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Physiological responses of habitat-forming seaweeds to increasing temperatures

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Abstract

Kelps and fucoids are dominant habitat-forming seaweeds along temperate rocky coastlines. Here, we tested the physiological performance of a dominant kelp (*Ecklonia radiata*) and two fucoids (*Scytothalia dorycarpa* and *Sargassum fallax*), distributed along the southwest coast of Australia. Photosynthesis and respiration were measured against increments in temperature for seaweeds collected along a latitudinal gradient in ocean temperature from Kalbarri (warm) to Hamelin Bay (cool). We found a similar decrease in photosynthetic activity from cooler to warmer latitudes in all three species. Seaweeds collected from warmer locations had significantly lower chlorophyll *a* concentration compared to cooler locations which could explain the lower levels of photosynthetic activity at warmer latitudes. The Q_{10} values for photosynthesis and respiration tended to decrease from cooler to warmer locations. For all species, the optimum temperature for net photosynthesis remained similar across the locations. However, within locations, the optimum temperature for *S. fallax* (25.2°C) was significantly higher than *E. radiata* (24.0°C) and *S. dorycarpa* (23.6°C). The reduction rates of net photosynthesis observed after optimum temperature showed the greatest variation among the species within and across locations. A thermal performance breadth analysis revealed a broader performance range for *S. fallax* (21.5–28.4°C) followed by *E. radiata* (21.2–26.5°C) and *S. dorycarpa* (21.4–25.8°C). These results highlight the differences in temperature sensitivity among the three species which help explain their current distributional patterns and have potential implications for future responses to future ocean warming.

Temperature is an important physical factor determining the biogeographic distribution of marine species (Hoek 1982; Perry et al. 2005; Wernberg et al. 2013*b*). Physiological adjustments to temperature regimes across large spatial scales play a vital role in controlling species ranges through regulating the temperatures under which normal cellular function can take place. Persistence usually depends on the temperature regimes an organism can physiologically tolerate (Osovitz and Hofmann 2007; Somero 2010).

In recognition of the risks of losing valuable ecosystem services to climate change (Smale et al. 2013; Costanza et al. 2014; Bennett et al. 2016), studying the potential impact of ocean warming on ecologically and socioeconomically important marine organisms has gathered momentum in recent years (Boyce et al. 2010; Cantin et al. 2010; Cheung et al. 2013). In this context, however, the response of marine organisms to discrete short-term and sudden environmental changes, such as heat spikes or heatwaves, is considerably less well known than responses to gradual change in mean conditions (Wernberg et al. 2012; Coble et al. 2016; Hobday et al. 2016). In particular, understanding the biochemical and physiological responses to the interplay between long-term and short-term variations in temperature regimes is important because extreme events are increasingly superimposed onto rising mean temperatures (Poloczanska et al. 2012).

Kelps and fucoids are ecologically and socioeconomically important large brown seaweeds that are abundant in temperate reef ecosystems (Smale et al. 2013; Steneck and Johnson 2013; Bennett et al. 2016). These habitat-forming seaweeds are under threat from increasing ocean temperatures, which have contributed to significant range shifts (Lima et al. 2007; Wernberg et al. 2011a; Straub et al. 2016). Substantial declines in kelp and fucoid covers have been recorded in Europe, North America, Asia, and Australia where many populations have gone, or are on the verge of going, locally extinct due to increasing temperatures

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(Johnson et al. 2011; Tanaka et al. 2012; Raybaud et al. 2013; Smale and Wernberg 2013; Voerman et al. 2013; Filbee-Dexter et al. 2016 ,Wernberg et al. 2016).

The western Australian coast is a tropical–temperate transition zone with high species richness and endemism (Phillips 2001; Bennett et al. 2016). A recent study of the habitat structure of seaweed forests along the west coast south of ~ 28°S revealed significant temperature-related variation in the distribution *Ecklonia radiata*, *Scytothalia dorycarpa* and *Sargassum* spp., three of the most abundant and dominant seaweeds in the region (Wernberg et al. 2011b). The kelp *E. radiata* was abundant across all latitudes while fucoid canopies changed gradually from *Sargassum* spp. to *S. dorycarpa* from warm to cool latitudes (Wernberg et al. 2011b). Subsequently, in early 2011, the marine ecosystems along the west coast of Australia experienced the highest-magnitude warming event on record. Temperature anomalies 2–4°C above long-term means persisted for more than 10 weeks and caused substantial impacts on the marine ecosystem (Pearce and Feng 2013; Wernberg et al. 2013a ,Wernberg et al. 2016). Among the most prominent changes seen were ~ 100 km range contractions of *E. radiata* and *S. dorycarpa*, with local extinctions in Kalbarri and Jurien Bay respectively, and a concurrent expansion of *Sargassum* spp. canopies (Smale and Wernberg 2013; Wernberg et al. 2013a; Bennett et al. 2015b ,Wernberg et al. 2016). Similar transitions from kelp to *Sargassum* dominance have been seen in Japan, another warming region (Tanaka et al. 2012).

These distribution patterns and responses to extreme warming are likely related to the temperature tolerances of the seaweeds, reflecting their biogeographic and evolutionary histories. *E. radiata* is a warm temperate kelp species whereas *Sargassum* spp. is a predominantly tropical genus, that dominates the tropical seaweed flora at Ningaloo Reef to the north (Fulton et al. 2014). *S. dorycarpa*, in contrast, belongs to a monospecific genus endemic to southern Australia (Womersley 1987) and is likely to have evolved from the cool, temperate Tethyan marine flora on the southern coast (Phillips 2001).

Constant fluctuations are superimposed onto the progressively changing environment. The capacity of species and populations to withstand these fluctuations depend on their thermal safety margins (distance between ambient and lethal temperature) (Bennett et al. 2015a). Consequently, assessing the impacts of ocean warming on habitat-forming seaweeds requires an understanding of physiological responses to short-term temperature variability under different climatic conditions. Photosynthesis, the basis of primary productivity, is a core metabolic process often measured as an indicator of seaweed stress-responses (Hurd et al. 2014). Specifically, high temperatures can result in denaturation of proteins and damage to heat-labile enzymes or membranes of the photosynthetic apparatus (Daniel et al. 1996). There is currently a limited understanding of how well different seaweeds cope with temperature variability and the consequences of long-term temperature increases (Bennett et al. 2015a). Recent studies have documented a broad range of responses from physiological adjustments to maintain performance to physiological collapse and range contraction of ecologically important seaweeds (Smale and Wernberg 2013; Tait and Schiel 2013; Colvard et al. 2014; Jueterbock et al. 2014).

The current study tested the effect of increasing ocean temperatures on key metabolic processes in the fully grown macroscopic stages of *E. radiata*, *S. dorycarpa* and *S. fallax* from different temperature regimes. In doing so, this study aimed to provide knowledge on the short-term temperature conditions each species can tolerate, and how this might change under different long-term growth temperatures. This provides an understanding of the physiological mechanisms which underpin current distribution patterns, seaweed responses to extreme events such as the 2011 marine heatwave and the future distribution of these ecologically important seaweeds.

Materials and methods

Study location and collection of seaweed species

The temperature conditions of the western Australian coastline are strongly influenced by the Leeuwin Current, which is a southward flow of warm, low-nutrient water along the continental shelf (Pearce 1991). The Leeuwin Current creates a natural temperature gradient along the coast, and a remarkable opportunity to study the influence of ocean temperature on physiological and ecological processes (Smale and Wernberg 2009; Stæhr and Wernberg 2009; Wernberg et al. 2010).

Seaweed samples were collected along a 2–4°C temperature gradient covering a stretch of about ~ 700 km coastline from Kalbarri (27°67′ S, 114°15′ E), Jurien Bay (30°26′ S, 114°97′ E), Marmion (31°85′ S, 115°70′ E) and Hamelin Bay (34°21′ S, 115°01′ E) (see Fig. 1). Five replicates (independent thalli a few meters apart) of each available species were collected from 10 m to 12 m deep reefs at each location between December 2012 to March 2013 (austral summer). *Sargassum fallax* was found at all four locations, *Ecklonia radiata* was found at Jurien Bay, Marmion and Hamelin Bay, and *Scytothalia dorycarpa* was found only at Marmion and Hamelin Bay. All freshly collected algal thalli were transported to the laboratory and maintained under dim light (~ 20 μmol photons m^{-2} s^{-1}; similar to natural sub-canopy conditions at 10–12 m depth, Wernberg et al. 2005) and natural photoperiod (~ 12 : 12 L : D) at 12°C for 24 h before being used in experiments. This temperature is close to the lowest temperatures experienced by these species across their distribution in Australia and was chosen to acclimatise the tissues to the starting conditions of the experiments.

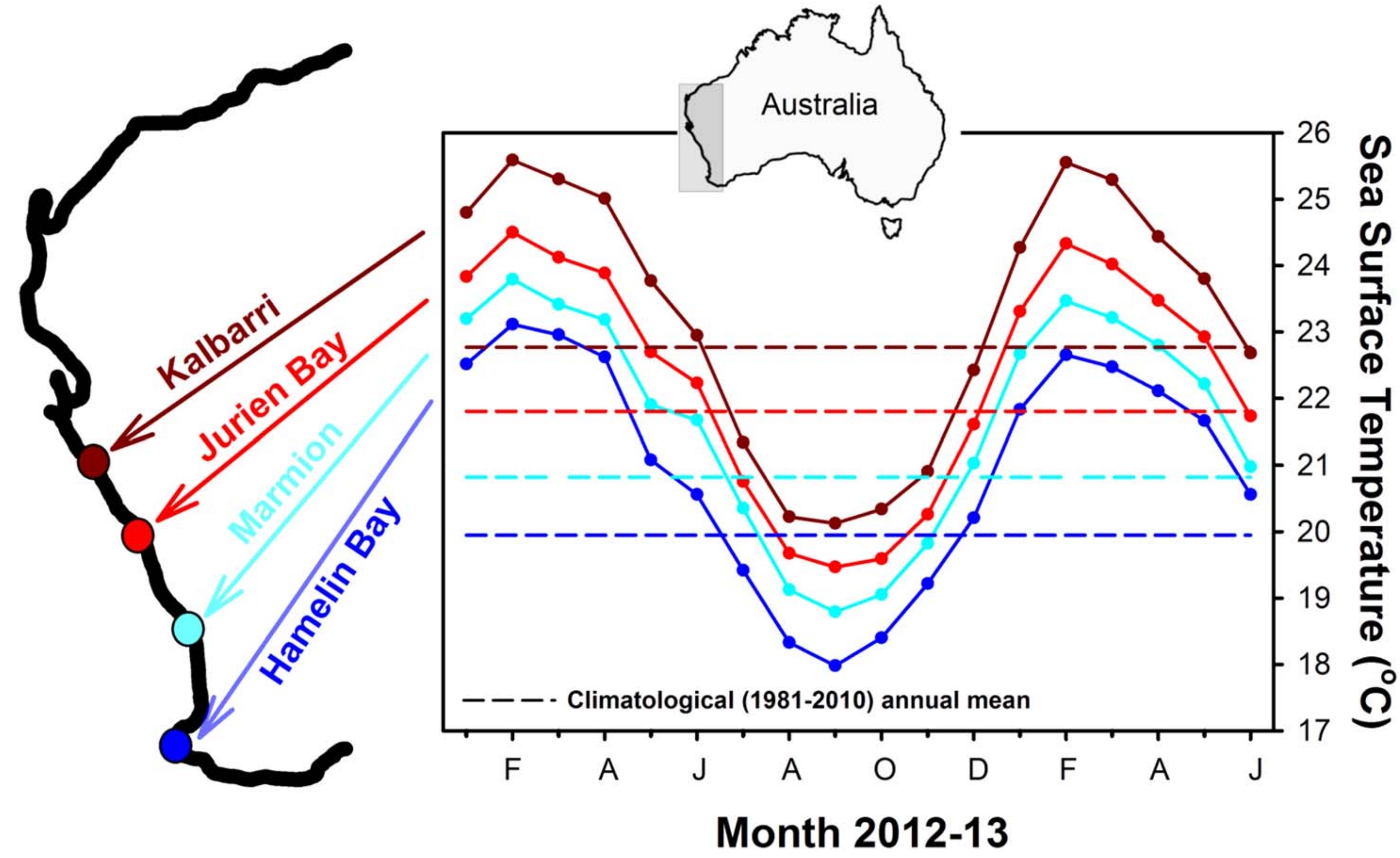

Fig. 1. Seaweed collection sites along the southwest Australian coast. The plot shows the satellite derived monthly sea surface temperature (SST) from January 2012 to June 2013 and the annual climatological means for the 30-yr period 1981–2010. [Color figure can be viewed at wileyonlinelibrary.com]

To demonstrate ambient water temperatures for the sampling sites during and prior to the sampling period, we obtained sea surface temperatures (SST) from January 2012 to June 2013 (Fig. 1). Climatological annual mean temperatures from 1981 to 2012 were also obtained to illustrate long-term differences across locations (Fig. 1). Temperature data was obtained from the National Oceanic and Atmospheric Administration (NOAA) optimum interpolation (OI) version 2 data which is computed on a 1-degree grid and combines satellite data with in situ observations. Satellite SST's are known to be a good proxy for in situ temperatures, although shot-term (days) events might not be fully captured (Smale and Wernberg 2009).

Photosynthesis and respiration

To standardise sampling, epiphyte-free pieces of tissue (220 ± 48 mg dry weight, mean ± SE) from the lower half of the thallus were used to measure net photosynthesis and respiration following the protocol of Stæhr and Wernberg (2009). All tissue samples were measured in a temperature-controlled bath which allowed simultaneous incubation of 10 individual tissue samples, five blackened and five clear at 530 μmol photons m^{-2} s^{-1}, similar to open canopy light conditions at 10–12 m depth (Wernberg et al. 2005). The samples were incubated in 120 mL flasks under gentle shaking for ~ 45 min at each successive measurement temperature (10°C, 15°C, 20°C, 22°C, 24°C, 26°C, 28°C, and 30°C). Subsequently, photosynthesis and dark respiration were measured via oxygen exchange using an YSI Pro oxygen probe (California, U.S.A.). The probe was calibrated regularly.

Pigment analyses

The photosynthetic pigments chlorophyll *a* (Chl *a*) and chlorophyll *c* (Chl *c*) were extracted from tissues of a subset of three randomly selected individuals. Extractions were done with 90% acetone in the dark and kept overnight at 4°C. The extract was centrifuged ($5000 \times g$) and absorption measured spectrophotometrically. Pigment concentrations were calculated following the method of Jeffrey and Humphrey (1975).

Parameter calculations

The maximum rate of gross photosynthesis (GP_{max}) was determined by nonlinear regression of net photosynthesis (NP) at irradiance (E) normalised to dry weight according to a saturating exponential model (Webb et al. 1974). Dark respiration (R_D) is the respiration rate at $E = 0$. The maximum rate of net photosynthesis (NP_{max}), was calculated as GP_{max}-R_D. For each specimen and temperature treatment, optimum temperature (T_{opt}) for net photosynthesis was calculated using a Gaussian fit to each temperature-response curve. To assess the differences in the temperature response between the species at each location and the same species at different locations, Q_{10} was calculated according to the equation:

$$Q_{10} = (\text{Rate}_2/\text{Rate}_1)^{\left[\frac{10}{T_2 - T_1}\right]} \quad (1)$$

where, Rate_1 and Rate_2 were reaction rates measured at temperatures T_1 (low temperature) and T_2 (high temperature), respectively. The Q_{10}, defined as the change in rate of a reaction with a rise in temperature of 10°C, was calculated for the temperature intervals from 10°C to 20°C for net photosynthesis and dark respiration. To understand the effect of increasing temperature above T_{opt}, the decrease in rate from T_{opt} to 30°C was calculated from the slope of each temperature-response curve using a Gaussian fit.

Thermal performance curves were constructed (Eggert et al. 2003), to determine the thermal performance breadth of each species, defined as the temperature range at which performance meets or exceeds a threshold (arbitrarily set at 80% of performance at maximum net photosynthesis). Marmion and Hamelin Bay were selected for this analysis as all three seaweeds were only available from these two locations. A Gaussian fit was used to estimate the temperature range and a curve was constructed for each species from the average rates of maximum net photosynthesis from these two locations.

Statistical analyses

Differences in oxygen metabolism between temperature treatments and estimates of temperature-response curves were tested with one-way analysis of variance (ANOVA). To compare the effect of the treatment temperature on metabolic response variables, the effect of increasing temperature on all species in each location and each species in all locations was analysed. All data was tested for homogeneity of variances (Levene's test) and data were transformed ($\log_{10}$) when normal distribution was not supported. Pair-wise comparisons (Tukey's test, $p < 0.05$) were carried out to ascertain which treatments differed from one another. All data analysis was performed using SPSS Statistics 22 (IBM Corp. 2013).

Results

Effect of temperature on net photosynthesis and respiration rates

Water temperatures along the coastal gradient ranged from 22.5–25.5°C (Kalbarri) to 20.5–22.5°C (Hamelin Bay) during the collection of seaweeds (December to March, Fig. 1). Irrespective of the location from which they were collected, an increase in incubation temperature resulted in an increase in the net photosynthetic rate in *Scytothalia dorycarpa, Ecklonia radiata*, and *Sargassum fallax* up to a temperature optimum (Fig. 2A–D) beyond which there was a decline in net photosynthetic rates. In general, the net rate of photosynthesis in each species decreased with decreasing latitude (and increasing ocean temperature) from Hamelin Bay to Kalbarri. In all the three species, net photosynthesis rates in samples collected from cool-acclimated conditions (Hamelin Bay) were more sensitive (steeper slopes) to the short-term successive increases in measurement temperature than samples collected from warm-acclimated conditions (Marmion to Kalbarri) (Fig. 2).

In contrast to net photosynthetic rates, dark respiration rates increased at successive temperature increases up to 30°C with no indication of an optimum temperature (Fig. 2E–H). Similar to photosynthesis, respiration at most measurement temperatures was higher in samples from lower latitudes. At lower measurement temperatures, respiration rates tended to be similar across species, but at higher measurement temperatures, *S. fallax* respired more slowly than the other species (Fig. 2E–H).

Effect of temperature on photosynthetic parameters

Q_{10} values for net photosynthesis were 13% higher at Hamelin Bay and showed a decreasing trend towards the warmer locations (Fig. 3A). The Q_{10} values were significantly different ($p < 0.05$) for *S. fallax* when compared across all the locations but *E. radiata* and *S. dorycarpa* did not show significant latitude-dependant variation (Table 1). Furthermore, Q_{10} values for the different species at each location were not significantly different (Table 1). Q_{10} values for dark respiration also showed a decreasing trend from cooler to warmer locations (Fig. 3B). However, no significant latitude-dependant differences were observed within or between species (Table 1).

Optimum temperature (T_{opt}) for photosynthesis in *S. dorycarpa*, *E. radiata*, and *S. fallax* displayed differences between species but not across latitude (within species). T_{opt} of *S. fallax* was significantly higher ($p < 0.05$) than *E. radiata* and *S. dorycarpa* (Fig. 3C; Table 2) in Marmion and Hamelin Bay but no significant difference was observed between *E. radiata* and *S. fallax* in Jurien Bay. Once averaged across locations *S. fallax* had the highest T_{opt} for net photosynthesis (25.2°C) followed by *E. radiata* (24.0°C) and *S. dorycarpa* (23.6°C). The reduction rate (slope of the net photosynthesis decreases above T_{opt}) showed the greatest variation among the photosynthetic parameters studied (Fig. 3D). The reduction rate was significantly different ($p < 0.05$) across locations within each species (Table 2; Fig. 3D). The reduction rate was also significantly different between species collected from Hamelin Bay and Marmion (Table 2). The reduction rate was higher in Hamelin Bay (~ 20%) and decreased gradually toward warmer locations.

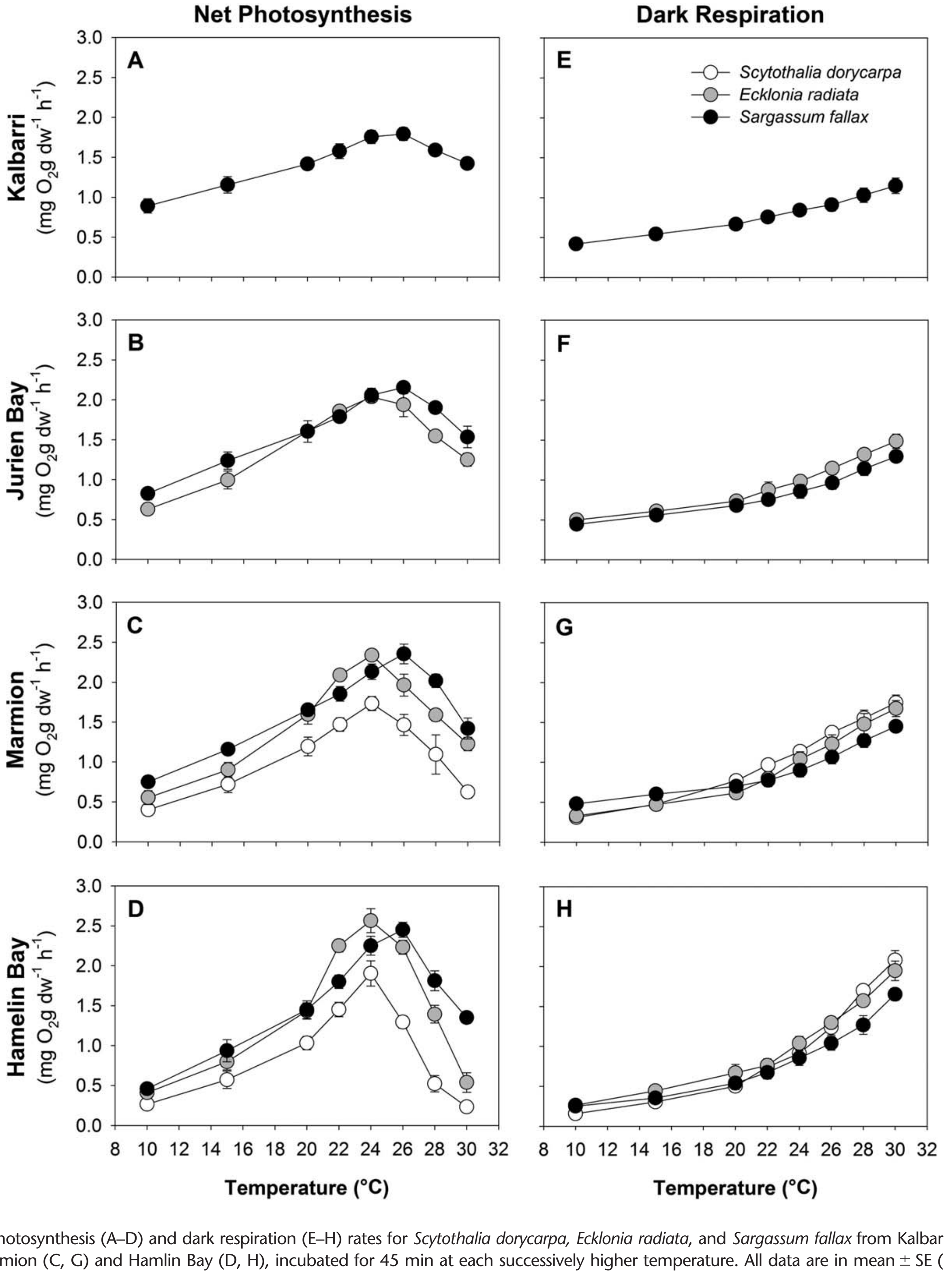

Fig. 2. Net photosynthesis (A–D) and dark respiration (E–H) rates for *Scytothalia dorycarpa, Ecklonia radiata*, and *Sargassum fallax* from Kalbarri (A, E), Jurien Bay (B, F), Marmion (C, G) and Hamlin Bay (D, H), incubated for 45 min at each successively higher temperature. All data are in mean ± SE ($n = 5$).

The breadth of temperature performance, defined as the temperature range over which net photosynthesis is at least 80% of maximum rate of net photosynthesis was greatest for *S. fallax* (21.5–28.4°C) followed by *E. radiata* (21.2–26.5°C) and in *S. dorycarpa* (21.4–25.8°C) (Fig. 4). The breadth of temperature performance (Fig. 4) provided further information on temperature sensitivity of the three species (complementary to T_{opt} results). Again, it showed the high

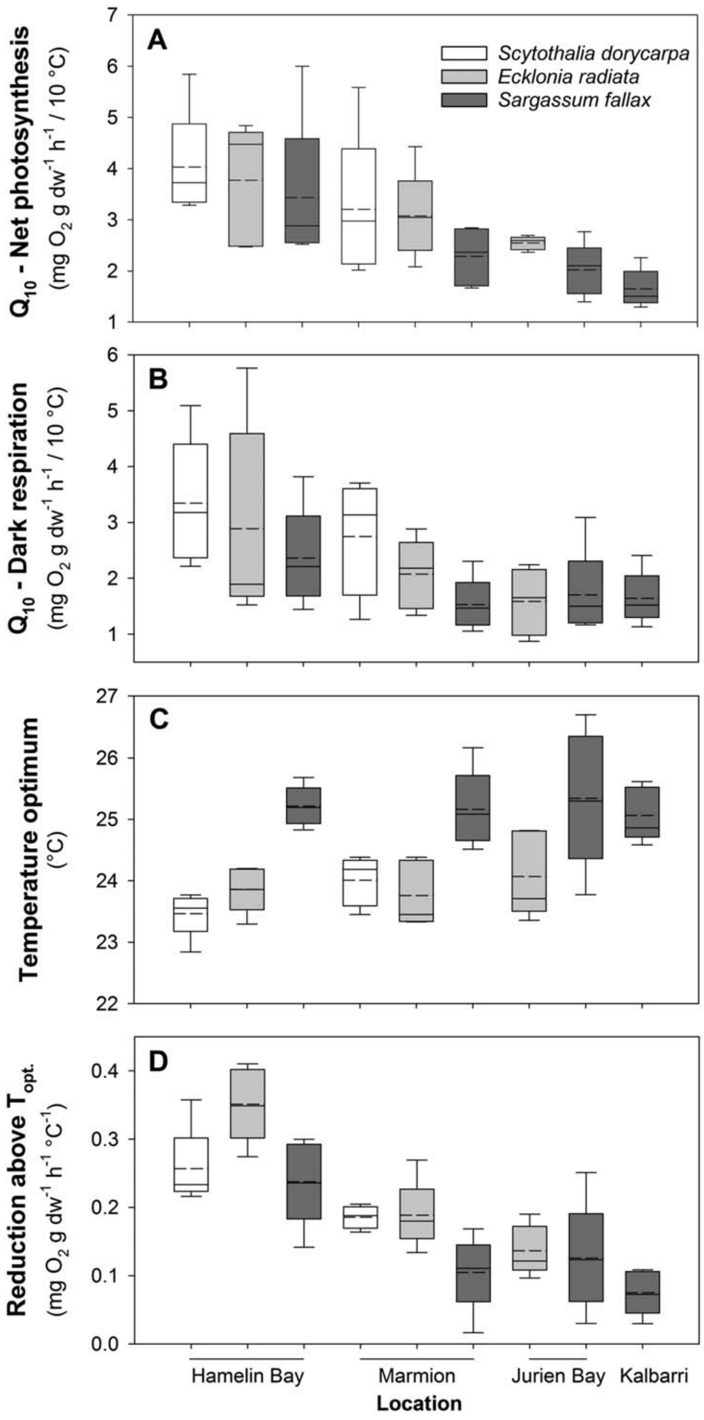

Fig. 3. Box plots of temperature-response parameters of *Scytothalia dorycarpa, Ecklonia radiata*, and *Sargassum fallax*. The bottom line of the box represents the 25th percentile, the centre line of the box represents the median value and the top line of the box represents the 75th percentile. The lower and upper whiskers represent the lowest and the highest values in the data. The dotted line inside the box represents the arithmetic mean. All data are in mean ± SD ($n = 5$).

temperature tolerance of *S. fallax* (Figs. 2, 3C) but highlighted a difference in temperature sensitivity between *E. radiata* and *S. dorycarpa* not found previously. There was a ~ 1°C difference in the breath of temperature performance between *E. radiata* (5.3°C) and *S. dorycarpa* (4.4°C) towards the warmer temperatures (similar lower limit: respectively 21.4°C and 21.2°C).

Effect of temperature on pigment content

The chlorophyll concentration gradually increased from warmer to cooler locations in all three species (Table 3). There was a significant difference in Chl *a* content in each species across the sampled locations (Table 4). Chl *c* concentration also showed a similar trend like Chl *a*, but the decline was not as strong as for Chl *a*, resulting in a downward trend for Chl *a* : Chl *c* ratio.

Discussion

Our study demonstrated that *Ecklonia radiata*, *Scytothalia dorycarpa*, and *Sargassum fallax*, the three dominant large brown seaweeds in southwestern Australia, showed variation in physiological responses to short-term temperature increases along a latitudinal temperature gradient. The observed differences were consistent with the biogeographic and evolutionary history of these seaweeds, and their responses to a recent warming event, suggesting these traits could have implications for the competitiveness and distribution of these species in a warmer future.

The three seaweeds had similar optimum temperature (T_{opt}) for photosynthesis across locations. However, within locations *S. fallax* exhibited significantly higher T_{opt} compared to *E. radiata* and *S. dorycarpa*. Significant differences between species and locations in the reduction rate above T_{opt} highlighted the negative impact of supra-optimal temperatures on the overall photosynthetic performance for all species. We also observed lower pigment concentrations and Q_{10} values for net photosynthesis and dark respiration at warmer locations compared to cooler locations. The thermal performance breadth analysis revealed a wider operating range for *S. fallax* compared to *E. radiata* and *S. dorycarpa*. Collectively, these results show a clear thermal performance hierarchy across these species (*S. fallax* > *E. radiata* > *S. dorycarpa*) and general physiological adjustments in response to long-term growth temperatures. Interestingly, warm-adjusted seaweeds were less responsive to short-term changes in temperature and the differences among species were more related to performance at supra-optimal conditions than optima per se.

Net rate of photosynthesis increased with increasing incubation temperature up to a temperature optimum for all species in this study. These temperature optima (23.6–25.2°C) were very close to the observed maximum summer temperatures (22.5–25.5°C) suggesting all species currently persist close to the limit of optimal performance where the observed physiological differences could play a role in

Table 1. Results of one-way ANOVA of Q_{10} calculated for net photosynthesis (NP) and dark respiration (RD).*

	Q_{10} NP					Q_{10} RD			
Source	**df**	**MS**	***F***	***p***	**Pair-wise test**	**df**	**MS**	***F***	***p***
Kalbarri—species	Nd	nd	nd	nd	nd	nd	nd	nd	nd
Jurien Bay—species	1	0.26	0.61	0.456	ns	1	0.03	0.07	0.800
Marmion—species	2	0.37	0.33	0.724	ns	2	1.86	3.34	0.070
Hamelin Bay—species	2	0.40	0.30	0.749	ns	2	1.21	0.69	0.519
Scytothalia dorycarpa—location	1	1.71	1.11	0.324	ns	1	0.89	0.76	0.409
Ecklonia radiata—location	2	1.89	2.63	0.113	ns	2	2.16	1.67	0.230
Sargassum fallax—location	3	2.95	4.15	**0.024**	Ham > Kal	3	0.71	1.51	0.249

*Values that were significantly different ($p < 0.05$) are indicated in bold. (nd, not determined; ns, not significant; Kal, Kalbarri; Ham, Hamelin Bay).

Table 2. Results of one-way ANOVA of temperature optimum (T_{opt}) for net photosynthesis and reduction rate in net photosynthesis observed after T_{opt}.*

	T_{opt} NP					Reduction rate after T_{opt}				
Source	**df**	**MS**	***F***	***p***	**Pair-wise test**	**df**	**MS**	***F***	***p***	**Pair-wise test**
Kalbarri—species	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd
Jurien Bay—species	1	4.10	4.79	0.060	ns	1	0.00	0.09	0.768	ns
Marmion—species	2	2.68	5.25	**0.023**	Sar > Eck, Scy	2	0.01	5.48	**0.020**	Sar < Eck, Scy
Hamelin Bay—species	2	4.20	33.82	**<0.001**	Sar > Eck, Scy	2	0.02	5.10	**0.025**	Sar < Eck
Scytothalia dorycarpa—location	2	0.29	0.52	0.493	ns	1	0.01	7.10	**0.029**	Ham > Mar
Ecklonia radiata—location	2	0.06	0.22	0.806	ns	2	0.06	27.40	**< 0.001**	Ham > Mar, Jur
Sargassum fallax—location	3	0.07	0.15	0.931	ns	3	0.03	7.00	**0.003**	Ham > Jur, Mar, Kal

*Values that were significantly different ($p < 0.05$) are indicated in bold (nd, not determined; ns, not significant; Kal, Kalbarri; Jur, Jurien Bay; Mar, Marmion; Ham, Hamelin Bay; Scy, *Scytothalia dorycarpa*; Eck, *Ecklonia radiata*; Sar, *Sargassum fallax*).

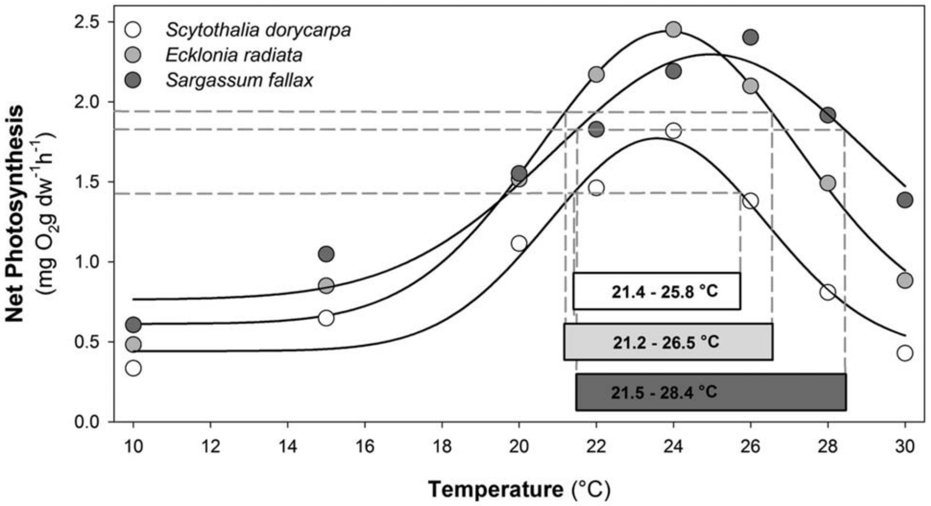

Fig. 4. The breadth of thermal performance of *Scytothalia dorycarpa, Ecklonia radiata*, and *Sargassum fallax* collected from Marmion and Hamelin Bay. The temperature range over which net photosynthesis is at least 80% of maximum net photosynthesis is shown for each species.

determining current and future distribution patterns. For example, an additional 1–2°C warming as predicted for the coming decades (Lough et al. 2012) would cause a substantial decline in performance of *S. dorycarpa* and *E. radiata* but not necessarily in *S. fallax* thus increasing its relative competitive advantage. Moreover, these physiological differences help

Table 3. Chl *a* and *c* concentration (μg g^{-1} dwt) of the three species collected at four locations. Data are mean ± SE ($n = 3$).

Species	Location	Chl *a*	Chl *c*	Chl *a* : Chl *c* ratio
Scytothalia dorycarpa	Marmion	1.95 ± 0.10	1.36 ± 0.07	1.44 ± 0.10
	Hamelin Bay	2.45 ± 0.14	1.45 ± 0.04	1.67 ± 0.05
Ecklonia radiata	Jurien Bay	1.73 ± 0.11	1.30 ± 0.07	1.33 ± 0.15
	Marmion	1.99 ± 0.13	1.39 ± 0.08	1.45 ± 0.16
	Hamelin Bay	2.53 ± 0.04	1.49 ± 0.10	1.71 ± 0.12
Sargassum fallax	Kalbarri	1.82 ± 0. 18	1.57 ± 0.11	1.15 ± 0.13
	Jurien Bay	1.98 ± 0.23	1.59 ± 0.09	1.23 ± 0.07
	Marmion	2.06 ± 0.10	1.65 ± 0.07	1.25 ± 0.11
	Hamelin Bay	2.67 ± 0.13	1.77 ± 0.13	1.51 ± 0.05

Table 4. Results of one-way ANOVA of chlorophyll concentration (μg·g^{-1} dwt) of three species collected at four locations.*

		Chl *a*					Chl *c*				Chl *a* : Chl *c*			
Source		**df**	**MS**	**F**	***p***	**Pair-wise test**	**df**	**MS**	***F***	***p***	**df**	**MS**	***F***	***p***
Kalbarri	species	nd	Nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd
Jurien Bay	species	1	0.09	0.92	0.392	ns	1	0.12	5.44	0.080	1	0.02	0.35	0.585
Marmion	species	1	0.01	0.24	0.796	ns	2	0.08	4.14	0.074	2	0.04	0.70	0.533
Hamelin Bay	species	2	0.04	0.91	0.450	ns	2	0.09	2.70	0.146	2	0.03	1.47	0.302
Scytothalia dorycarpa	location	1	0.37	7.85	**0.049**	Ham > Mar	1	0.01	1.22	0.332	1	0.08	3.87	0.120
Ecklonia radiata	location	2	0.50	15.02	**0.005**	Ham > Jur	2	0.03	1.03	0.411	2	0.11	1.70	0.260
Sargassum fallax	Location	3	0.41	4.77	**0.034**	Ham > Kal	3	0.02	0.71	0.572	3	0.07	3.49	0.070

*Values that were significantly different ($p < 0.05$) are indicated in bold (nd, not determined; ns, not significant; Kal, Kalbarri; Jur, Jurien Bay; Mar, Marmion; Ham, Hamelin Bay).

explain the disappearance of *S. dorycarpa* and *E. radiata* over 100 km coastline from their northern (warm) distribution limits, and the concurrent increase in *Sargassum* spp. abundance during the 2011 marine heatwave (Smale and Wernberg 2013; Bennett et al. 2015b, Wernberg et al. 2016). Interestingly, *E. radiata* and *S. dorycarpa* had similar temperature tolerance and physiological adjustment with latitude (given by their Q_{10}, T_{opt} and reduction rate) yet the distribution of *E. radiata* extends farther north than *S. dorycarpa* and the two species were affected differently by the marine heatwave in Jurien Bay. Where *S. dorycarpa* was completely wiped out *E. radiata* underwent a 40% reduction in percent cover (Wernberg et al. 2013a). These observations are, however, consistent with our analysis of thermal performance breadth which showed a broader tolerance range for *E. radiata* (21.2–26.5°C) than *S. dorycarpa* (21.4–25.8°C) and the outcomes of longer-term growth experiments (Xiao et al. 2015).

Dark respiration increased in response to increasing incubation temperature without a clear optimum in any of the three species. This has also been show for other seaweeds (Stæhr and Wernberg 2009; Tait and Schiel 2013) and could reflect oxygen-dependent thermal tolerance (Zou et al. 2007). The increase in dark respiration rates at temperatures above T_{opt} for photosynthesis would have contributed to the decrease in net photosynthesis, demonstrating how the metabolic costs keep going up whereas metabolic gains decline resulting in a negative balance at higher temperatures. Among the various acclimation hypotheses discussed in Deere and Chown (2006), “colder is better” suits all the three species across the latitudinal gradient of this study characterised by the performance advantage at cooler locations compared to warmer locations where the T_{opt} does not change but the overall performance curve increases.

Seaweeds from cooler locations had higher concentrations of pigments compared to the seaweeds collected from the warmer locations. These effects are not likely to have been caused by systematic differences in light conditions as the latitudinal differences in insolation (~ 8%) are much smaller than variations in light received by individuals within and across sites (~ 25%) caused by differences in collection depth and turbidity, neither of which co-vary with latitude (Stæhr and Wernberg 2009). Cellular concentrations of photosynthetic pigments are known to be directly affected by growth temperature (Davison 1987) and higher concentrations are known to occur in large brown seaweeds in cooler waters or during the winter months (Stengel and Dring 1998; Campbell et al. 1999; Fairhead and Cheshire 2004). In our study, lower rates of photosynthesis in samples collected from warmer locations might be due to the decreasing concentration of Chl *a* which would lower the light harvesting capacity and therefore also the ability to respond to short-term changes in temperature as seen with the decreasing Q_{10} values.

In conclusion, the observed differences in thermal physiology of canopy-forming seaweeds likely contribute to the gradual changes in species distribution and population structure across the latitudinal gradient in Western Australia. Seaweeds that are able to efficiently photosynthesise at slightly higher temperatures and have a broader performance range will have a competitive edge over other species in a warming world, resulting in the extension of their ranges and colonisation of space previously occupied by species unable to cope with warming. Further studies based on long-term experiments will help separate pheno- and geno-typic components of these responses and further improve our understanding of the physiological ecology of these foundation species.

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Conflict of Interest

None declared.

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