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Narrow range of temperature and irradiance supports optimal development of *Lessonia corrugata* (Ochrophyta) gametophytes: implications for kelp aquaculture and responses to climate change

Ellie R. Paine[1] · **Matthias Schmid**[1] · **Juan Diego Gaitán-Espitia**[2] · **Joshua Castle**[1] · **Ian Jameson**[3] · **John C. Sanderson**[4] · **Catriona L. Hurd**[1]

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Abstract

The kelp *Lessonia corrugata* (Ochrophyta, Laminariales) is being developed for integrated multi-trophic aquaculture (IMTA) trials in the vicinity of salmon cages in Tasmania, Australia. Gametophytes are vegetally maintained before seeding on hatchery twine; however, the optimal temperature and light conditions for growth and sexual development are unknown. We measured vegetative size of female and male gametophytes and sexual development of females over a range of temperatures and irradiances using a temperature gradient table and neutral density light filters. Over a 4-week experiment, gametophytes were exposed to a combination of thermal (5.7–24.9 °C) and irradiance (10–100 μmol photons m^{-2} s^{-1}) gradients, to assess biological performance. At the temperature extremes (hottest = 24.9 °C, coldest = 5.7 °C), we observed the critical thermal limits for this species and the results reveal a narrow optimal temperature range for growth and sexual development between 15.7 and 17.9 °C, with irradiances between 40 and 100 μmol photons m^{-2} s^{-1} resulting in fertile female gametophytes. *Lessonia corrugata* inhabits a small geographic range, found only around Tasmania, south of the Australian mainland, hence oceanic changes such as ongoing increases in sea surface temperatures (SSTs), and altered irradiance regimes may limit recruitment of the early microscopic life stages in the future. Our findings provide optimised culture conditions for aquaculture and information to predict the future geographic range of *L. corrugata* under ocean global change.

Keywords Gametophytes · Irradiance · Laminariales · *Lessonia corrugata* · Macroalgae · Temperature

Introduction

Brown macroalgae of the order Laminariales (true kelps) are important in temperate marine ecosystems as they form dense forests providing food, habitat and key ecosystem services for a great diversity of organisms (Bennett and Wernberg 2014; Bennett et al. 2016). They also take up nutrients including nitrogen and phosphorus, and as such, kelps are increasingly being used in integrated multi-trophic aquaculture (IMTA) systems where seaweeds are grown in conjunction with finfish and shellfish to take up excess nutrients produced by the fed species (Buschmann et al. 2001; Chopin et al. 2001; Hurd et al. 2014; Buck et al. 2017; Roleda and Hurd 2019). However, the development of IMTA and kelp aquaculture may be hindered by environmental changes in sea surface temperature (SST), nutrients (primarily nitrogen) and irradiance, which currently limit seaweed recruitment and biogeographic distribution of kelp forests in coastal marine waters around the world (Deysher and Dean 1986; Steneck et al. 2002; Mabin et al. 2019; Smale 2020).

Kelp forests currently experience multiple anthropogenic stressors including ocean warming and altered underwater irradiance regimes which may be exacerbated in the future (Smale et al. 2013; Krumhansl et al. 2016; Smale 2020). Global SSTs have increased ~ 0.11 °C per decade since the industrial revolution and the east coast of Tasmania, Australia, is predicted to experience warming ~ 3.8 times the global

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✉ Ellie R. Paine
ellie.paine@utas.edu.au

[1] Institute for Marine and Antarctic Studies, University of Tasmania, Hobart TAS 7001, Australia

[2] SWIRE Institute of Marine Sciences & School of Biological Sciences, The University of Hong Kong, Pokfulam Road, Hong Kong, SAR, China

[3] CSIRO Oceans and Atmosphere, Castray Esplanade, Hobart TAS 7001, Australia

[4] Tassal Group Limited, Hobart TAS 7001, Australia

average (2–3 °C) making this one of the fastest warming regions in the southern hemisphere—a global 'hotspot' (Ridgeway 2007; Johnson et al. 2011; IPCC 2014). Increased SSTs have the potential to impact seaweeds by impairing respiration, photosynthesis, basic cellular maintenance and juvenile recruitment (Wernberg et al. 2010). As the kelp canopy is destabilised by increased SST, higher irradiances penetrate the understorey algal community, including juvenile kelps and gametophytes (Wernberg et al. 2010). Furthermore, changes to underwater irradiance regimes caused by increased precipitation, storm events and pollution may affect kelp survival by reducing the irradiance available (Tait 2019; Blain and Shears 2020). Understanding how temperature and irradiance that are likely to interact and influence the microscopic life stage of kelps is crucial for determining productivity of the order Laminariales both in natural populations and in an aquaculture setting into the future.

The kelp life cycle is a heteromorphic alteration of generations (Hurd et al. 2014). Mature diploid sporophylls (2n) produce and release zoospores (n) which settle and germinate into dioecious haploid gametophytes (n). Gametophytes mature into female and males before reproduction is induced (Lüning and Dring 1975; Lüning and Neushul 1978; Gerard 1990). During reproduction, eggs produced in the female oogonium are fertilised by sperm produced in the male antheridium, driving the formation of the zygote and re-starting the sporophyte (2n) stage (Maier et al. 1987; Müller et al. 1979). The development of the gametophyte and fertilisation of the egg is, however, affected by environmental factors, particularly temperature and irradiance (Matson and Edwards 2007; Cie and Edwards 2008; Mohring et al. 2013; Bringloe et al. 2018). Environmental extremes in either sides of their optimal range can reduce gametophyte growth and sexual development, which may hinder population recruitment (Augyte et al. 2019).

Temperature has a significant regulatory effect on the growth and sexual development of the microscopic life stages of kelp through changes to zoospore germination success, morphology and development of gametophytes, as well as growth of juvenile sporophytes (Lüning and Neushul 1978; Nelson 2005; Oppliger et al. 2012; Murúa et al. 2013). Lower and upper critical temperatures vary depending on species and biogeographic location; only within the optimal temperature window can gametophytes germinate, become sexually mature and fertilise into zygotes (tom Dieck 1993). This optimal temperature window highlights the importance of physiological plasticity and local adaptation in kelps as recruitment varies in respect to seasonality and latitudinal distribution (Lee and Brinkhuis 1988; Martínez 1999; Oppliger et al. 2012; Murúa et al. 2013; Mohring et al. 2014).

Organisms respond to their environments according to their tolerances and sensitivities, and these responses can be described through performance curves that represent the degree of physiological plasticity of species and populations (Fernández et al. 2020). The performance curves depict the tolerance range and critical zones where organisms can enter into stress and be lethal (Gaitán-Espitia et al. 2013). Although temperature is recognised as the main environmental factor shaping these performance curves (and thus plasticity), for kelps, these curves can additionally be shaped by the interactions with other factors such as irradiance, nutrients and salinity (Gaitán-Espitia et al. 2014b; Fernández et al. 2020).

The order Laminariales contains 113 species in 33 genera globally (Bolton 2010), one of which is *Lessonia corrugata* A.H.S. Lucas, an endemic kelp found around Tasmania, a temperate island at the southern tip of Australia (Scott 2017). *Lessonia corrugata* commonly grows at 1–4 m depth but has been recorded to 18 m (Scott 2017). It is being grown around finfish farms in Tasmania as part of a trial IMTA system. Gametophyte cultures are initiated and maintained in a laboratory before being sprayed onto twine and spun around rope suspended from buoys adjacent to the fish farms (Barrington et al. 2009; Edwards and Watson 2011; Flavin et al. 2013). However, despite being an ecosystem dominant in Tasmania, *L. corrugata* is poorly studied and the temperature and irradiance conditions necessary for optimal gametophyte growth are unknown. Therefore, the aim of this study was to identify the thermal performance range (minimum, maximum and optimal temperatures) for gametophyte growth and sexual development under a range of irradiances (10, 40, 70 and 100 μmol photons m^{-2} s^{-1}). The results of this study will help to future proof the seaweed aquaculture industry of Tasmania under future oceanic change by providing optimal culture conditions for gametophyte germplasm preservation (i.e. zoospores or haploid gametophytes stored in a lab, also known as a 'seed bank') (Edwards 2000; Wade et al. 2020) and provide information that will enable predictions of the future biogeographic range of *L. corrugata* as the oceans continue to warm.

Methods

Seaweed collection and zoospore release

Lessonia corrugata sori were collected using snorkel from Crayfish Point (43° 01′ S, 147° 33′ E), South-Eastern Tasmania on the 28th of May 2018 (late Autumn; *L. corrugata* is found to have reproductive sori year-round; J.C. Sanderson, pers. obs.). Specimens were found growing sub-tidally on rock substratum between 2 and 6 m and once removed from the water were promptly placed into a dark cool box and transported to the laboratory (20 min away).

For zoospore release from kelp tissue, we followed the protocols described by Edwards and Watson (2011) and Flavin et al. (2013). In the laboratory, sorus tissue containing fertile sporangia were cut and isolated from the nonreproductive tissue and cleaned using tweezers to remove any obvious epiphytes before being placed in an iodine bath for 30 s (5 mL L^{-1} Betadine and filtered seawater 0.22 μm) (Flavin et al. 2013). Once removed from the iodine bath, sori were rinsed and soaked in sterilized seawater for 5 min then wiped with paper towel. This process was repeated three times each in fresh filtered seawater (0.22 μM), to ensure clean sori. Sorus tissue was then placed between sheets of clean, damp paper towel and left in a cool room (12 °C) overnight for slow, gentle desiccation. The following day, 1-L beakers were filled with filtered seawater (15 °C) in a laminar flow hood into which sorus tissue was immersed. Sori were stirred occasionally and left for 2 h for zoospore release. The initial zoospore density was estimated at 160,000 zoospores per millilitre by counting of zoospores using a haemocytometer under a light microscope (Nikon ECLIPSE Ts2). The following experiment was initiated the afternoon of the zoospore release.

Experimental design

An aluminium temperature gradient table was used for the temperature × irradiance experiment (Edwards and van Baalen 1970). The temperature gradient along the table was created by a heating unit set at 28 °C at one end and a cooling unit set at − 8 °C at the other end of the aluminium block. The temperature table had a total of 72 wells (12 along the temperature gradient with six replicate wells per temperature), which fit 70-mL polypropylene specimen containers (Techno Plas). The table was set up to create 12 ecologically relevant temperature treatments, 5.7, 8.3, 11.0, 13.2, 15.3, 16.9, 18.5, 19.9, 21.1, 22.4, 23.6, and 24.9 °C, which were monitored using a spike probe thermometer (Testo 826-T4—IR and Probe Thermometer) over a 24-h period (SD ± 0.3 °C) prior to the experiment.

A LED panel light (Lumex NovaBlade) illuminated the base of the wells in the table from below. Neutral density filters were placed at the base of each well creating four irradiance treatments, 10, 40, 70, and 100 μmol photons m^{-2} s^{-1}. Irradiance in each well was measured using a LI-COR Light Meter (LI-250A) with a flat quantum sensor attached. Due to logistical restraints of the 12 × 6 well temperature gradient table and in order to have three replicates for each factorial treatment, the irradiance treatments alternated with each temperature treatment (Fig. 1). We grouped 10 μmol photons m^{-2} s^{-1} and 70 μmol photons m^{-2} s^{-1} treatments as well as the 40 μmol photons m^{-2} s^{-1} and 100 μmol photons m^{-2} s^{-1} irradiance treatments and alternated them with each temperature treatment (Fig. 1). The light:dark cycle was 12:12 which was chosen to approximate the seasonal conditions on collection.

For the temperature × irradiance experiment, aliquots of the zoospore solution (438 μL) were added to each of the 72 containers and filled to 10 mL with F/2 enriched filtered seawater to achieve a density of ca 7000 zoospores per millilitre (~ 36 spores per mm^2 once settled) (Tatsumi and Wright 2016). F/2 culture medium was used as it is known to support good gametophyte development (Nelson 2005; Ratcliff et al. 2017). The experiment was run for 4 weeks, and the culture medium in each of the 72 culture containers was exchanged with fresh F/2 enriched seawater every week following methods outlined in other gametophyte studies (tom Dieck 1987; Wiencke 1990; Nelson 2005; Murúa et al. 2013; Müller et al. 2019).

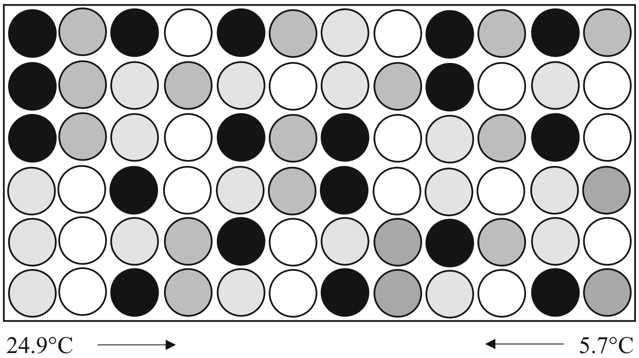

Fig. 1 Schematic showing temperature and irradiance combinations across the temperature gradient table (not to scale). Black = 10 μmol photons m^{-2} s^{-1}, dark grey = 40 μmol photons m^{-2} s^{-1}, light grey = 70 μmol photons m^{-2} s^{-1} and white = 100 μmol photons m^{-2} s^{-1}. Each irradiance had three replicates. Temperatures ranged between 24.9 and 5.7 °C. The temperature increment between treatments was ~ 1.75 °C. Once in position, replicates were kept in that position because of the difficulty of moving light filters

Measurement of gametophyte surface area and sexual development

To determine the combined effects of temperature and irradiance on gametophyte size (a measure of growth) and sexual development, three photographs were taken using an inverted light microscope at × 100 magnification (bright field; Leica Microsystems-Labovert) in each replicate container at the end of the experiment (day 30) (Fig. 2). Photographs were randomly taken along a pre-determined radial line at the base of each container. For each of the three photographs, five male and five female gametophytes were randomly selected and their surface area (mm^2) measured in the software Fiji (Schindelin et al. 2012). These values were then averaged for each photo, then each container, to give three values per temperature × irradiance treatment (i.e. one value of surface area for each of the three replicate containers). The total number of oogonia on female gametophytes per mm^2 (i.e. area of microscope field of view at × 100 magnification) was counted for each photo to determine sexual development of female gametophytes (Fig. 3). Again, oogonia count was averaged for each photo, then each container, to give one value per replicate container (i.e. three values per temperature ×

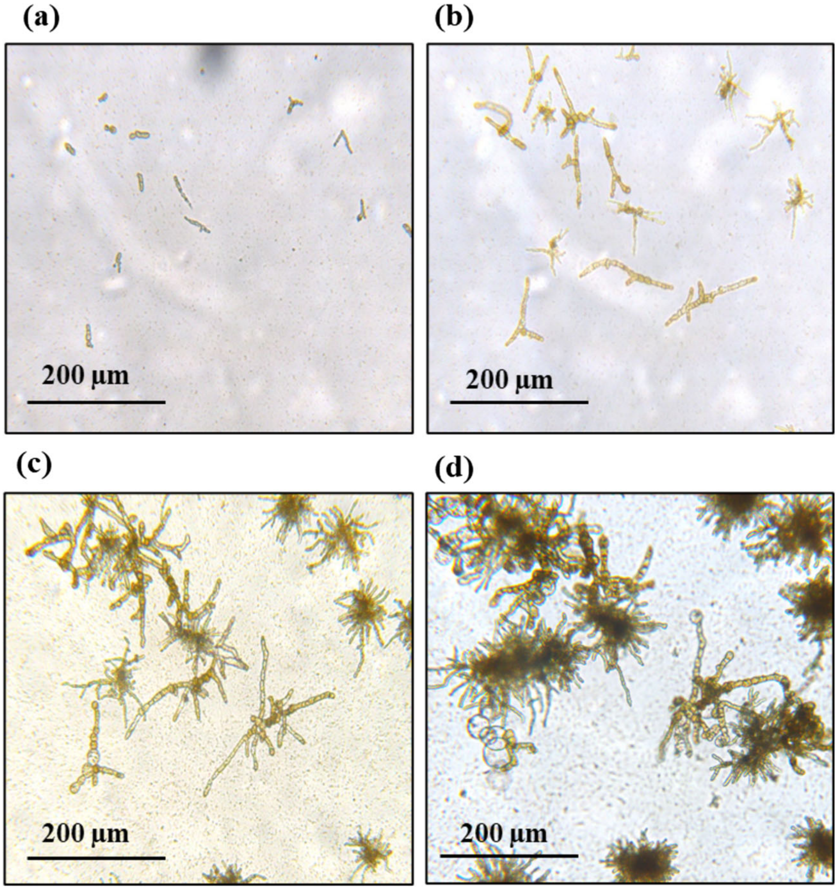

Fig. 2 Growth of *L. corrugata* gametophytes under 70 µmol photons m^{-2} s^{-1} at 16.9 °C; **a** week 1, **b** week 2, **c** week 3 and **d** week 4 development of individual gametophytes

irradiance treatment). For all the traits analysed, the mean and variance of each replicate (i.e. each container) were included in the model fitting step of the performance curves.

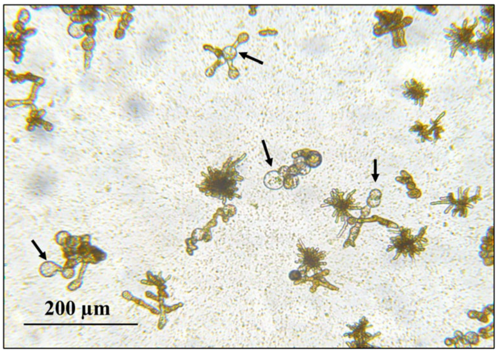

Fig. 3 Sexual maturation of *L. corrugata* gametophytes after 3 weeks; arrows highlight oogonia formation on female gametophytes at 18.5 °C under 100 µmol photons m^{-2} s^{-1}

Data analysis

The non-linear relationship between gametophyte size and the experimental factors (temperature and irradiance) was analysed following the method described in Fernández et al. (2020). Briefly, a continuous reaction norm or performance curve was constructed for female and male gametophyte surface area as well as for the number of oogonia using a model-fitting approach (Gaitán-Espitia et al. 2014a). Here, several non-linear functions (e.g. Gaussian, exponential modified Gaussian, Quadratic Lorentzian, Weibull) were tested using the *lsfit* function implemented in the *easynls* R package v.5.0 (Arnhold 2017) and the GraphPad Prism software (v.7.03). Thermal performance curve (TPC) parameters of the curve (maximal measurement—μ_{max}, thermal optimum—T_{opt}, critical thermal maximum and minimum at which gametophyte growth decreases—CT_{min} and CT_{max}) were numerically derived from the best-fitted models considering the y_{max} and the intersection points of the resulting curve with the temperature axis ($\mu = 0$). The best fit models were assessed using the

Akaike Information Criterion (AIC) (Angilletta 2006). Parameters of the curves were compared among treatments through the confidence intervals (CI) computed from the likelihood profile and using AIC and the extra sum-of-square *F* test. Finally, in order to better visualise the overall biological performance of *L. corrugata* gametophytes across the temperature ×irradiance environmental seascape, we used surface plots implemented in the R plotly package v. 4.9.2.1 (Sievert 2020). Comparison of functions used to describe the performance curves for size of female and male gametophytes retrieved the lowest Akaike's information criterion (AIC) for the exponential modified Gaussian function (best-fitted model). For sexual development, the AIC retrieved the Gaussian function as the best-fitted model. These functions were used to fit the data for all the treatments in the corresponding datasets.

Results

Gametophyte size

The size of female and male gametophytes at a range of temperatures followed the typical bell shape curve described for ectothermic organisms (Angilletta Jr et al. 2002). However, these curves were influenced by irradiance showing a clear interaction between both factors. At the lowest irradiance (10 μmol photons m^{-2} s^{-1}) gametophytes exhibited no-to-slow growth nor sexual development across the thermal gradient which revealed a sub-optimal irradiance response independent of temperature (Fig. 2a). The T_{opt}, CT_{max} and μ_{max} of the TPCs for both female and male gametophyte sizes were the highest under 70 μmol photons m^{-2} s^{-1}; however, there was no statistical difference in the CT_{min} between all irradiances (Table 1). The graphs clearly indicate that the overall pattern of the TPCs is driven by temperature, and that variability around the curve is driven by irradiance and sexual dimorphism of the gametophyte. In cultures kept at 22.4 °C and above, zoospores did not survive, and no gametophytes were recorded in these cultures.

The TPCs for female gametophytes were similar to each other at the higher irradiances (40–100 μmol photons m^{-2} s^{-1}; Fig. 2a). However, female gametophytes cultured at 70 μmol photons m^{-2} s^{-1} showed higher T_{opt} (16.52 °C) and CT_{max} (22.30 °C) compared with their counterparts at the other two irradiances (40 μmol photons m^{-2} s^{-1}: T_{opt} = 15.82 °C, CT_{max} = 21.31 °C and 100 μmol photons m^{-2} s^{-1}: T_{opt} = 15.69 °C, CT_{max} = 21.12 °C; $F_{18,48} = 11.26$; $P = 0.001$; Table 1).

The TPCs for male gametophyte size showed similar T_{opt} (16.17–16.54 °C) under each of the higher irradiances (40–100 μmol photons m^{-2} s^{-1}; Table 1; Fig. 2b). Significant differences in thermal performance were detected for μ_{max} (i.e. maximum size) and CT_{max}. Male gametophytes at 100 μmol photons m^{-2} s^{-1} showed the lowest thermal performance (μ_{max} = 6.95 mm^2 and CT_{max} = 21.1 °C) compared with those at 40 μmol photons m^{-2} s^{-1} (μ_{max} = 9.01 mm^2 and CT_{max} = 21.23 °C) and 70 μmol photons m^{-2} s^{-1} (μ_{max} = 10.9 mm^2 and CT_{max} = 22.1 °C) ($F_{18,48} = 7.16$, $P < 0.001$).

The modelled surface plots for *L. corrugata* gametophytes across the temperature × irradiance environmental seascape revealed the narrow optimal range for female and male gametophyte size (Fig. 3 a and b). The differences in parameters of the TPCs (Table 1) were significant within sex (females and males compared separately), but not between the sexes (i.e. comparison between female and male TPCs, $P > 0.05$) (Figs. 4, 5 and 6). The difference between sexes was non-significant despite the visual differences in the shape of the TPCs between female and male gametophytes with the different irradiance levels (Fig. 2 a and b).

Table 1 TPC traits (i.e. modelled data) for the size and sexual development of *L. corrugata* gametophytes under the different irradiances—T_{opt} (°C) = thermal optimum, CT_{min} (°C) and CT_{max} (°C) = critical thermal maximum and minimum and μ_{max} = maximal measurement

Parameter	Treatment	T_{opt} (°C)	CT_{min} (°C)	CT_{max} (°C)	μ_{max}
Female gametophyte size (mm^2)	40 μmol photons m^{-2} s^{-1}	15.82	5.02	21.31	7.89
	70 μmol photons m^{-2} s^{-1}	16.52	5.53	22.30	8.83
	100 μmol photons m^{-2} s^{-1}	15.69	4.98	21.12	7.64
Male gametophyte size (mm^2)	40 μmol photons m^{-2} s^{-1}	16.25	5.27	21.23	9.01
	70 μmol photons m^{-2} s^{-1}	16.54	5.15	22.12	10.94
	100 μmol photons m^{-2} s^{-1}	16.17	5.03	21.08	6.95
Female gametophyte maturation (oogonia per mm^2)	40 μmol photons m^{-2} s^{-1}	16.31	9.93	22.25	12.79
	70 μmol photons m^{-2} s^{-1}	17.91	11.74	23.19	11.12
	100 μmol photons m^{-2} s^{-1}	16.28	9.94	22.28	10.62

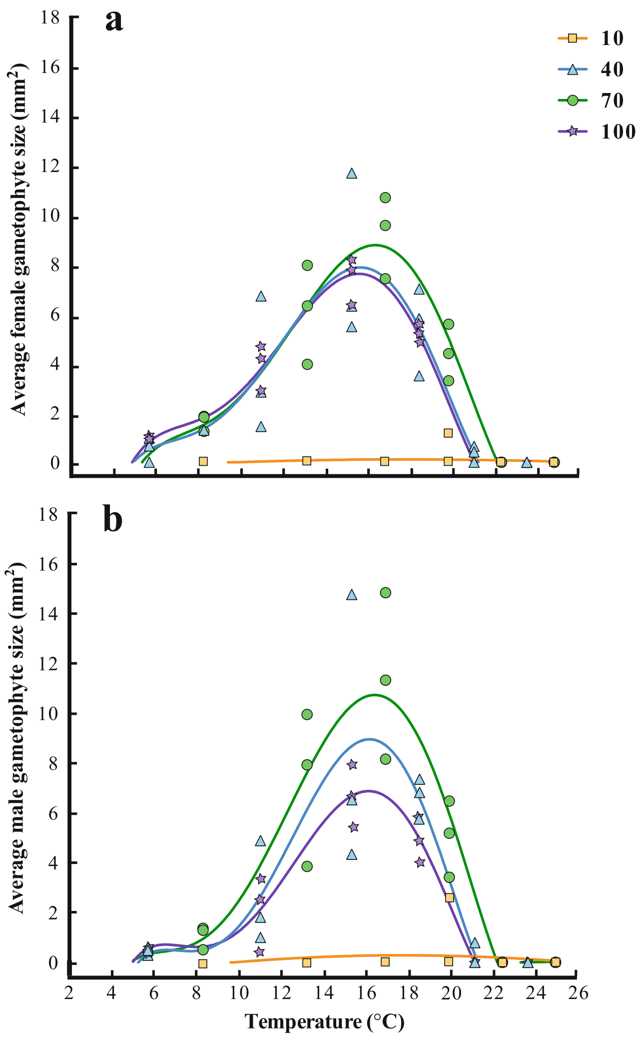

Fig. 4 Temperature-size response curves of **a** female and **b** male *L. corrugata* gametophytes incubated under four irradiances (orange square = 10 μmol photons m^{-2} s^{-1}, blue triangle = 40 μmol photons m^{-2} s^{-1}, green circle = 70 μmol photons m^{-2} s^{-1}, purple star = 100 μmol photons m^{-2} s^{-1}). Each point represents the average surface area of gametophytes in a replicate container i.e. $n = 3$ at each temperature treatment (5.9–24.9 °C)

Female gametophyte sexual development

Sexual development, reflected in female gametophyte oogonia count (per mm^2), was strongly influenced by both temperature and irradiance (Fig. 4). The T_{opt} was between 16.2 and 17.9 °C at 40, 70 and 100 μmol photons m^{-2} s^{-1}. No oogonia were observed under 10 μmol photons m^{-2} s^{-1} at any of the experimental temperatures. In terms of the TPCs for each irradiance, the best-fitted model for oogonia count followed the Gaussian function evidencing different shapes among treatments ($F_{9.6}$ = 11.36; $P < 0.001$).

Discussion

We found that gametophyte development for *L. corrugata*, a kelp with a narrow geographic range that is endemic to the island of Tasmania, Australia, has a narrow range of thermal tolerance and high sensitivity to changes in temperature and irradiance. This finding supports the idea of local thermal adaptation in species with a narrow biogeographic range (Bennett et al. 2019) and has also been documented in endemic brown seaweeds from other temperate and polar regions, for example, *Durvillaea poha* in New Zealand (Thomsen et al. 2019) and *Laminaria solidungula* in the Arctic (Roleda 2016). Compared with other kelp species that also grow in Tasmania but have very broad geographic distribution, *Ecklonia radiata* (T_{opt} range of ~ 18 to 23 °C) (Mohring et al. 2014) and *Undaria pinnatifida* (a non-indigenous kelp in Tasmania, which has successfully invaded coastal areas around the world due to its wide temperature tolerance; $\mathrm{CT}_{\max}$ of 27–28 °C and up to 33 °C under short term exposure) (Henkel and Hofmann 2008; Morita et al. 2003), *L. corrugata* has a narrow optimal

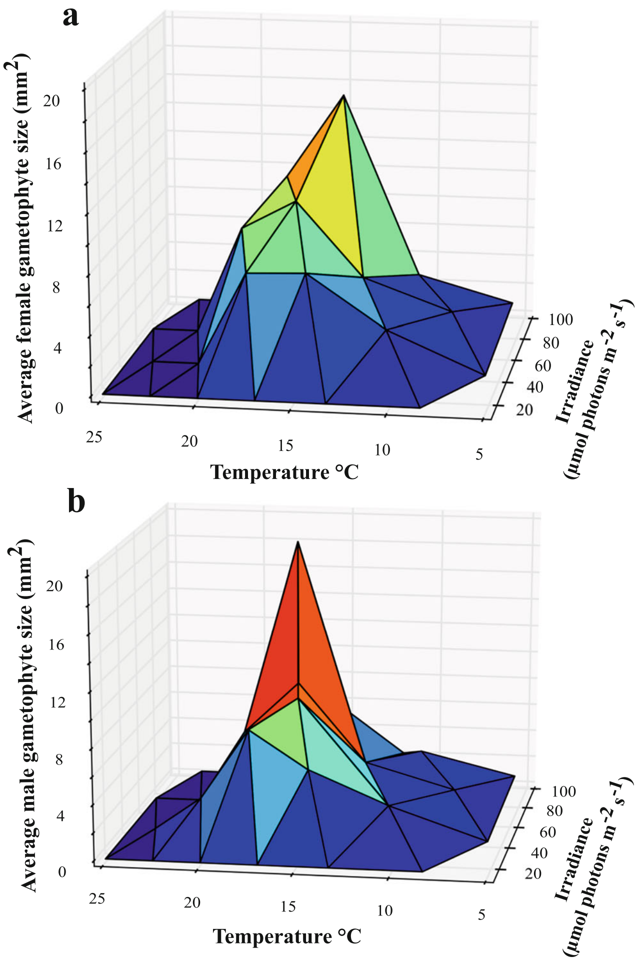

Fig. 5 Modelled 3D surface plot of **a** female gametophyte size and **b** male gametophyte size under different temperatures and irradiances

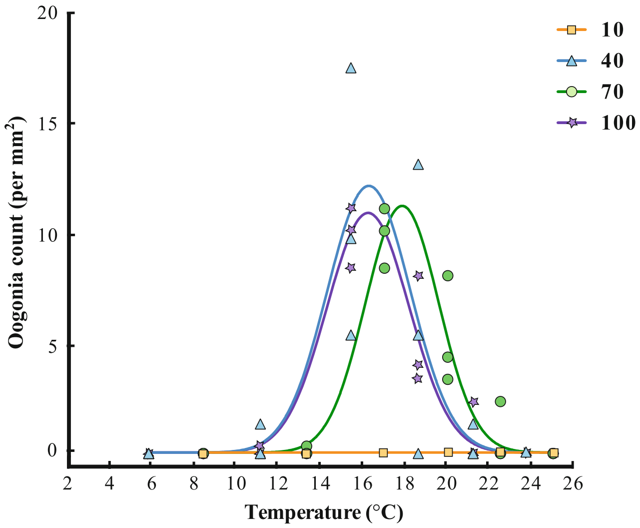

Fig. 6 Temperature response curve of number of oogonia per mm^2 of female *L. corrugata* gametophytes incubated under four irradiances (orange square = 10 μmol photons m^{-2} s^{-1}, blue triangle = 40 μmol photons m^{-2} s^{-1}, green circle = 70 μmol photons m^{-2} s^{-1}, purple star = 100 μmol photons m^{-2} s^{-1}). Each point represents the average count of oogonia per mm^2 in a replicate container i.e. n = 3 at each temperature treatment (5.9–24.9 °C)

thermal range (15.7–17.9 °C) for gametophyte growth and sexual development.

No differences were observed for the TPC traits between male and female gametophytes of *L. corrugata*. This contrasts with *Undaria pinnatifida* male gametophytes, which had both a higher temperature and irradiance tolerance than female gametophytes (Sato et al. 2020) and *Ecklonia radiata* males which had a higher temperature tolerance (Mabin et al. 2019). At temperatures > 21.1 °C, zoospores were unable to survive with a 100% mortality rate observed after 1 week. In the only prior study of *L. corrugata* gametophytes, an upper survival temperature of 23 °C was recorded (tom Dieck 1993) but that experiment used gametophytes previously grown vegetally in long-term laboratory culture under red light, whereas our study followed gametogenesis directly from freshly collected zoospores. The differences between our results which recorded zoospore mortality > 21.1 °C and the upper survival temperature of 23 °C found by tom Dieck (1993) suggest that *L. corrugata* zoospores are more susceptible to degradation and senescence under sub-optimal environmental conditions compared with gametophytes of *L. corrugata*.

The mortality of zoospores > 21.1 °C and small optimal temperature range for *L. corrugata* gametophyte size suggest that the species may be negatively impacted by the predicted 2–3 °C increase in SSTs by the end of the century (Allen et al. 2018). Many seaweed species in mainland Australia have experienced southward migration to lower latitudes as a result of increased SSTs (Wernberg et al. 2011), but *L. corrugata* is at its geographic limit in Tasmania as there is no suitable habitat further south. Our results suggest it is unlikely that *L. corrugata* will successfully recruit under these predicted temperatures, and a bottleneck for survival may occur with a local extinction of the species and subsequent range constriction (Wernberg et al. 2010; Harley et al. 2012). A mechanism by which *L. corrugata* may survive future water warming is vertical migration to cool, deeper waters as SSTs increase (Jorda et al. 2020). However, our results suggest that *L. corrugata* requires moderate irradiances for size and sexual development (discussed below), and migrating to cooler temperatures at depths could reduce the density of the population due to light limitation (Jorda et al. 2020). Additionally, although *L. corrugata* zoospores at low temperatures (< 8.3 °C) underwent gametogenesis, gametophytes remained small (< 1.64 mm^2), did not become sexually mature and had a very slow growth rate (~ 2.8 μm day^{-1}). These results suggest that *L. corrugata* gametophytes can survive in temperatures lower than those currently experienced in Tasmanian waters. As our experiment was run at the start of winter and seasonal changes would be expected to alter the thermal plasticity of kelp gametophytes, seasonal studies may elucidate annual responses of *L. corrugata* gametophytes to thermal ranges. Furthermore, *L. corrugata* has a broad genetic variability (Durrant et al. 2015), and this study provides a basis for future population studies around Tasmania. It would additionally be beneficial for future research to study the thermal range of the mature *L. corrugata* sporophyte to further understand the species biogeography and response to increase in SSTs.

Our results revealed a trade-off between maximal size (μ_{max}) and optimal temperature (T_{opt}) for sexual development but not for gametophyte size. Sexual development of cultures at 70 μmol photons m^{-2} s^{-1} exhibited higher T_{opt} and CT$_{max}$ than those at 40 and 100 μmol photons m^{-2} s^{-1}; however, the greatest number of oogonia per mm^2 was found under 40 μmol photons m^{-2} s^{-1}. This trade-off between μ_{max} and T_{opt} for sexual development may have implications for *L. corrugata* under future ocean predictions. For example, the greatest number of oogonia formed under mid-low irradiance conditions (i.e. 40 μmol photons m^{-2} s^{-1}) but was at the cost of a lower T_{opt}. This temperature and irradiance interaction may be beneficial for *L. corrugata* gametophytes in terms of vertical migration to depth and competition under the canopy (Bennett and Wernberg 2014; Bennett et al. 2015); however, a higher T_{opt} would be most beneficial under future SSTs (Harley et al. 2012). Moreover, mid-high irradiance (70 μmol photons m^{-2} s^{-1}) supported a great number of oogonia yet with a higher T_{opt} which would be beneficial under future SSTs. However, the CT$_{min}$ at this irradiance was also higher than the other treatments which suggests that irradiance had a significant regulatory effect on the sexual development of *L. corrugata*. This finding indicates that moderate irradiances are optimal as the higher T_{opt} at these irradiances provides higher chances of survival and fertilisation in changing environments (de Bettignies et al. 2018). On the other hand, no trade-offs were detected for gametophyte size and the optimal irradiance was between 70 and 100 μmol photons m^{-2} s^{-1}. However, size of gametophytes under 70 μmol photons m^{-2} s^{-1} evidenced broader thermal breath than their counterparts at 100 μmol photons m^{-2} s^{-1}, suggesting higher thermal plasticity and performance.

Conclusions

Our results suggest that growth and sexual development of *L. corrugata* gametophytes are highly sensitive to fluxes in temperature and irradiance. Understanding how this habitat-forming species will respond to increases in SSTs and alterations to irradiance regimes will help conserve the biodiversity of the temperate reefs that *L. corrugata* supports and aid in management decisions regarding the species' aquaculture potential. Future experiments should analyse the thermal range of *L. corrugata* sporophytes and sporangia development as microscopic reproduction may have a lower thermal performance window than adult sporophyte size and survival (Ling et al. 2008; Andrews et al. 2014). Warming events may act as a strong selective force on thermal tolerant genotypes of *L. corrugata*, and further research is required to better understand the thermal responses of adult sporophytes. This future research will enhance our ability to predict the species vulnerability to climate change and marine heatwaves (Bennett et al. 2019). Finally, our study highlights the importance of including multiple environmental factors which co-vary seasonally in determining potential drivers of change in kelp forests, and our results may be used to assist in predicting distributional changes in *L. corrugata* biogeography as well as establishing and optimising kelp aquaculture practices.

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Author contributions E. Paine: experimental design, conducted experiments, drafting and editing of manuscript; M. Schmid: experimental design, laboratory assistance, editing manuscript; J. D. Gaitán-Espitia: data analysis and graph creation; J. Castle: analysis of images; Ian Jameson: laboratory facilities and assistance; J. C. Sanderson: original concept, experimental design; C. Hurd: original concept, experimental design, editing manuscript.

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