Functional responses of juvenile kelps, Laminaria ochroleuca and Saccorhiza polyschides, to increasing temperatures

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A B S T R A C T
We tested the ability of juvenile sporophytes of two coexisting kelps native to Portugal, Laminaria ochroleuca and Saccorhiza polyschides, to adjust their photosynthesis and respiration to increasing sea water temperatures. These responses were measured for S. polyschides from both the subtidal and the intertidal habitat, and for L. ochroleuca from the intertidal habitat. L. ochroleuca showed a reduced ability to acclimatize to changing conditions, whereas S. polyschides demonstrated a larger physiological flexibility. These findings are connected with the life-history traits of these species. Additionally, optimum temperatures for the primary production of kelps were assessed, indicating higher values for inter- than subtidal S. polyschides. Significant physiological differences between inter- and subtidal S. polyschides were observed, based on metabolic rates of primary production and dark respiration. This study suggests that, under a warming climate scenario, responses can significantly vary for each species, and that L. ochroleuca is more susceptible to ocean warming than S. polyschides, due to larger acclimatization capacity of the latter.

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1. Introduction

Although environmental effects of climate change are complex and diverse, there is general consensus on increasing atmospheric and sea surface temperatures (SST) over the past decades. Anthropogenic activities, such as greenhouse gas emissions, are mostly considered responsible for a global average increase of SST in the last century of 0.6 ± 0.2 °C (IPCC, 2007). The rate of warming is not constant throughout the globe, creating high risk areas, which include polar and cold-temperate regions. For example, SST has risen at a mean rate of 0.27 ± 0.13 °C per decade in the eastern Atlantic since 1982, which is more than the global average (Lima and Wethey, 2012); importantly, the IPCC (2007) predicts a rise in temperature between 2 °C and 4 °C in the northeast Atlantic by 2100.

The increase of temperature is potentially the most important change occurring in the oceans in the last decades, as it influences physiological and ecological processes at all biological levels, from genes to ecosystems (Kordas et al., 2011; Smale et al., 2011). In addition to a gradual increase in temperature, a key element of climate change is an increase in climate variability; more specifically, an increase in the frequency and magnitude of warming events (e.g. Lima and Wethey, 2012; Wernberg et al., 2013). Effects of temperature changes on communities and ecosystems are well known for terrestrial plants and pelagic systems (e.g. Parmesan, 2006), while relatively few studies have explicitly examined effects of global warming on coastal marine communities (Wernberg et al., 2012). Among all studies on climate-related changes in natural communities, on the expected biological responses to temperature increases and on the eco-physiological mechanisms behind these, only 5% refer to marine systems. Nevertheless, recent studies have indicated that one of the main consequences of rising ocean temperature is distributional range shifts of species worldwide (O’Connor et al., 2012). Cases of latitudinal shifts of rocky shore species have been documented in Europe, along the Atlantic and Pacific coasts of North America and in the southern hemisphere (Lima et al., 2007; Wernberg et al., 2011). These were considered as primarily driven by changes in patterns of recruitment and survival of populations that are strongly affected by temperature (Barry et al., 1995).

Kelp beds are key organisms across temperate rocky shores in both hemispheres (Steneck et al., 2002). Being cool-water adapted species, they are particularly sensitive to sea temperature rise, which can negatively affect their growth, survival, reproduction and recruitment (Wernberg et al., 2010). In the northern hemisphere and under predicted warming, such effects may lead to further decreases in abundance of kelp species at their southern range edges and to their retreat northward in the near future. For
example, a trend northward shifts of kelp distribution in the past decades is supported by local communities’ awareness, through personal and anecdotic observations, along the entire Portuguese coastline (Assis et al., 2009). Abundant and dense kelp beds that were present along the Portuguese coast in previous decades (Ardré, 1971) are currently reduced to patches with irregular distribution (Assis et al., 2009) and almost restricted to northern Portugal (Tuya et al., 2012). As ‘foundation species’ in temperate regions (Wernberg et al., 2010), kelps play a crucial role in primary production and habitat provision for associated biota. Moreover, the ecological function of kelp beds might be amplified in the future, as they were shown to be able to buffer the negative effects of climate-related disturbance and mitigate environmental stress (Bertocci et al., 2010; Wernberg et al., 2010). As a result, conservation of the marine environment and possible mitigation of climate change will critically depend on understanding the response mechanisms of these species to future environmental scenarios (Wernberg et al., 2012).

When exposed to environmental conditions outside their normal physiological range, populations of macroalgae can react in one of four possible ways: migration (dispersal toward a more favorable area), adaptation (selection of the phenotypic traits of individuals that match the new environment), extinction (algae are not capable to migrate and/or to adapt; therefore, the species becomes extinct) (Clarke, 1996), or acclimatization (the organism adjusts its physiological or morphological traits to gradual changes of the environment, which leads to increased tolerance) (O’Connor et al., 2012). Persistence of kelp beds is often achieved through acclimatization, which in contrast to adaptation does not involve genetic differentiation within species, but occurs within a lifetime of an individual (Wernberg et al., 2010). When exposed to altered environmental conditions, kelps may demonstrate resilience by altering their metabolic responses or undergoing structural changes and adjusting physiological processes in order to maintain efficiency. In this process, organisms show a certain flexibility of their metabolism, which is however possible only to a limited extent of environmental changes, e.g. temperature rise (Wernberg et al., 2010). Nevertheless, this process can have costs in terms of offsetting some physiological constrains of kelps, including, for example, a lower resilience of adults to concomitant perturbations, or a reduced ecological performance of recruits (Staehr and Wernberg, 2009; Wernberg et al., 2010). As a consequence, exposure to elevated temperatures, although buffered by acclimatization, will increase the sensitivity of kelps to other concomitant sources of environmental pressure, such as extreme storms or reduced water quality (Roleda and Dethleff, 2011; Wernberg et al., 2013). In addition, some species are more vulnerable than others (Roleda, 2009; Roleda et al., 2010), due to their limited acclimatization capabilities, which eventually will lead to distributional range shifts and substantial changes in local communities (Graham, 2004). For example, when acclimatization cannot buffer the negative effects of environmental pressure, retreat and migration occurs, as documented for some kelp populations on the northern coast of Spain (Fernández, 2011).

The coast along continental Portugal has overlapping distributions of species of both boreal and Lusitian origins (Lima et al., 2007; Tuya et al., 2012) and is included within the South European Atlantic Shelf ecoregion. A large number of cold- and warm-water marine species have their southern or northern distributional range edges along this stretch of coastline (Lima et al., 2007), while other species show latitudinal clines in abundance (Boaventura et al., 2002; Tuya et al., 2012).

The life cycle of kelps is composed of two altering stages: a microscopic, haploid gametophyte and a macroscopic, diploid sporophyte. Mature sporophyte produces spores, which, after settling on a substrate, develop into either male or female haploid gametophytes. Male gametophytes produce sperm cells and female gametophytes egg cells. After fertilization, these create a zygote that develops into a new diploid sporophyte that starts a new cycle (Pereira et al., 2011). Based on the life span of the sporophyte, kelp species can be identified as annual or perenniannual (perennial) (Birkett et al., 1998; Pereira et al., 2011). Saccorhiza polyschides (order: Tilipteridales, family: Phyllariaceae), which is the most abundant kelp in southern Europe (Raffaelli and Hawkins, 1996), is an annual seaweed. Its sporophyte grows quickly in spring and summer and start decaying in autumn. Most individuals are detached from the rocky substrate during winter storms. In contrast, Laminaria ochroleuca (order: Laminariales, family: Laminariaceae) is a pluriannuall alga, with a life cycle that can span up to 18 years, becoming fertile after 2–6 years (Birkett et al., 1998).

The aim of this study was to test the effects of increasing sea water temperature on the physiological performance of juvenile sporophytes of the native kelps, *L. ochroleuca* and *S. polyschides*, from continental Portugal. We expected that kelps would show an increase in physiological responses with increasing temperatures. Furthermore, we investigated possible variation in these responses between both kelp species from the intertidal and between inter- and subtidal sporophytes of *S. polyschides*. We expected some variability in physiological responses between these two kelp species and between habitats, due to differences in optimal temperatures, life cycles and distribution of both kelps, and different conditions between the inter- and subtidal. Changes in metabolic rates caused by increasing temperature were expected to be higher for *S. polyschides* than *L. ochroleuca*, due to the annual life cycle of the former species. Furthermore, we expected differences in metabolism sensitivity between inter- and subtidal *S. polyschides*, where the former was expected to be less affected by adverse abiotic changes (here, SST increases), because of the natural exposure to the harsher conditions of the intertidal.

2. Materials and methods

2.1. Distribution range of kelp species

The distribution range of *S. polyschides* stretches from the west coast of Norway, through the British Isles, extending along the western coast of the Iberian Peninsula, with the southern limit located in the warm–temperate waters of the Moroccan coast (Birkett et al., 1998; Pereira et al., 2011). The distribution range of *L. ochroleuca* stretches from the British Isles in the north to the Moroccan coast in the south (Birkett et al., 1998; Pereira et al., 2011), where it shares the southern distribution limit with *S. polyschides* (Pereira et al., 2011).

2.2. Collection of algal material

Juveniles (20–25 cm of total length) of *L. ochroleuca* (*n* = 108) and *S. polyschides* (*n* = 108) were collected from low intertidal areas (between 0 m and 0.20 m above Chart Datum) and shallow subtidal rocky reefs (3–8 m depth) for *S. polyschides* (*n* = 108), along about 20 km of coastline in northern Portugal (southernmost point of sampling: 41°37′6″ N 8°49′4″ W and northernmost: 41°47′2″ N 8°53′6″ W) between 21st of March and 2nd of April 2012. The sea water temperature at the sampling locations was around 12–13°C (Aqua MODIS SST, NASA). Collected algal material was transported to the laboratory and kept in a tank (300 l capacity, protected from excess of sun light) with aerated sea water at around 12°C. Every two days, 30 ml of a macro-nutrients solution (NO<sub>3</sub>−, PO<sub>4</sub>−) were added to provide conditions without nutrient-limited stress.
2.3. Productivity and respiration

Primary productivity was determined by measurement of the concentration of dissolved O₂, using whole juvenile plants in a temperature-controlled incubation unit, with 400 W Halogen Osram® bulbs and neutral filters. The incubator allowed simultaneous and independent measurements on algal material exposed to six light intensities (0, 30, 90, 210, 710 and 1445 µEinsteins m⁻² s⁻¹), covering an entire PAR light range, from light-limited conditions (dark incubation) to photo-inhibition; this allowed to plot conventional photosynthesis–irradiance curves. All algal material was given a short period of ~15 min of aclimatisation in the incubation tank before measurements under selected temperatures: 5, 10, 15, 20, 25 and 30 °C, representative of the range of temperatures normally experienced by kelps in this region during an annual cycle (Tuya et al., 2012) and two extremes: 5 and 30 °C. Pre-cooled, or pre-warmed, water was used for each incubation; all incubations were done using filtered seawater (1 and 5 µm) to avoid the influence of phytoplankton photosynthesis on final results and 3 individual plants – replicates – were used for incubations for each species and temperature. Changes in O₂ concentrations were measured continuously using a multi HQ40D (Hach Lange®) oxygen probe for each incubation, which had a duration of ~20 min. After the incubations, seaweeds were oven-dried at 45 °C for 48 h and the dry weight recorded. All data from the oxygen probes was corrected with the algal dry weight (DW) and the volume of the incubation tank to express all functional response variables per g DW of algae 1⁻¹ h⁻¹ (Staehr and Wernberg, 2009). To be able to discard possible procedural artifacts we performed additional blind incubations to examine respiration/production rates in the filtered seawater used in our incubations and found negligible values.

The maximum rate of gross productivity (GPₚₓᵢₐₓ) was calculated by adding the absolute value of respiration (Rₓ) to values recorded for net primary productivity from all light intensities. Three additional parameters were determined by non-linear regression of gross photosynthesis (GPP) normalized by dry weight (DW) and irradiance (E), according to the model of Eilers and Peeters (1993):

\[
GPP = \frac{GP_{\text{max}} 2(1 + \beta)(E/E_{\text{opt}})}{2E/E_{\text{opt}} + 1}
\]

where \(GP_{\text{max}}\) is the maximum productivity at selected irradiance and temperature, \(E_{\text{opt}}\) is the optimum light intensity and, in case of photo-inhibition due to excess of light, the slope of photo-inhibition (β) was also determined (modeled with the R v2.15.0 open software, The R Foundation for Statistical Computing 2012).

Furthermore, the light saturated gross productivity (\(GP_{\text{max}}\)) dependency on temperature was plotted through piecewise regression (‘segmented’ package, R v2.15.0). This model determines the ‘breakpoint’ of the regression, which is the optimum temperature (\(T_{\text{opt}}\)) for photosynthesis, and its initial slope (Muggeo, 2008). However, algorithms used by the piecewise model were exclusively applied to kelps from the intertidal, as the model was not able to detect the ‘breakpoint’ for subtidal \(S.\) polyschides, due to the restrictions on the flat relationship determination of the algorithm (Vito Muggeo, pers. com.). Therefore, \(T_{\text{opt}}\) for subtidal \(S.\) polyschides was based on mean values of gross primary production along the increasing temperature, where the highest value was chosen as the optimum temperature.

Differences in the temperature responses of GPP and NPP below the optimum temperature were assessed with \(Q_{10}\) values, which were calculated as:

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

where rate 1 and 2 are metabolic rates for productivity measured at temperatures \(T_2\) (higher temperature) and \(T_1\) (lower temperature), respectively. \(Q_{10}\) is the increase factor in the rate of a chemical reaction when temperature increases (Van’t Hoff, 1898). Because the arbitrary selection of \(T_1\) and \(T_2\) has a systematic effect on the \(Q_{10}\) estimation, all calculations were done for each 5 °C interval (from 5 °C up to determined \(T_{\text{opt}}\) for each of the 3 cases (intertidal \(L.\) ochroleuca, inter- and subtidal \(S.\) polyschides) and then the mean values were calculated as the final, reported, \(Q_{10}\). In order to test which was the effect of supra-optimal (i.e. above \(T_{\text{opt}}\)) temperatures on productivity, the reduction above \(T_{\text{opt}}\) was calculated the same way as \(Q_{10}\), but for 5 °C intervals from \(T_{\text{opt}}\) to 30 °C (Staehr and Wernberg, 2009).

Two-way analysis of variance (ANOVA) was used to test the effects of increasing temperatures on the functional variables and estimates (GPₚₓᵢₐₓ, \(R_d\), \(Q_{10}\) and reduction of \(Q_{10}\)) Temperature (six levels: 5, 10, 15, 20, 25, 30 °C) and the group case (intertidal \(L.\) ochroleuca, inter- and subtidal \(S.\) polyschides) were treated as crossed, fixed factors. Some of the data did not conform to the assumptions of ANOVA; the significance of results were interpreted according to Underwood (1997), i.e. when data violated the assumption of homogeneous variances, the significance was set at the α = 0.01 level to decrease a type I error rate. Tukey’s tests were used as pairwise comparisons to resolve differences among levels of significant factors. Statistical analyses were performed using the STATISTICA 8 software package (Stat Soft, Inc., 2007).

3. Results

Gross primary productivity gradually rose until the optimum temperatures, i.e. around 16 °C for \(L.\) ochroleuca and \(S.\) polyschides from the intertidal and 10 °C for subtidal \(S.\) polyschides (Table 1), above which the rate of photosynthesis decreased (Fig. 1). For both kelp species from the intertidal, optimum temperature was determined through the piecewise regression model. For subtidal \(S.\) polyschides, the breakpoint was based on mean of \(GP_{\text{max}}\) values (Fig. 1C). For dark respiration, no optimum temperature was observed, as the rate of \(R_d\) was steadily rising until 30 °C (Fig. 2). \(GP_{\text{max}}\) reached ca. 8, 18, and 15 mg O₂ g⁻¹ DW h⁻¹ for intertidal \(L.\) ochroleuca, and inter- and subtidal \(S.\) polyschides, respectively (Fig. 1). These values were significantly different between intertidal \(L.\) ochroleuca and inter- and subtidal \(S.\) polyschides (two-way ANOVA, Table 2), with a significant higher value for intertidal \(S.\) polyschides than \(L.\) ochroleuca (Tukey’s post hoc test, p < 0.001). The difference in productivity between inter- and subtidal \(S.\) polyschides was not so pronounced, but still statistically significant (Tukey’s post hoc test, p < 0.001).

Experimental temperatures significantly affected the rates of respiration (two-way ANOVA, Table 2, Fig. 2), with intertidal \(S.\) polyschides having the strongest increase. Additionally, post hoc Tukey’s tests showed significantly higher values for intertidal \(S.\) polyschides than \(L.\) ochroleuca (p < 0.001) and for subtidal \(S.\) polyschides (p < 0.029).

\(Q_{10}\) values for both NPP and GPP differed between cases (two-way ANOVA, Table 2); the highest value was recorded for subtidal \(S.\) polyschides, which was significantly different from both kelp species from the intertidal (Tukey’s post hoc, p < 0.001, Tables 1 and 2). In the intertidal, \(Q_{10}\) tended to be, although not statistically significant, higher for \(L.\) ochroleuca than \(S.\) polyschides (Tables 1 and 2). The values of reduced \(Q_{10}\) estimates (calculated for temperatures above \(T_{\text{opt}}\) to 30 °C) showed a significant decrease in metabolic rates for all cases under increasing temperatures (two-way ANOVA, Table 2). Importantly, \(L.\) ochroleuca showed the strongest drop in metabolism above the optimum temperature (Table 1), which was significantly larger than subtidal \(S.\) polyschides.
Table 1

Estimates from fitted temperature-response curves for gross (GPP) and net (NPP) photosynthesis and respiration ($R_d$) of intertidal $L$. ochroleuca and inter- and subtidal $S$. polyschides. $T_{opt}$ (°C) is the temperature at which maximum rates were found, $Q_{10}$ is the relative change in metabolism with a 5 °C increase in experimental temperatures. Reduction of $Q_{10}$ above $T_{opt}$ is the relative decrease of metabolism from $T_{opt}$ to 30 °C (mean ± SE, na – not applicable).

<table>
<thead>
<tr>
<th>NPP</th>
<th>$T_{opt}$ (°C)</th>
<th>$Q_{10}$</th>
<th>Reduction of $Q_{10}$ above $T_{opt}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intertidal $L$. ochroleuca</td>
<td>16.090 ± 2.239</td>
<td>2.484 ± 0.948</td>
<td>1.149 ± 0.576</td>
</tr>
<tr>
<td>Intertidal $S$. polyschides</td>
<td>16.410 ± 2.500</td>
<td>2.597 ± 1.078</td>
<td>0.936 ± 0.031</td>
</tr>
<tr>
<td>Subtidal $S$. polyschides</td>
<td>10.000 ± 2.587</td>
<td>6.546 ± 0.000</td>
<td>0.812 ± 0.119</td>
</tr>
</tbody>
</table>

4. Discussion

We hypothesized that Portuguese native kelp species would show an increase in functional responses with increasing temperatures and our results supported our expectations. We tested the consistency of these physiological responses to temperature between juvenile sporophytes of $L$. ochroleuca and $S$. polyschides from the intertidal. Our results showed that, due to their different reproductive strategies, the functional responses to temperature vary, including rates of productivity at optimum temperatures. Moreover, this study showed that there is significant variability in the functional response of $S$. polyschides when exposed to increasing temperature between individuals from the inter- and subtidal.

The optimal temperature for productivity for intertidal $L$. ochroleuca and $S$. polyschides was around 16 °C and 10 °C for subtidal $S$. polyschides. Similar values were reported by Izquierdo et al. (2002), where optimum temperatures for $L$. ochroleuca ranged from 15 °C to 18 °C. In this study, we observed a significant difference between optimum temperatures for inter- and subtidal $S$. polyschides. This supports the notion of the highly adaptable capacity of this species to environmental conditions. Plastic responses, expressed as physiological variations to changing environmental conditions, are key mechanisms for macroalgae to occupy a broad

(Tukey’s post hoc, $p < 0.0025$), and larger, although not statistically significant, than intertidal $S$. polyschides.

Table 2

Two-way ANOVA testing the effect of temperature and group case (intertidal $L$. ochroleuca, inter- and subtidal $S$. polyschides) on $G_{max}$, $R_d$, $Q_{10}$, and reduced $Q_{10}$. Effects that were found significant are in bold, ns—not significant (at $p > 0.05$).

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>$F$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$G_{max}$</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td>5</td>
<td>58.303</td>
<td>11.062</td>
<td>&lt;0.001</td>
</tr>
<tr>
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<td>332.868</td>
<td>63.156</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Temp $\times$ Group</td>
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<td>23.098</td>
<td>4.383</td>
<td>&lt;0.001</td>
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<td>Residual</td>
<td>36</td>
<td>5.271</td>
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<td></td>
</tr>
<tr>
<td>$R_d$</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
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<td>5.514</td>
<td>39.077</td>
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<tr>
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<td>0.141</td>
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<td></td>
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<tr>
<td>$Q_{10}$</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td>5</td>
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<td>0.000</td>
<td>ns</td>
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<tr>
<td>Group</td>
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<td>Temp $\times$ Group</td>
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<td>0.000</td>
<td>ns</td>
</tr>
<tr>
<td>Residual</td>
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<td>4.597</td>
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<td></td>
</tr>
<tr>
<td>Reduction of $Q_{10}$</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td>5</td>
<td>0.000</td>
<td>0.000</td>
<td>ns</td>
</tr>
<tr>
<td>Group</td>
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<td>0.564</td>
<td>6.932</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Temp $\times$ Group</td>
<td>10</td>
<td>0.000</td>
<td>0.000</td>
<td>ns</td>
</tr>
<tr>
<td>Residual</td>
<td>36</td>
<td>0.081</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Fig. 1. Temperatures dependency of photosynthesis for (a) intertidal $L$. ochroleuca, (b) intertidal $S$. polyschides and (c) subtidal $S$. polyschides. $G_{max}$ is in mg O$_2$ g$^{-1}$ DW h$^{-1}$. For detailed optimum temperature ($T_{opt}$) determined by the model/calculation see Table 1.
sporogenesis only after the second year (Birkett et al., 1998; Bartsch et al., 2008). Pereira et al. (2011) compared the ability of L. ochroleuca and S. polyschides to recover after disturbances, emphasizing the pioneer and opportunistic nature of the latter due to its annual life cycle.

The sensitivity of kelps’ metabolism to temperatures below and above $T_{opt}$ was modeled through the $Q_{10}$ parameter. Subtidal S. polyschides showed higher values than intertidal individuals, indicating its faster onset of primary production. This finding suggests that subtidal S. polyschides would be more sensitive to temperature changes. Compared to the intertidal, the subtidal is relatively more stable in terms of potential sources of stress and disturbance, including temperature fluctuations (e.g. Moran, 1999). This would explain a lower acclimation capacity of S. polyschides from the subtidal to environmental fluctuations, compared to intertidal specimens. Intertidal S. polyschides showed a trend for higher metabolic rates under low (i.e. below the optimum) temperatures than L. ochroleuca, but these did not exceed those observed for subtidal S. polyschides. This further supports the idea that intertidal specimens are more adapted than those from the subtidal to environmental changes (Somero, 2002), and that differences between the two intertidal kelps may be mostly driven by species-specific reproductive strategies (Pereira et al., 2011).

The response of macroalgae to supra-optimal temperature was also tested and expressed as a reduction of $Q_{10}$ values above the $T_{opt}$. The strongest decrease in both gross (GPP) and net (NPP) primary productivity was recorded for L. ochroleuca, in agreement with previous findings documenting up to four times higher mortality rates due to higher temperatures for L. ochroleuca than S. polyschides (Pereira et al., 2011). This physiological limitation of L. ochroleuca (Rolda et al., 2004) and its restricted capability to acclimatize to high temperatures (Bolton and Lüning, 1982; Izquierdo et al., 2002) could have a reflection on its distribution. Further south from the sampling location, populations of L. ochroleuca occur mainly at depths below 40 m (Tittley et al., 2005), as the upper parts of the shore might be exposed periodically to high temperatures (Van den Hoek, 1982; Pereira et al., 2011) or in areas associated with intense upwelling (Fernández, 2011). In contrast, across the same latitudes, S. polyschides is capable of growing almost until the surface, and so subjected to higher temperature fluctuations (Van den Hoek, 1982). In the future, under predicted scenarios of ocean warming, this might lead to a change in the distribution range of L. ochroleuca (northward retreat) and/or limit the existing populations to deeper habitats (Rolda et al., 2004).

In summary, we have demonstrated that distinct kelp species inhabiting the same geographical area may have different functional responses to increasing temperatures, and so they will not be equally affected by predicted ocean warming. In particular, L. ochroleuca has a more limited physiological plasticity than S. polyschides, and might therefore be more susceptible to the effects of ocean warming.

Fig. 2. Temperature-dependency of dark respiration for (a) intertidal L. ochroleuca ($y = 0.048x - 0.057, R^2 = 0.659, p\text{-value} = 0.050$), (b) intertidal S. polyschides ($y = 0.066x + 0.169, R^2 = 0.736, p\text{-value} = 0.029$) and (c) subtidal S. polyschides ($y = 0.067x - 0.291, R^2 = 0.809, p\text{-value} = 0.015$). Dark respiration is in mg O$_2$ g$^{-1}$ DWh$^{-1}$.

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Metabolic rates ($GP_{max}$ and $R_q$) of intertidal S. polyschides were higher than L. ochroleuca; these findings likely reflect the different life spans of these kelps. Annual S. polyschides must develop all life stages, including sporophyte growth, gametophyte formation and reproduction, within several months. In spring, fast growth prepares kelps for maturation and sporogenesis, followed by decay (senescence) in autumn. In contrast, the metabolism of perennial L. ochroleuca does not require such intensive pace, as it starts
References


