (1983) The nitrogen relationships of marine macroalgae. In: Carpenter E, Capone D (eds) *Nitrogen in the marine environment*. Academic Press, New York, NY, p 699–730
- Hatcher BG (1977) An apparatus for measuring photosynthesis and respiration of intact large marine algae and comparison of results with those from experiments with tissue segments. *Mar Biol* 43:381–385
- Hatcher BG, Kirkman H, Wood W (1987) Growth of the kelp *Ecklonia radiata* near the northern limit of its range in Western Australia. *Mar Biol* 95:63–72
- Hepburn CD, Holborow JD, Wing SR, Frew RD, Hurd CL (2007) Exposure to waves enhances the growth rate and nitrogen status of the giant kelp *Macrocystis pyrifera*. *Mar Ecol Prog Ser* 339:99–108
- Hochachanka PW, Somero GN (1984) *Biochemical adaptation*. Princeton University Press, Princeton, NJ
- Holthuijsen L (2007) *Waves in oceanic and coastal waters*. Cambridge University Press, Cambridge
- Howarth RW (1988) Nutrient limitation of net primary productivity in marine ecosystems. *Annu Rev Ecol Syst* 19:89–110
- Hoyo-Meléndez JM, Mecklenburg MF, Doménech-Carbó MT (2011) An evaluation of daylight distribution as an initial preventive conservation measure at two Smithsonian Institution Museums, Washington DC, USA. *J Cult Herit* 12:54–64
- Hughes L (2000) Biological consequences of global warming: is the signal already apparent. *Trends Ecol Evol* 15:56–61
- Hurd C (2000) Water motion, marine macroalgal physiology and production. *J Phycol* 36:453–472
- Jackson GA (1977) Nutrients and production of giant kelp, *Macrocystis pyrifera*, off southern California. *Limnol Oceanogr* 22:979–995
- Kain JM (1989) The seasons in the subtidal. *Br Phycol J* 24:203–215
- Keesing JK, Heine JN, Babcock RC, Craig PD, Koslow JA (2006) *Strategic Research Fund for the Marine Environment Final Report, Vol 2: The SRFME Core Projects*. Strategic Research Fund for the Marine Environment, Perth, WA
- Kirk JTO (1994) *Light and photosynthesis in aquatic environments*. Cambridge University Press, Cambridge
- Kirkman H (1984) Standing stock and production of *Ecklonia radiata* (C.Ag.) J. Agardh. *J Exp Mar Biol Ecol* 76:119–130
- Kirkman H (1989) Growth, density and biomass of *Ecklonia radiata* at different depths and growth under artificial shading off Perth, Western Australia. *Aust J Mar Freshw Res* 40:169–177
- Kuha J (2004) AIC and BIC: comparisons of assumptions and performance. *Sociol Methods Res* 33:188–229
- Lapointe BE, Littler MM, Littler DS (1992) Nutrient availability to marine macroalgae in siliciclastic versus carbonate-rich coastal waters. *Estuaries* 15:75–82
- Larkum AWD (1986) A study of growth and primary production in *Ecklonia radiata* (Laminariales) at a sheltered site in Port Jackson, New South Wales (Australia). *J Exp Mar Biol Ecol* 96:177–190
- Lourey MJ, Kirkman H (2009) Short-lived dissolved nitrate pulses in a shallow Western Australian coastal lagoon. *Mar Freshw Res* 60:1068–1080
- Lourey MJ, Dunn JR, Waring J (2006) A mixed-layer nutrient climatology of Leeuwin Current and Western Australian shelf waters: seasonal nutrient dynamics and biomass. *J Mar Syst* 59:25–51
- Lumley T (2009) *Leaps: Regression subset selection*. R package version 2.0. Available at <http://cran.r-project.org/web/packages/leaps/index.html>
- Luning K (1980) Critical levels of light and temperature regulating the gametogenesis of three *Laminaria* species. *J Phycol* 16:1–15
- Luning K (1984) Temperature tolerance and biogeography of seaweeds: the marine algal flora of Helgoland (North Sea) as an example. *Helgol Meeresunters* 38:305–317
- Maegawa M, Yokohama Y, Aruga Y (1987) Critical light conditions for young *Ecklonia cava* and *Eisenia bicyclis* with reference to photosynthesis. *Hydrobiologia* 151/152:447–455
- Mann KH, Kirkman H (1981) A biomass method for measuring productivity of *Ecklonia radiata* with the potential for adaptation to other large brown algae. *Aust J Mar Freshw Res* 32:297–304
- Mass T, Genin A, Shavit U, Grinstein M, Tchernov D (2010) Flow enhances photosynthesis in marine benthic autotrophs by increasing the efflux of oxygen from the organism to the water. *Proc Natl Acad Sci USA* 107:2527–2531
- McGlathery K, Pedersen M, Borum J (1996) Changes in intracellular nitrogen pools and feedback controls on nitrogen uptake in *Chaetomorpha linum* (Chlorophyta). *J Phycol* 32:393–401
- Miller SM, Hurd CL, Wing SR (2011) Variations in growth, erosion, productivity, and morphology of *Ecklonia radiata* (Alariaceae; Laminariales) along a fjord in southern New Zealand. *J Phycol* 47:505–516
- Moore LR, Goericke R, Chisholm SW (1995) Comparative physiology of *Synechococcus* and *Prochlorococcus*: influence of light and temperature on growth, pigments, fluorescence and absorptive properties. *Mar Ecol Prog Ser* 116:259–275
- Novaczek I (1984) Response of *Ecklonia radiata* (Laminariales) to light at 15°C reference to the field light budget at Goat Island Bay, New Zealand. *Mar Biol* 80:263–272
- Pearce A, Feng M (2007) Observations of warming on the Western Australian continental shelf. *Mar Freshw Res* 58:914–920
- Pedersen MF, Borum J (1996) Nutrient control of algal growth in estuarine waters. Nutrient limitation and the importance of nitrogen requirements and nitrogen storage among phytoplankton and species of macroalgae. *Mar Ecol Prog Ser* 142:261–272
- Pedersen MF, Borum J, Fotel FL (2010) Phosphorus dynamics and limitation of fast- and slow-growing temperate seaweeds in Oslofjord, Norway. *Mar Ecol Prog Ser* 399:103–115
- Poloczanska ES, Babcock RC, Butler A, Hobday AJ and others (2007) Climate change and Australian marine life. *Oceanogr Mar Biol Annu Rev* 45:409–480
- Quinn G, Keough M (2002) *Experimental design and data*

- analysis for biologists. Cambridge University Press, Cambridge
- R Development Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rinde E, Sjutun K (2005) Demographic variation in the kelp *Laminaria hyperborea* along a latitudinal gradient. *Mar Biol* 146:1051–1062
- Schils T, Wilson S (2006) Temperature threshold as a biogeographic barrier in northern Indian Ocean macroalgae. *J Phycol* 42:749–756
- Smale DA, Wernberg T (2009) Satellite-derived SST data as a proxy for water temperature in nearshore benthic ecology. *Mar Ecol Prog Ser* 387:27–37
- Staehr PA, Wernberg T (2009) Physiological responses of *Ecklonia radiata* (Laminariales) to and latitudinal gradient in ocean temperature. *J Phycol* 45:91–99
- Symonds G, Zhong L, Mortimer NA (2011) Effects of wave exposure on circulation in a temperate reef environment. *J Geophys Res* 116:C09010, doi:10.1029/2010JC006658
- Theodorou ME, Elrifi IR, Turpin DH, Plaxton WC (1991) Effects of Phosphorus limitation on respiratory metabolism in the green alga *Selenastrum minutum*. *Plant Physiol* 95:1089–1095
- Thompson PA, Baird ME, Ingleton T, Doblin MA (2009) Long-term changes in temperate Australian coastal waters: implications for phytoplankton. *Mar Ecol Prog Ser* 394:1–19
- van den Hoek C (1982) Phytogeographic distribution of groups of benthic marine algae in the North Atlantic Ocean. A review of experimental evidence from life history studies. *Helgol Meeresunters* 35:153–214
- Vanderklift MA, Lavery PS, Waddington KI (2009) Intensity of herbivory on kelp by fish and sea urchins differs between inshore and offshore reefs. *Mar Ecol Prog Ser* 376:203–211
- Watson RJ, Butler ECV, Clementson LA, Berry KM (2005) Flow-injection analysis with fluorescence detection for the determination of trace levels of ammonium in seawater. *J Environ Monit* 7:37–42
- Wernberg T, Goldberg N (2008) Short-term temporal dynamics of algal species in a subtidal kelp bed in relation to changes in environmental conditions and canopy biomass. *Estuar Coast Shelf Sci* 76:265–272
- Wernberg T, Kendrick GA, Phillips JC (2003) Regional differences in kelp-associated algal assemblages on temperate limestone reefs in south-western Australia. *Divers Distrib* 9:427–441
- Wernberg T, Thomsen MS, Tuya F, Kendrick GA, Staehr PA, Toohey BD (2010) Decreasing resilience of kelp beds along a latitudinal temperature gradient: potential implications for a warmer future. *Ecol Lett* 13: 685–694
- Winer BJ (1971) Statistical principles in experimental design. McGraw-Hill, New York, NY
- Wolters M (2003) QuikChem method 31-114-27-1-D. Determination of silicate in brackish or seawater by flow-injection analysis. Lachat Instruments, Loveland, CO
- Womersley HBS (1981) Aspects of the distribution and biology of Australian marine macro-algae. In: Pate JS, McComb AJ (eds) *The biology of Australian plants*. University of Western Australia Press, Nedlands, WA, p 294–305

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