THERMAL ECOPHYSIOLOGY OF *LAURENCIA PACIFICA* AND *LAURENCIA NIDIFICA* (CERAMIALES, RHODOPHYTA) FROM TROPICAL AND WARM-TEMPERATE REGIONS¹

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Laurencia is a globally distributed genus with about 80 species (order Ceramiales) that inhabit tropical, subtropical, and warm-temperate regions of both sides of the Atlantic and Indo-Pacific oceans. This study investigated how two species of *Laurencia* distributed in different thermal environments (California and Hawaii) varied in their photosynthetic responses to temperature. The thermal ecophysiology of both species was investigated at different temporal scales (short-term responses and seasonal acclimatization) using oxygen evolution and pulse-amplitude-modulated (PAM) fluorometry. Our results indicated that seasonal acclimatization of both species of *Laurencia* influenced the short-term photosynthetic response at both locations. Greater seasonal differences in the photosynthetic performance were observed for *L. pacifica* Kylin, which reflects the ability of this species to acclimatize to local environmental conditions characterized by short-term fluctuations and a broader annual temperature range. Photosynthetic performance of *L. nidifica* J. Agardh was consistent with the less variable local environment (no short-term fluctuations and a narrower temperature range). These results suggest that acclimatization to temperature variability in the environment can influence the degree of flexibility of physiological responses of species in this genus.

Key index words: acclimatization; photosynthesis; short-term responses; thermal ecophysiology

Abbreviations: F_v/F_m , dark-adapted yield; PAM fluorometry, pulse-amplitude-modulated fluorometry; $P_{net,max}$, maximum net photosynthesis; P-PFD curve, photosynthesis versus photon flux density curve; rETR, relative electron transport rate

On a large spatial scale (equator to the poles), ocean temperatures generally dictate patterns of seaweed distribution (Van Den Hoek 1975, Breeman 1988, Lüning 1990, Druehl 2000). Temperature is a very dynamic factor (McGowan et al. 1998) that can control the rate of photosynthesis (Davison 1991), growth (Gerard and Du Bois 1988), reproduction,

and survival of marine macroalgae (Breeman 1988). Temperature effects on photosynthetic metabolism can be reflected in light-use characteristics (Davison et al. 1991, Kübler and Davison 1995), enzyme activity and concentration (Davison 1987, Davison and Davison 1987, Descolas-Gros and De Billy 1987, Gao et al. 2000), damage to the PSII apparatus (Morris and Kromkamp 2003), electron transport (Kübler and Davison 1993, Eggert et al. 2003, Morris and Kromkamp 2003), and the solubility of the thylakoid membrane (Lynch and Thompson 1984).

Different species and even different populations of a given species may have different optimal temperatures for photosynthesis (Davison 1991) and growth (Breeman 1988). In addition, different life stages may possess different thermal tolerances that can limit distribution and abundance over time (Lüning 1990). Temperature tolerance of seaweeds can depend on genetic adaptation and on the ability to acclimatize to temperature fluctuations (Kübler et al. 1991).

The range of temperatures experienced by algae can vary both spatially and temporally at different scales. A few species of seaweeds may tolerate a wide range of environmental conditions and are distributed worldwide. Algae with a broader biogeographic range are thought to acclimatize (change in response to environmental fluctuation) better than seaweeds from habitats with narrower temperature ranges (Dawes 1989).

Previous studies have examined the thermal acclimation (phenotypic change occurring under laboratory conditions) between ecotypes (Gerard and Du Bois 1988, Pakker et al. 1996, Eggert et al. 2003) and closely related species of algae (Dawes 1989, Kübler et al. 1991, Breeman et al. 2002, Eggert et al. 2003) from environments with different temperature regimes. These studies have shown that adaptation to the local temperature conditions can strongly influence the temperature tolerance of these species. For instance, individuals exposed to larger temperature differences between summer and winter generally have greater thermal tolerance.

Laurencia is a globally distributed genus with about 80 species, inhabiting tropical, subtropical, and warm-temperate regions (Lüning 1990) and distributed commonly in the lower intertidal and subtidal zones (Abbott and Hollenberg 1976, Abbott 1999). This study investigates how two

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species of *Laurencia* distributed in different thermal environments vary in their seasonal photosynthetic responses to temperature. California and Hawaii are locations where *Laurencia* is common; approximately 13 species of *Laurencia* are found in California (Abbott and Hollenberg 1976), and at least 17 species are present in the Hawaiian Islands (Abbott 1999). For this study, we chose one species of *Laurencia* that represented native (i.e., nonintroduced) species from each location. *Laurencia pacifica* is distributed from the Monterey Peninsula, California, to Isla Magdalena, Baja California (type locality: La Jolla, CA; Abbott and Hollenberg 1976). Thalli are erect, between 6 and 16 cm tall, and with cylindrical branches 2 mm in diameter. *Laurencia nidifica* is widely distributed in tropical and subtropical zones of the Pacific and Indian oceans (type locality: Oahu, HI; Abbott 1999). The thalli are erect, up to 10 cm tall, and also with cylindrical axes that are 0.5–1 mm in diameter. The genus *Laurencia* is a broadly distributed genus with several species encountering extremely different environments. Specifically, we examined the photosynthetic response to temperature, thermal limits of photosynthesis, and the capabilities of each species to respond to seasonal temperature fluctuations in their respective environments. The following questions were addressed: (i) Does the short-term photosynthetic response to temperature differ between *L. pacifica* (from California) and *L. nidifica* (from Hawaii)? (ii) Does this response differ between seasons for either species? (iii) Is there a relationship between the phenotypic plasticity displayed and thermal variability experienced for either species?

The thermal ecophysiology of these two species was investigated at different temporal scales (short-term response and seasonal acclimatization, which is the phenotypic change under environmental conditions) using oxygen evolution and pulse-amplitude-modulated (PAM) fluorometry. The use of both techniques allowed a quantification of the phenotypic changes at different levels of the photosynthetic process. Oxygen evolution is an overall measure of the light-dependent reactions of photosynthesis. Measures using PAM fluorometry indicate the efficiency of PSII photochemistry, electron transport rate (ETR), and maximum quantum efficiency of PSII [dark-adapted yield (F_v/F_m)], which is a sensitive indicator of photosynthetic performance (Maxwell and Johnson 2000).

MATERIALS AND METHODS

Study sites. Algal collection and physiological experiments were performed at Santa Catalina Island (California), located in the warm-temperate NE Pacific region (33°27' N, 118°30' W), and Kaneohe Bay (Oahu, HI), located in the tropical Indo-West Pacific region (19°43' N, 155°4' W). Santa Catalina Island is characterized by a broader seawater temperature range (14°C–21°C). Kaneohe Bay has a narrower temperature range (24°C–28°C) with lower temperature variability throughout the year.

Laurencia spp. were collected from a depth of 2–3 m in both locations during summer (2003) and winter (2004). Although we did not differentiate between tetrasporophytes and gametophytes, we believe that tetrasporophytes were mostly used in the experiments, as this stage is the dominant phase and gametophytes are rarely found in these locations (J. L. Padilla-Gamiño and K. A. Miller, personal observation; Abbott 1999). *Laurencia pacifica* was collected from Big Fisherman's Cove and Bird Rock (a small bedrock island located north of Big Fisherman's Cove). *Laurencia nidifica* was collected from the Kaneohe Bay barrier reef flat.

Photosynthetic performance. Physiological experiments were performed when field temperatures were close to the minimum and maximum values within the annual temperature range (August and September during summer, and January and February during winter). Oxygen evolution and chl fluorescence were used to estimate the physiological performance (photosynthesis and respiration) at six different temperatures (10, 15, 20, 25, 30, and 35°C). These temperatures were chosen to represent a range that encompassed, but was broader than, the environmental conditions in both locations.

At least 12 h prior to measuring the physiological performance, pieces were cut from fresh algae (sections 1 cm long, approximately 2–3 cm below branch apices) and returned to sea tables to allow wound healing. Respiration rates after excision were used to assess the timing of wound healing. Preliminary studies showed that respiration was highly variable immediately after wounding, but relatively consistent after ~4–5 h. Independent sections (from different thalli) were used for the physiological experiments ($n = 5$ –10 per temperature treatment).

First, the sections of thalli were exposed in the dark (for 1 h) to one of the experimental temperatures in a temperature-controlled water bath. Then, algae were transferred to a Clark-type oxygen electrode system (Rank Brothers, Botolphsham, England) at the same temperature, and dark respiration was estimated by recording changes in dissolved oxygen for 5 min. Dark-adapted yield (F_v/F_m) was obtained after the respiration measurements using a PAM fluorometer (Model 210, Walz, Effeltrich, Germany). After measuring F_v/F_m , a photosynthesis versus photon flux density (P-PFD) curve was estimated (5 min incubation at each light level). An actinic lamp provided the light source for the seven PFD levels (10, 20, 50, 100, 200, 500, and 1000 $\mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) used to estimate the P-PFD curve, and a fiber-optic quantum sensor of an underwater fluorometer (Diving PAM, Walz) was used to measure PFD inside the incubation chamber. Oxygen evolution was measured for 5 min using an A/D card (Cyber-Research, Branford, CT, USA) at a sampling rate of 0.2 Hz. After the P-PFD curve was recorded, the algal sample was placed in the dark (at the experimental temperature) for 5 min and then transferred back to the incubation chamber to obtain the ETR. A PAM fluorometer (Model 210, Walz) was used to estimate the ETR curve using 11 PFD levels (1 min. duration at each PFD). Absorption factors were difficult to estimate due to the complexity of the thallus structure of *Laurencia* spp.; therefore, ETR was expressed as the relative electron transport rate ($\text{rETR} = \text{yield} \cdot \text{PAR}$) when yield (Φ_{PSII}) was > 0.1 (Beer and Axelsson 2004). Filtered seawater (filter size: 1–5 μm ; General Electric, Louisville, KY, USA) and flow inside the chamber (provided by a magnetic stirrer) were used to obtain all the physiological measurements. To correct for bacterial respiration and electrode oxygen consumption, control incubations were performed between samples.

Photosynthetic pigment composition. Freshly collected algal samples were used to estimate photosynthetic pigment concentrations from each site in both seasons ($n = 10$ –30 for each site and season). Chlorophyll *a* and accessory pigments were

extracted from two samples from each thallus (sections 1–2 cm long). For chl extractions, samples were ground using a mortar and pestle with 90% acetone and an MgCO_3 solution. Phycobiliprotein samples were ground with a cold phosphate buffer (Beer and Eshel 1985). After extraction in the dark for 24 h at 4°C, absorbance at the appropriate wavelengths of each extract was quantified using a spectrophotometer (Beckman DU-600, Beckman Instruments, Fullerton, CA, USA), and photosynthetic pigment concentrations were estimated according to the equations of Jeffrey and Humphrey (1975) for chl, and Beer and Eshel (1985) for phycobiliproteins.

Data analysis. From the P-PFD curves, maximum net photosynthesis ($P_{\text{net,max}}$) and photosynthetic efficiency at low light intensities (α) were estimated. The $P_{\text{net,max}}$ ($\text{mg O}_2 \cdot \text{g DM}^{-1} \cdot \text{h}^{-1}$) was the value obtained at saturating PFD ($>500 \mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$). Photosynthetic efficiency [$\text{mg O}_2 \cdot \text{g DM}^{-1} \cdot \text{h}^{-1} / (\mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1})$], or the initial slope of the P-PFD curve, was estimated by fitting a linear regression to the initial values of the P-PFD curve. A hyperbolic tangent nonlinear regression model developed by Jassby and Platt (1976) was used to estimate the maximum $r\text{ETR}_{\text{max}}$.

To evaluate the effects of season (fixed factor) and temperature (fixed factor) on $P_{\text{net,max}}$, respiration, α , dark-adapted yield, and $r\text{ETR}_{\text{max}}$, a two-way analysis of variance (ANOVA) was used. Data from pigment extractions were log-transformed, and a *t*-test was used to analyze seasonal differences in chl *a* and accessory pigment content for each species at each site.

RESULTS

Photosynthetic performance. A characteristic photosynthesis-temperature response was observed for values of $P_{\text{net,max}}$ of both species of *Laurencia*. The $P_{\text{net,max}}$ increased progressively with increasing temperature up to an optimum temperature, beyond which it decreased quickly. Within their respective environmental temperature ranges, *L. pacifica* from California had higher rates of $P_{\text{net,max}}$ ($\sim 7 \text{ mg O}_2 \cdot \text{g DM}^{-1} \cdot \text{h}^{-1}$) than *L. nidifica* from Hawaii ($\sim 3 \text{ mg O}_2 \cdot \text{g DM}^{-1} \cdot \text{h}^{-1}$) during the summer (Fig. 1, a and b). In the winter, however, similar values were observed for both species (~ 2 – $3 \text{ mg O}_2 \cdot \text{g DM}^{-1} \cdot \text{h}^{-1}$). The relationship between $P_{\text{net,max}}$ and temperature varied between seasons only for *L. pacifica* (Table 1), which acclimatized within the temperature range in the field (14°C–21°C). Within this range, higher values of $P_{\text{net,max}}$ for *L. pacifica* were measured in the summer than in the winter. There was no evidence of seasonal acclimatization within the range of field temperatures (24°C–28°C) for *L. nidifica*.

In general, values of photosynthetic efficiency (α) did not show a distinctive pattern across temperatures (Fig. 1, c and d). Values of α for *L. pacifica* were higher and more variable during summer than winter. There was no effect of seasonal differences across temperatures on the photosynthetic efficiency of *L. pacifica* ($P > 0.05$; Table 1), but the independent effect of season was significant (Table 1). In contrast, the relationship between α and temperature varied between seasons for *L. nidifica* (Table 1; Fig. 1). For both species, α decreased at temperatures above 30°C during the winter.

FIG. 1. Short-term temperature response of (a,b) maximum net photosynthesis ($P_{\text{net,max}}$; $\text{mg O}_2 \cdot \text{g DM}^{-1} \cdot \text{h}^{-1}$), (c, d) photosynthetic efficiency (α ; $\text{mg O}_2 \cdot \text{g DM}^{-1} \cdot \text{h}^{-1} / [\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}]$), and (e, f) respiration ($\text{mg O}_2 \cdot \text{g DM}^{-1} \cdot \text{h}^{-1}$) of *Laurencia pacifica* and *Laurencia nidifica* during summer and winter. Error bars indicate ± 1 SE from the mean ($n = 5$ – 10 at each temperature). Areas between dotted vertical lines represent annual temperature ranges at the collection sites. DM, dry mass.

TABLE 1. Two-way ANOVA of maximum net photosynthesis ($P_{\text{net,max}}$; $\text{mg O}_2 \cdot \text{g DM}^{-1} \cdot \text{h}^{-1}$), photosynthetic efficiency (α ; $\text{mg O}_2 \cdot \text{g DM}^{-1} \cdot \text{h}^{-1} / \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), and respiration ($\text{mg O}_2 \cdot \text{g DM}^{-1} \cdot \text{h}^{-1}$) of *Laurencia pacifica* (California) and *Laurencia nidifica* (Hawaii) during summer and winter.

Source	<i>Laurencia pacifica</i>			<i>Laurencia nidifica</i>		
	df	F-ratio	P-value	df	F-ratio	P-value
$P_{\text{net,max}}$						
Temperature	5	45.55	<0.01	5	63.09	<0.01
Season	1	34.97	<0.01	1	17.82	<0.01
Temp $\times$ seas	5	12.68	<0.01	5	3.48	<0.01
Error	85			103		
α						
Temperature	5	0.67	0.64	5	19.00	<0.01
Season	1	12.97	0.01	1	25.13	<0.01
Temp $\times$ seas	5	0.93	0.47	5	4.89	<0.01
Error	88			103		
Resp.						
Temperature	5	20.45	<0.01	5	21.23	<0.01
Season	1	0.03	0.87	1	5.46	<0.05
Temp $\times$ seas	5	3.25	<0.01	5	0.33	0.91
Error	89			92		

Analysis of dark-adapted yield values for *L. pacifica* and *L. nidifica* revealed a significant interaction term (Table 2), indicating that seasonal acclimatization influenced the responses across temperatures. The F_v/F_m values for *L. pacifica* were different between seasons across all experimental temperatures, with larger F_v/F_m values obtained in summer (Fig. 2, a and b; Table 2). The F_v/F_m values of *L. nidifica* did not differ between seasons or temperatures, except at 35°C (indicating warm acclimatization). For both species, F_v/F_m generally began decreasing at 30°C and drastically decreased at 35°C.

Seasonal acclimatization of $rETR_{\max}$ (Fig. 2, c and d) was evident for both species (Table 2). Patterns of $rETR_{\max}$ across temperatures for *L. pacifica* (Fig. 2, c and d) were similar to those of $P_{\text{net}_{\max}}$ and F_v/F_m . Values of $rETR_{\max}$ were higher in summer than in winter across all temperatures (except 10°C). Values of $rETR_{\max}$ for *L. nidifica* within the field temperature range were higher during winter than during summer (Fig. 2). For both species (except *L. nidifica* in the summer), $rETR_{\max}$ decreased above 25°C. At extreme cold temperatures, $rETR_{\max}$ did not differ between seasons (10°C for *L. pacifica* and 10°C–15°C for *L. nidifica*).

Respiration values did not differ across temperatures until high values were reached (30°C–35°C); at these temperatures, an increase in respiratory rates was observed (Fig. 1, e and f), reaching ~4 and 1.5 mg O₂·g DM⁻¹·h⁻¹ (*L. pacifica* and *L. nidifica*, respectively). The relationship between respiration rates and temperature for *L. pacifica*

TABLE 2. Two-way ANOVA of dark-adapted yield (F_v/F_m), maximum relative electron transport rate ($rETR_{\max}$), and minimal level of fluorescence (F_0) of *Laurencia pacifica* (California) and *Laurencia nidifica* (Hawaii) during summer and winter.

Source	df	<i>Laurencia pacifica</i>		df	<i>Laurencia nidifica</i>	
		F-ratio	P-value		F-ratio	P-value
F_v/F_m						
Temperature	5	43.986	<0.001	5	63.549	<0.001
Season	1	103.674	<0.001	1	2.155	0.145
Temp × seas	5	4.249	0.002	5	6.622	<0.001
Error	81			101		
$rETR_{\max}$						
Temperature	5	30.138	<0.001	5	56.712	<0.001
Season	1	71.279	<0.001	1	2.655	0.106
Temp × seas	5	6.178	<0.001	5	4.007	0.002
Error	95			103		

varied significantly between seasons (Table 1). No evidence of this relationship was determined for *L. nidifica*, but significant effects of temperature and season were detected (Table 1).

Photosynthetic pigment composition. Chlorophyll *a* content for *L. pacifica* and *L. nidifica* did not differ significantly between winter and summer (Table 3). Phycocyanin (PC) and allophycocyanin (APC) concentrations for *L. pacifica* were significantly higher in summer than in winter (PC: $t = 7.52$, $df = 24$, $P < 0.001$; APC: $t = 2.46$, $df = 24$, $P < 0.05$; Table 3). Phycoerythrin (PE) concentrations, however, did not differ between seasons for *L. pacifica* (Table 3). Concentrations of all phycobiliproteins of *L. nidifica* were significantly higher in winter than in summer (Table 3).

DISCUSSION

Short-term responses between seasons. Seasonal acclimatization and short-term responses were observed for different aspects of photosynthetic metabolism ($P_{\text{net}_{\max}}$, α , F_v/F_m , and $rETR_{\max}$). Our results indicate that seasonal acclimatization of both species of *Laurencia* influences the short-term photosynthetic response.

Laurencia pacifica had significantly higher values of $P_{\text{net}_{\max}}$, F_v/F_m , and $rETR_{\max}$ during summer (ambient temperature 21°C) than during winter (ambient temperature 14°C), and in most cases, maximum values of these parameters were observed between 20°C and 30°C. This discrepancy of having the maximum photosynthetic temperature outside the normal environmental temperature range also has been shown in other studies of algae growing in colder regions (Lüning 1990). Seaweeds from polar regions often have photosynthetic maxima well above normal environmental temperatures (Lüning 1990, Tang and Vincent 2000). Drew (1977) demonstrated that the optimum temperature for photosynthesis of *Himantothallus grandifolius* (A. Gepp et E. S.

FIG. 2. Short-term temperature response of (a, b) dark-adapted yield (F_v/F_m) and (c, d) relative electron transport rate ($rETR_{\max}$) of *Laurencia pacifica* and *Laurencia nidifica* during summer and winter. Error bars indicate ± 1 SE from the mean ($n = 5-10$ at each temperature). Areas between dotted vertical lines represent annual temperature ranges at the collection sites.

TABLE 3. Photosynthetic pigment content of *Laurencia pacifica* and *Laurencia nidifica* between different seasons.

Pigments	<i>Laurencia pacifica</i>		<i>Laurencia nidifica</i>	
	Summer (n = 10)	Winter (n = 17)	Summer (n = 30)	Winter (n = 14)
Chl <i>a</i>	2598 ± 183 ^{ns}	2214 ± 94 ^{ns}	1279 ± 65 ^{ns}	1146 ± 64 ^{ns}
PC	11.727 ± 0.726 ^a	6.368 ± 0.335 ^b	7.807 ± 0.415 ^a	10.193 ± 0.705 ^b
APC	5.284 ± 0.429 ^a	4.129 ± 0.202 ^b	5.024 ± 0.303 ^a	6.576 ± 0.549 ^b
PE	16.029 ± 0.714 ^{ns}	15.442 ± 0.532 ^{ns}	9.937 ± 0.411 ^a	13.136 ± 0.808 ^b

Values are means ± SE. Chl *a*, chlorophyll *a* ($\mu\text{g} \cdot \text{g DM}^{-1}$); PC, phycocyanin ($\text{mg} \cdot \text{g DM}^{-1}$); APC, allophycocyanin ($\text{mg} \cdot \text{g DM}^{-1}$); PE, phycoerythrin ($\text{mg} \cdot \text{g DM}^{-1}$). Different superscripts represent significantly different pigment concentrations between seasons ($P < 0.05$); ns, not significant.

Gepp) *Zinova*, *Desmarestia anceps* Mont., and *Palmaria decipiens* (Reinsch) R. W. Ricker is 15°C, a temperature higher than that experienced in Antarctic waters.

Light-harvesting efficiency (α) was extremely variable for *L. pacifica* in the summer and generally not affected by short-term changes in temperature (except for a decrease at temperatures above 30°C during the winter for both species). Seasonal acclimatization influenced the values of α for *L. pacifica*; higher values were observed during the summer than in the winter. The increase in α during summer could be attributed in part to an increase in PC and APC (light-harvesting accessory pigments), which reflect alterations in the photosynthetic unit (PSU) size. Acclimation to increased growth temperature has been related previously to increased photosynthetic pigment content. In the kelp *Laminaria*, these changes in pigment content also have been associated with changes in photosynthetic efficiency (Davison et al. 1991). In this study, both species of *Laurencia* showed seasonal differences in phycobiliprotein content. However, these differences were not attributed only to seasonal differences in temperature; thus the seasonal acclimatization of pigment content of this species may reflect a covariation in temperature and other factors, such as photoacclimation to different PFD, day length (Falkowski and Raven 1997), and nutrient availability (Zimmerman and Kremer 1984). Algal densities and sizes of *L. pacifica* at Santa Catalina Island increased during the summer (J. L. Padilla-Gamiño, personal observation), and it is possible that in a denser mat, self-shading of thalli could lead to higher phycobilisome number and/or size. In contrast, *L. nidifica* from Kaneohe Bay did not show dramatic changes in size or density between seasons.

Both species exhibited a similar response above 30°C, where a drastic decline in all photosynthetic parameters was observed. Reduction of $P_{\text{net,max}}$ at high temperatures (25°C–30°C) can be attributed to an increase in respiratory rates. However, response of $P_{\text{net,max}}$ to cold temperatures was not dependent on respiration. The effect of temperature on seasonal acclimatization of respiration was observed only at temperatures above 25°C for *L. pacifica* and above 30°C for *L. nidifica*. When measured within

the local temperature ranges, respiration rates for both species did not differ between seasons. At warm temperatures (above 25°C), respiration rates of *L. pacifica* were higher than those for *L. nidifica*. Differential effects of temperature on respiration were measured by Davison et al. (1991) when they acclimated sporophytes of the kelp *L. saccharina* (L.) J. V. Lamour. at high and low temperatures. Lower respiration rates were observed in warm-acclimated algae (15°C), which also were less sensitive to changes in assay temperature than cold-acclimated algae (5°C). This suggests that warm acclimatized algae can increase the amount of fixed carbon available for growth (at higher temperatures) owing to a reduction in losses of fixed carbon during the dark period (Davison 1991).

Phenotypic plasticity and temperature variability. To assess how future temperature stresses due to climate change may impact the distribution of organisms and their physiological status, it is important to define environmental optima and tolerance limits for different physiological processes (Somero 2000, 2002). By comparing two closely related species, we were able to quantify the phenotypic plasticity of these species from locations with different thermal fluctuations.

Subtidal populations of *L. pacifica* at Santa Catalina Island experience a temperature range between 14°C and 21°C and shorter-term changes in temperature related to monthly temperature variability. At this site, temperature can drop by 3°C in 3 d, and short-term decreases of 3°C every 4 h occur (Zimmerman and Robertson 1985). In contrast, subtidal populations of *L. nidifica* in the Kaneohe Bay barrier reef flat experience a narrower range between 24°C and 28°C, and no short-term fluctuations of temperature occur (Bathen 1968).

Seasonal differences in photosynthetic performance were more pronounced for *L. pacifica*. This species had a greater tolerance for cold temperatures and demonstrated significant changes in photosynthetic performance between seasons. These physiological responses reflect the ability of *L. pacifica* to withstand temperature fluctuations at different time scales. The weaker seasonal acclimatization of *L. nidifica* may reflect a more general-purpose genotype for local conditions with a narrower temperature range (Lynch 1984).

Short-term photosynthetic responses were useful to compare the phenotypic plasticity and physiological characteristics within and outside the range of temperatures to which both species are normally exposed. However, these short-term responses do not necessarily reflect the upper and lower limits for survival, growth, and reproduction of these species (Breeman 1988, Lüning 1990, Kübler et al. 1991, Eggert et al. 2003). The gametophyte stage of *Laurencia* may have different acclimatization capabilities and/or thermal tolerances. In both locations, tetrasporophytes were more common, which suggests that gametophytes are restricted by physical and/or biotic factors at these two sites. Furthermore, both species of *Laurencia* used in this study can also be distributed in the low intertidal at the study sites (Abbott and Hollenberg 1976, Abbott 1999), which can be exposed to rapid and extreme fluctuations in temperature twice daily because of semidiurnal tidal emersion. Future studies are required to understand the effects of these thermal fluctuations on *Laurencia* spp. Sudden increases in temperature (due to tidal immersion/emersion) affect photosynthesis of the ecologically and economically important red alga *Chondrus crispus* Stackh. (Kübler and Davison 1993). Algae acclimated to summer seawater temperatures were able to tolerate extreme temperatures better than those acclimated to winter temperatures. The ability of *C. crispus* to photosynthesize at high temperatures enables it to survive extreme temperatures for limited periods of time and recover from stress on reimmersion.

CONCLUSION

Our results demonstrate that seasonal acclimatization influences the thermal responses of the photosynthetic performance of both species. However, acclimatization was greater in individuals exposed to greater thermal variability (*L. pacifica*). Because thermal acclimatization may be a common phenomenon in photosynthetic organisms (Kübler and Davison 1995), future studies assessing changes in biogeographic distribution owing to natural and/or anthropogenic thermal fluctuations should recognize that temperature may influence species in different ways depending on their acclimatization capabilities. The results of this study suggest that *L. nidifica* (a tropical alga) may be more impacted by changes in local temperature than *L. pacifica* (a temperate alga) because it has a narrower temperature tolerance, lives closer to its upper thermal limits, and has less acclimatization potential.

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