



ELEVATED TEMPERATURE AFFECTS PHENOTYPIC PLASTICITY IN THE BULL KELP (*NEREOCYSTIS LUETKEANA*, PHAEOPHYCEAE)¹

Varoon P. Supratya ,² Liam J.M. Coleman , and Patrick T. Martone

Department of Botany and Beaty Biodiversity Research Centre, University of British Columbia, Vancouver, British Columbia V6T1Z4, Canada

The sensitivity of kelps to elevated temperatures has been linked to recent declines in some kelp populations, with cascading impacts on marine communities. However, it remains unclear how thermal stress affects the ability of kelps to respond to other environmental factors, which could influence their vulnerability to climate change. We investigated the effect of thermal stress on the ability of the bull kelp *Nereocystis luetkeana* to acclimate to its surrounding hydrodynamic environment through tension-regulated plasticity in blade morphology. We first determined optimal and stressful temperatures for *N. luetkeana* by measuring growth over nine temperatures from 5°C to 22°C. We then exposed *N. luetkeana* blades to a factorial combination of temperature (13°C and 20°C) and tension (0.5 N and 2.0 N) simulating different flow conditions, and measured changes in blade length and width after 7 days. The temperature at which *N. luetkeana* exhibited maximum growth was estimated to be ~11.9°C, though growth was high over a relatively wide temperature range. When thermally stressed, *N. luetkeana* maintained morphological responses to simulated high flow, but were inhibited from acclimating to low flow, indicated by an inability of blades to widen. Our results suggest that *N. luetkeana* in sheltered habitats may be particularly vulnerable to climate warming, where an inability to adjust blade morphology to local hydrodynamic conditions could drive declines at sublethal levels of warming. As ecologically important foundation species, declines in sheltered kelp populations could result in major biodiversity loss and disrupt ecosystem function.

Key index words: climate change; growth; kelp; light; macroalgae; morphology; *Nereocystis*; nutrients; plasticity; temperature

Abbreviations: L_f, final blade length; L_i, initial blade length; W_f, final blade width; W_i, initial blade width

Climate change is a major threat to marine ecosystems worldwide (Harley et al. 2006, Poloczanska et al.

2013). As ecologically important sources of habitat and primary productivity (Duggins et al. 1989, Teagle et al. 2017), marine macroalgae are of notable concern, as the effects of climate change may cascade to the multitudes of species that depend on them for survival (Harley et al. 2012). Kelps (order Laminariales) are among the largest and most structurally complex marine algae. As dominant components of temperate rocky coasts (Steneck et al. 2002), kelps support nearshore food webs and create habitat for many other organisms, both directly through the provision of structure and indirectly by chemical and hydrodynamic modification of the surrounding environment (Dayton 1985, Duggins et al. 1989, Smale et al. 2013, Teagle et al. 2017). Many kelps are sensitive to elevated temperatures (>15°C), which reduce growth rates, weaken tissues, increase mortality, and generally limit their biogeographic distributions to temperate ecosystems (Fortes and Lüning 1980, Bolton and Lüning 1982, Kirkman 1984, Lüning and Freshwater 1988, Steneck et al. 2002, Andersen et al. 2013, Simonson et al. 2015). With ongoing oceanic warming, kelps are likely to experience thermal stress with increasing frequency and severity. Increasing temperatures have already been implicated in kelp declines in Australia, Europe, and Eastern and Western North America (Andersen et al. 2013, Yesson et al. 2015, Wernberg et al. 2016a, Pfister et al. 2018, Rogers-Bennett and Catton 2019, Starko et al. 2019).

Kelps face rising temperatures in the context of a heterogeneous physical and chemical environment (Wernberg et al. 2010, Harley et al. 2012), and the response of kelps to elevated temperatures may depend upon other environmental conditions (Harley et al. 2012). Kelps frequently grow in current-swept, hydrodynamically energetic coastal environments (Koehl and Wainwright 1977, Friedland and Denny 1995, Gaylord and Denny 1997, de Bettignies et al. 2013), where forces exerted by waves and currents may represent a major source of mortality due to dislodgement from the substratum (Seymour et al. 1989, Dudgeon and Johnson 1992, Denny and Gaylord 2002, Pratt and Johnson 2002, Mach et al. 2007). At the same time, water motion also benefits kelps by increasing gas exchange and nutrient uptake (Hepburn et al. 2007). Kelps may reduce the effects of hydrodynamic forces by having drag-

¹Received 3 December 2019. Accepted 12 June 2020.

²Author for correspondence: e-mail varoon.p@alumni.ubc.ca.
Editorial Responsibility: M. Edwards (Associate Editor)

minimizing, streamlined blade morphologies (Martone et al. 2012, Starko and Martone 2016). However, streamlined blade morphologies have a reduced capacity for photosynthesis and nutrient uptake due to their limited surface area and, in kelps with multiple blades, tendency to self-shade (Koehl et al. 2008). Many kelps balance this morphological trade-off with phenotypic plasticity in blade morphology (summarized in Koehl et al. 2008). High-flow environments promote the growth of narrow, strap-like blades which minimize drag, while low-flow environments result in wide, thin, ruffled blades which increase exposure to light and nutrient uptake but incur more drag (Koehl et al. 2008; Fig. 1). Phenotypic plasticity in blade form is manifested in new growth produced subsequent to changes in flow conditions, with morphological changes observable in a matter of days when growth is rapid (Koehl et al. 2008). Interestingly, a high-flow blade morphology can be artificially induced by mechanically loading blades with weights, suggesting that blade morphology in situ is regulated by tensile forces from hydrodynamic drag (Gerard 1987, Koehl et al. 2008). Changes in blade morphology may represent shifts in biomass allocation—not rates of tissue production—as length and width can be traded against one another, and narrower blades elongate more rapidly than wider blades (Gerard 1987).

Tension-regulated plasticity likely allows some kelp species to thrive in a wide range of hydrodynamic conditions. Furthermore, as wave energy increases due to oceanic warming (Young et al. 2013, Reguero et al. 2019), plasticity may shield kelp populations from the subsequent hydrodynamic

effects. However, it remains unknown if thermal stress may affect this critical ability to modify morphology, which may result in negative interactions between elevated temperatures and intensified hydrodynamic environments as ocean conditions change. Past research has demonstrated that such multi-stressor interactions may be common in marine ecosystems (Crain et al. 2008, Kroeker et al. 2017), and have the potential to markedly influence macroalgal responses to climate change (Harley et al. 2012). Compared to research investigating the impact of isolated factors however, research on the effects of multi-stressor interactions remains limited, and the outcomes of such interactions are difficult to predict (Crain et al. 2008, Harley et al. 2012, Kroeker et al. 2017).

We investigated the effect of thermal stress on tension-regulated blade plasticity in the bull kelp *Nereocystis luetkeana*, a large, subtidal species that occurs across a range of flow conditions from California to the Aleutian Islands (Gardner and Setchell 1925; Fig. 1). As a thermal performance curve has not been generated for sporophytes of *N. luetkeana*, we first measured the growth of *N. luetkeana* over a range of temperatures to determine the threshold for thermal stress. We then quantified morphological responses to tension at optimal and stressful temperatures to determine if elevated temperatures affect the ability of *N. luetkeana* to respond to simulated high- and low-flow conditions. Given that morphological plasticity of blades is dependent on the production of new tissue, we hypothesize that thermal stress may cause a decrease in plasticity proportional to the reduction in growth rates. Furthermore, any observations of decreased plasticity not proportional to decreased growth rates may point to the resilience or susceptibility of the mechanism of developmental plasticity. Should thermal stress inhibit the vital ability to develop flow-appropriate morphologies, elevated temperatures could drive kelp declines even at sublethal levels of warming by reducing resource acquisition efficiency or increasing exposure to hydrodynamic forces. This impact of climate change may be particularly pronounced for kelps growing in more exposed environments, where being incapable of minimizing hydrodynamic stress could act synergistically with thermal weakening of tissues (Simonson et al. 2015) and increased wave energy (Young et al. 2013, Reguero et al. 2019).

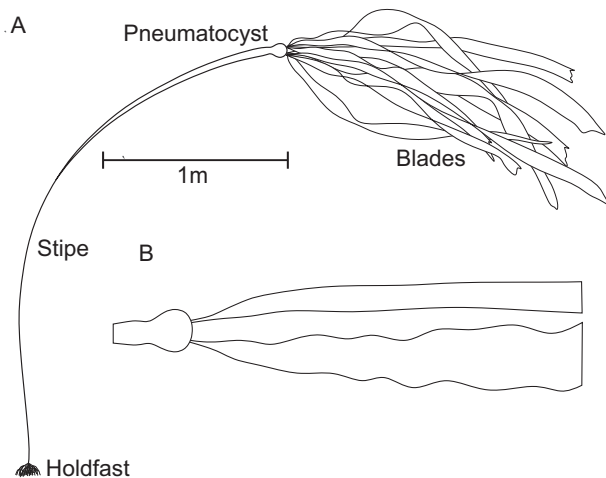


FIG. 1. (A) General morphology of *Nereocystis luetkeana*. The scale bar represents the approximate size of specimens collected from Stanley park. (B) Distinct morphologies of blades from different flow conditions; blades exposed to high-flow rates are flat and narrow (top) while blades from sheltered conditions are wider with ruffled margins (bottom).

MATERIALS AND METHODS

Specimen collection and acclimation. *Nereocystis luetkeana* sporophytes (50–100 mm pneumatocyst diameter) were haphazardly collected by wading between June 14 and October 4, 2018 from a small kelp bed near the Girl in a Wetsuit statue in Stanley Park, Vancouver, BC, Canada (49°18'9.4356" N, 123°7'33.4128" W). Specimens were generally growing in the shallow subtidal zone and had experienced little mechanical or thermal damage during past low tides; those that were damaged, reproductive, or covered in epiphytes were avoided.

Partial thalli consisting of the round portion of the pneumatocyst with attached blades truncated to 0.5 m length were transported to the University of British Columbia, where they were acclimated in illuminated ($\sim 110 \mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, 16:8 h light:dark photoperiod) sea tables containing recirculated seawater ($13 \pm 1^\circ\text{C}$, $\text{pH} = 7.75$, 34 salinity). Kelps collected for each experiment were used within 48 h post-collection to ensure the health of the blades.

Thermal performance curve. Growth of *Nereocystis luetkeana* blades was recorded as a proxy for stress over a range of temperatures in three custom recirculating climate-controlled growth flumes (Coanda Engineering, Burnaby, BC, Canada) that enabled the precise manipulation of water temperature, flow velocity, and flow direction (Fig. 2). We assumed that the thermal tolerance of *N. luetkeana* blade tissue was representative of that of the whole thallus. From each kelp, blades with the fewest sori and macroscopic epibionts, and least physical damage, were excised with a portion of the pneumatocyst attached to the base (Fig. 3). This pneumatocyst portion anchored the blades in the growth tanks and acted as a physical buffer against tissue degradation from the cut surfaces. The distal end of each blade was trimmed to a uniform initial length of 400 mm immediately prior to the start of a trial to simplify subsequent measurements of blade elongation. The flumes were filled with seawater ($\text{pH} = 7.75$, 34 salinity) enriched with Micro-Algae Grow™ Guillard f/2 growth medium (Florida Aqua Farms) and exposed to $\sim 90 \mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ for 16 h per d. At each of nine temperatures (5°C , 7°C , 10°C , 12°C , 13°C , 15°C , 17°C , 20°C , and 22°C), six blades were anchored by the base and left to grow in a uniform flow of $0.7 \text{ m} \cdot \text{s}^{-1}$ for 8 d, after which we recorded the final length of the blades rounded to the nearest 5 mm. Trials had to be conducted over four time blocks due to the limited number of flumes (10°C and 15°C initiated on June 15, 7°C and 22°C on June 29, 12°C and 20°C on July 12, and 5°C , 13°C and 17°C on August 10). Multiple blades were often derived from a single sporophyte due to a limited number of healthy individuals ($n = 24$). However, blades from an individual sporophyte were distributed such that no temperature treatment had more than one blade from an individual. Blade growth was expressed as an unbounded percentage of the initial blade length using the formula:

$$\Delta\% \text{Length} = \frac{L_f - L_i}{L_i} * 100\% \quad (1)$$

where L_f was the final length of the blade and L_i the initial length (standardized to 400 mm). We examined the relationship between temperature and blade growth with a quadratic linear mixed model using the “lme4” package (Bates et al. 2015), incorporating time block and sporophyte individual as random effects. Significance of fixed and random effects was determined with the “lmerTest” package (Kuznetsova et al. 2017). Homoscedasticity and normality of residuals were checked graphically with quantile–quantile and residual plots. A follow-up comparison of blade growth at $\sim 190 \mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ was conducted at 13°C to rule out the possibility of low light levels limiting growth at optimal temperatures, which was analyzed with a paired *t*-test. All statistical analyses were conducted using R statistical software version 3.6.1 (R Core Team 2019).

Plasticity experiments. We used a 2×2 factorial design to determine the effect of thermal stress on the tension-regulated plastic response of *Nereocystis luetkeana* blades. *Nereocystis luetkeana* blades were prepared as outlined previously for the creation of the thermal performance curve. However, blades were trimmed to an initial length of 350 mm instead. These

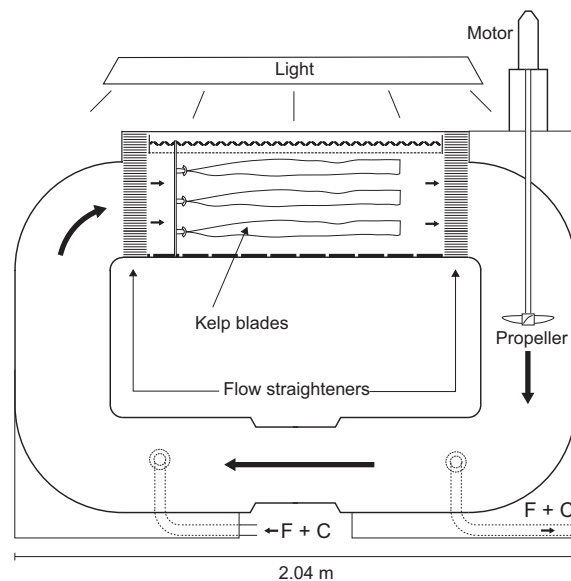


FIG. 2. A schematic diagram of a recirculating growth flume, with water flow indicated by solid arrows. Filtration and chiller units (F + C) not depicted.

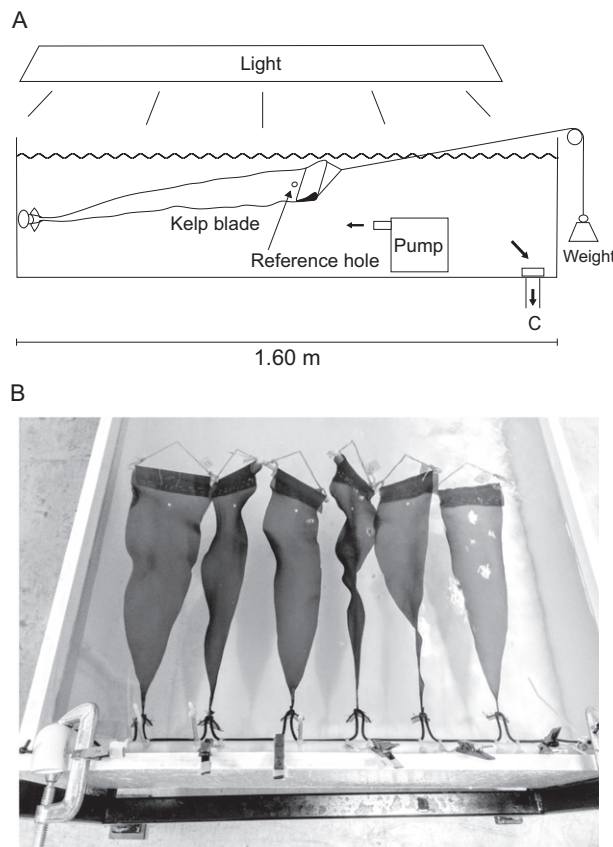


FIG. 3. (A) Schematic diagram of the setup used to apply tension to kelp blades. Aquarium pumps ensured constant but non-directional water motion. The water was circulated through a chiller (C) to maintain the correct temperatures. (B) A view from above of kelp blades under tension in the sea table.

experiments were conducted in sea tables filled with seawater (pH = 7.75, 34 salinity) enriched with Micro-Algae Grow™ Guillard f/2 growth medium as with the thermal performance curve (Fig. 3). Following Koehl et al. (2008), the distal end of the blade was folded on itself to form a loop, which was sewn together with cotton thread (Fig. 3). A small hole was punched through the distal blade at 300 mm length as a reference point for length measurements (Fig. 3). A nylon rod was pushed through the loop, and weights were suspended on a string tied to the rod (Fig. 3). Pneumatocyst pieces were anchored in slots on one end of the sea table and the blades were suspended horizontally by the weights hanging from the opposite edge of the sea table (Fig. 3). The way the blades were suspended resulted in a slight upwards angle. However, the angle was small (~5.6°), and the difference in distance to the light source between the base and the distal end was much smaller than intra-blade differences due to blade ruffling (Fig. 3). Weights were calibrated to apply either 0.5 N or 2.0 N of tension on the blades with a 5 N spring scale (OHAUS 8002-MN), simulating a sheltered environment with low drag and a current-swept environment with higher drag, respectively. These forces are within the range experienced by kelp blades in a natural setting (Charteris 1969, as cited in Gerard 1987). Weight treatments were alternated on blades suspended side by side (Fig. 3). Low (0.5 N) and high (2 N) tension blades were further subdivided into two temperature treatments selected based on the thermal performance curve: 13 ± 1°C (near optimal) and 20 ± 1°C (stressful but not immediately lethal). For each blade, the width 100 mm from the base was recorded to the nearest millimeter. Blades were subsequently allowed to grow in the treatment combinations for 7 d (~90 μmol photons · m⁻² · s⁻¹ 16 h light photoperiod). Blade width (100 mm from the base) was measured again at the end of the growth period, along with the final length of the blade (rounded to the nearest 5 mm). To increase the number of replicates, this experiment was conducted twice (block 1 on September 13 and block 2 on October 6, resulting in a pooled total of 12 blades each in the 13°C × 0.5 N and 13°C × 2 N treatments, but 11 and 10 blades in the 20°C × 0.5 N and 20°C × 2 N treatments, respectively, due to breakage during the growth period. In some cases, multiple blades were derived from a single sporophyte due to a limited number of healthy individuals (*n* = 14). However, no treatment combination had more than one blade from an individual. Blade elongation was calculated as an unbounded percentage of the initial blade length using the formula:

$$\Delta\% \text{Length} = \frac{L_f - L_i}{L_i} * 100\% \quad (2)$$

whereby L_f was the final length of the blade and L_i the initial length (standardized to 350 mm). The percent change in width was calculated as an unbounded percentage of the initial width with the formula:

$$\Delta\% \text{Width} = \frac{W_f - W_i}{W_i} * 100\% \quad (3)$$

whereby W_f was the final width of the blade at 100 mm and W_i the initial width. We analyzed the effect of temperature and tension on blade elongation and width with linear mixed models using the “lme4” package (Bates et al. 2015). We incorporated temperature, tension, and the two time blocks as fixed effects, and treated sporophyte individual as a random effect. Significance of fixed and random effects was determined with the “lmerTest” package, and homoscedasticity and normality of residuals were checked graphically with quantile–quantile and residual plots. The change in blade width in

each treatment combination was subsequently compared to a null value (0% width change) with one sample *t*-tests (four comparisons), and a student’s *t*-test was used to compare the two high tension treatments (one comparison). α -values for all *t*-tests were adjusted with a Bonferroni correction to $\alpha = 0.01$.

RESULTS

Thermal performance curve. The effect of temperature (5–22°C) on the growth of *Nereocystis luetkeana* could be expressed with the following quadratic function: Growth (%) = 4.40,860 + 12.13,513 (°C) – 0.51,191 (°C)² ($P < 0.01$, conditional $R^2 = 0.67$; Fig. 4). Maximum growth was predicted to occur at ~11.9°C (Fig. 4). Random effects of block (LRT = 0.92, $P = 0.34$) and sporophyte individual (LRT = 0.03, $P = 0.86$) were not significant. Light levels in the flumes were not limiting, as blades did not grow significantly more at ~190 μmol photons · m⁻² · s⁻¹ than at ~90 μmol photons · m⁻² · s⁻¹ (Paired *t*-test, $t_5 = -1.56$, $P = 0.18$).

Plasticity experiments. Initial blade widths did not significantly differ between treatments (ANOVA, $F_{3,44} = 0.26$, $P = 0.85$), and were as follows (mean ± SD): 60.5 ± 15.8 mm (13°C × 0.5 N), 56.8 ± 10.3 mm (13°C × 2 N), 56.8 ± 13.4 mm (20°C × 0.5 N), and 56.2 ± 13.5 mm (20°C × 2 N). Elevated temperature significantly reduced blade elongation (linear mixed model, $t_{26} = -5.13$, $P < 0.01$; Fig. 5): elongation at 13°C (69.3 ± 14.7%, mean ± SD) was greater than at 20°C (37.8 ± 7.5%). Tension had a significant effect on blade elongation (linear mixed model, $t_{25,4} = 3.60$,

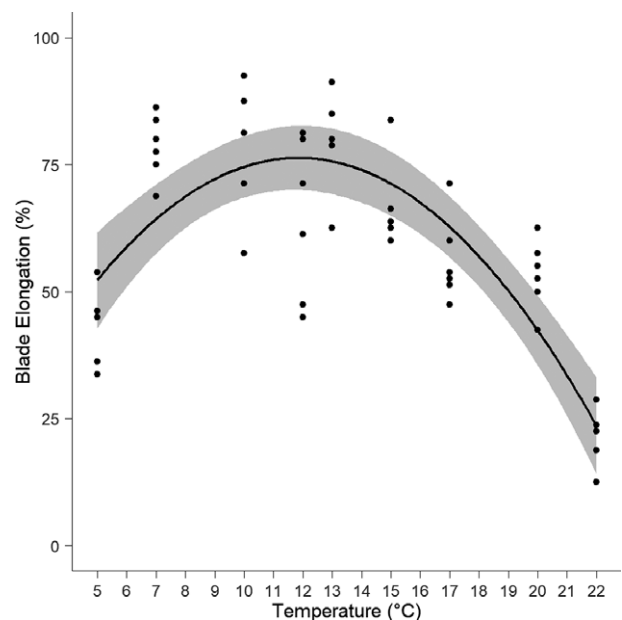


FIG. 4. Effect of temperature on blade elongation of *Nereocystis luetkeana* after 7 d. Each point represents an individual blade. The data were fitted to a quadratic model of the form $y = -ax^2 + bx + c$, with the shaded area representing 95% confidence intervals.

$P < 0.01$; Fig. 5), with blades experiencing 2 N tension elongating more ($60.8 \pm 21.5\%$) than blades experiencing 0.5 N tension ($48.6 \pm 16.4\%$). The effect of tension on blade elongation was not different between temperatures (linear mixed model, $t_{26.8} = -1.43$, $P = 0.16$; Fig. 5). Blade elongation was not different between time blocks (linear mixed model, $t_{31.3} = 0.10$, $P = 0.92$), nor did the effects of temperature and tension differ between blocks ($P > 0.76$ for all interactions). However, blade elongation differed across sporophyte individuals (LRT = 4.45, $P = 0.03$).

The effect of tension on *Nereocystis luetkeana* blade width depended upon temperature (linear mixed model, $t_{28.3} = 2.67$, $P = 0.01$; Fig. 5). Blades

experiencing 0.5 N widened significantly at 13°C (One-sample t -test, $15.8 \pm 13.3\%$, $t_{11} = 4.11$, $P < 0.01$; Fig. 5) but did not change in width at 20°C (one-sample t -test, $0.63 \pm 6.39\%$, $t_{10} = -0.32$, $P = 0.75$; Fig. 5). Blades experiencing 2 N of tension narrowed significantly at 13°C (one-sample t -test, $-9.9 \pm 9.9\%$; $t_{11} = -3.47$, $P < 0.01$; Fig. 5) and at 20°C (one-sample t -test, $-9.3 \pm 8.2\%$; $t_9 = -3.58$, $P < 0.01$; Fig. 5). Narrowing at 2 N tension was not significantly different between blades grown at 13°C and 20°C (Student's t -test, $t_{20} = 0.16$, $P = 0.88$; Fig. 5). The change in blade width was not different between time blocks (linear mixed model, $t_{33.7} = 0.75$, $P = 0.46$), nor did the effects of temperature and tension differ between blocks ($P > 0.31$ for all interactions). The change in blade width was not significantly different across sporophyte individuals (LRT₁ = 3.47, $P = 0.06$).

DISCUSSION

Anthropogenic warming has been linked to kelp declines across the globe (Andersen et al. 2013, Yesson et al. 2015, Krumhansl et al. 2016, Pfister et al. 2018, Rogers-Bennett and Catton 2019, Starko et al. 2019). However, responses to interactions between warming and other environmental factors, which may differ from responses to isolated factors, remain under-investigated despite their prevalence in marine ecosystems (Crain et al. 2008, Harley et al. 2012, Kroeker et al. 2017). In this study, we characterized the thermal performance of the kelp *Nereocystis luetkeana* and investigated the effect of thermal stress on the ability of *N. luetkeana* to respond to simulated high- and low-flow conditions. *Nereocystis luetkeana* growth exhibited a thermal optimum of $\sim 11.9^\circ\text{C}$. Thermally stressed *N. luetkeana* blades developed streamlined morphologies when subject to high tensile forces (as they would in high-flow, exposed habitats). However, they no longer widened when experiencing low tensile forces characteristic of low-flow, sheltered habitats.

The thermal optimum determined for *Nereocystis luetkeana* sporophytes was comparable to that of many other temperate kelp species (Fortes and Lüning 1980, Bolton and Lüning 1982, Andersen et al. 2013, Hargrave et al. 2017) and to *N. luetkeana* gametophytes (Lind and Konar 2017). However, unlike thermal performance curves generated for other kelp species that tended to show sharply increasing or decreasing growth on both sides of the optimum (Fortes and Lüning 1980, Bolton and Lüning 1982, Gao et al. 2013a), the growth of *N. luetkeana* was high over a wide range of temperatures. We considered the possibility that this plateau was caused by limited irradiance in the flumes, capping growth at optimal temperatures without affecting the shape of the curve at more stressful temperatures. However, follow-up experiments conducted at double the irradiance failed to produce

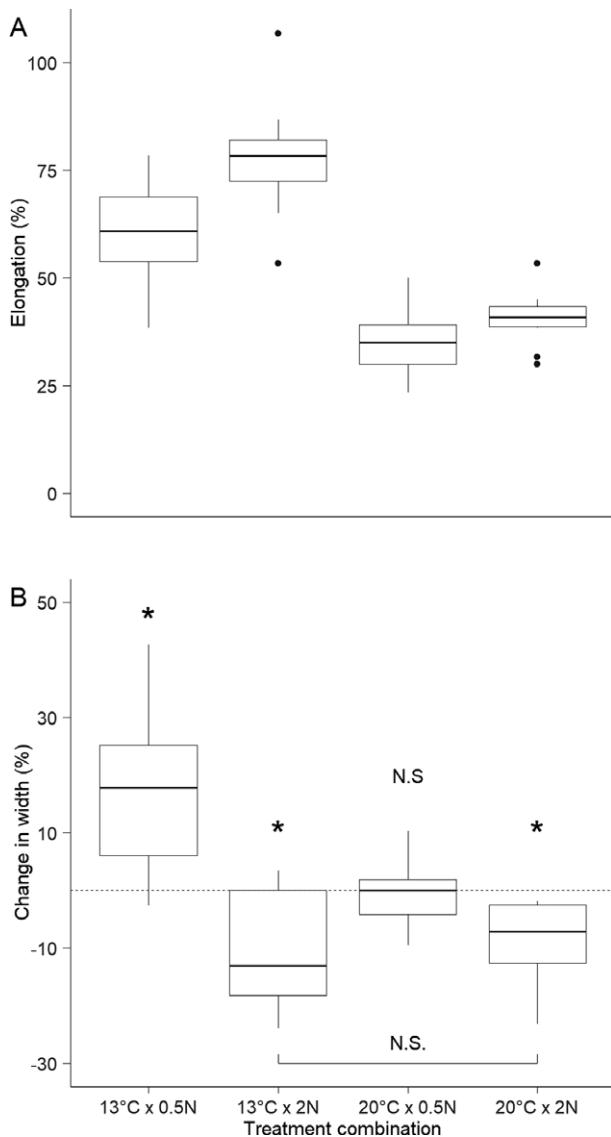


FIG. 5. (A) Relative elongation of *Nereocystis luetkeana* blades grown for 7 d in different combinations of temperature and tension. (B) Relative change in width of *Nereocystis luetkeana* blades grown for 7 d in different combinations of temperature and tension. Asterisks indicate significant changes from the starting blade widths, "N.S." indicate no difference.

higher growth rates. As many published thermal performance curves have fewer temperature points with large (3–5°C) increments (Fortes and Lüning 1980, Bolton and Lüning 1982, Gao et al. 2013a), we speculate that the apparent tendency for sharp thermal optima in other kelps may be the result of insufficient resolution. Other published thermal performance curves with more temperature points (including the one here for *N. luetkeana*) often demonstrate optimal growth over a wider range of temperatures (Gao et al. 2013b, Komazawa et al. 2015, but see Wernberg et al. 2016b). The wide thermal optimum may reflect the widespread distribution and generalist nature of *N. luetkeana*, allowing it to tolerate thermal environments from California to the Aleutian Islands (Gardner and Setchell 1925). However, significant ecotypic variation has been documented in kelps (e.g., Buschmann et al. 2004, Gao et al. 2013b), and future research will be required to determine the relative contribution of local adaptation to the thermal tolerance of *N. luetkeana* populations.

Despite a reduction in overall growth, thermally stressed *Nereocystis luetkeana* blades remained capable of responding to high tension by developing a narrower and more elongate blade form. In contrast, the effect of thermal stress was disproportionately pronounced in blades under low tension, which did not widen despite showing reduced rates of elongation. We speculate that this inability to widen may stem from a disruption of normal blade development. In kelps, new blade growth, initially narrow at the intercalary meristem at the base of the blade, widens as it is pushed distally (Kain Jones 1987). Elevated temperatures are known to physiologically disrupt kelps (Simonson et al. 2015, Nepper-Davidsen et al. 2019), and an inability to widen could indicate a disruptive effect of thermal stress on cell division or expansion perpendicular to the long axis of the blade. In low-flow conditions, where the development of wider blades is favored, being unable to widen would be especially conspicuous. However, for blades growing in conditions that would already promote blades to remain narrow, an inability to widen may not result in observable differences in blade morphology under thermal stress. This apparent decoupling of the trade-off between blade elongation and widening may possibly be due to reduced biomass gain under thermal stress, effects of tension on carbon uptake (Kraemer and Chapman 1991), or altered allocation of biomass into blade thickness instead of either length or width. Further research will be required to determine what mechanisms underlie tension-regulated plasticity in kelp blades, and how these mechanisms are compromised by thermal stress. Additionally, it may be worth investigating whether the sensitivity of these mechanisms to thermal stress varies across populations of *N. luetkeana*. Ecotypic adaptation to local thermal environments (see Buschmann et al.

2004, Gao et al. 2013b) could conceivably extend to the thermal sensitivity of tension-regulated plasticity.

Contrary to our predictions, a reduced capacity to develop a low-flow morphology may make thermally stressed *Nereocystis luetkeana* especially vulnerable to warming in sheltered habitats by impairing their ability to acquire resources under such conditions. Nutrient stress in warm, low-flow conditions may be further exacerbated by increased nitrogen requirements to maintain physiological function in elevated temperatures (Gerard 1997), rendering such areas inhospitable even at sublethal temperatures. A decline in intertidal kelp abundance has been observed in sheltered habitats following abnormally elevated temperatures, without a corresponding loss in nearby exposed areas (Starko et al. 2019). These declines were attributed to a lack of wave splash keeping exposed kelps cool during low tides, or to limited water motion allowing localized pockets of warm water to form (Starko et al. 2019). This study proposes an additional mechanism by which elevated ocean temperatures may affect kelps growing in sheltered areas, and suggests that temperature-driven kelp declines in sheltered habitats could include both intertidal and subtidal species.

In summary, phenotypic plasticity allows some kelp species to tune their blade morphology to match surrounding flow conditions, contributing to their ability to thrive in a wide range of hydrodynamic environments. Morphological responses to simulated high water flow were maintained under thermal stress despite reduced growth, but morphological responses to simulated low flow were significantly inhibited, as blades did not widen in such conditions. Our results suggest that the effect of oceanic warming on *Nereocystis luetkeana* will be particularly pronounced in sheltered habitats, where an inability to adjust blade morphology could lead to temperature-driven declines even before warming becomes lethal. Given the importance of healthy kelp populations in modifying coastal habitats and increasing biodiversity, declines in kelp abundance along sheltered coasts could result in significant biodiversity loss and community restructuring.

We are indebted to Alana Breitreutz, Matt Whalen, Joani Viliunas, and Ania Łoboda for assisting with the collection and processing of kelp. We are thankful for the input of Matt Whalen, Sam Starko, Lauran Liggan, Alana Breitreutz, and Christopher Harley with regards to interpreting and analyzing the data, and for the feedback of Sam Starko, Alana Breitreutz, and Joani Viliunas on the manuscript. This research was made possible by an NSERC Discovery grant and funding from the Canada Foundation for Innovation (#27431) awarded to PTM.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

- Andersen, G. S., Pedersen, M. F. & Nielsen, S. L. 2013. Temperature acclimation and heat tolerance of photosynthesis in Norwegian *Saccharina latissima* (Laminariales, Phaeophyceae). *J. Phycol.* 49:689–700.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67:1–48.
- Bolton, J. J. & Lüning, K. 1982. Optimal growth and maximal survival temperatures of Atlantic *Laminaria* species (Phaeophyta) in culture. *Mar. Biol.* 66:89–94.
- Buschmann, A. H., Vásquez, J. A., Osorio, P., Reyes, E., Filún, L., Hernández-González, M. C. & Vega, A. 2004. The effect of water movement, temperature and salinity on abundance and reproductive patterns of *Macrocystis* spp. (Phaeophyta) at different latitudes in Chile. *Mar. Biol.* 145:849–62.
- Crain, C. M., Kroeker, K. & Halpern, B. S. 2008. Interactive and cumulative effects of multiple human stressors in marine systems. *Ecol. Lett.* 11:1304–15.
- Dayton, P. K. 1985. Ecology of kelp communities. *Annu. Rev. Ecol. Syst.* 16:215–45.
- de Bettignies, T., Wernberg, T. & Lavery, P. S. 2013. Size, not morphology, determines hydrodynamic performance of a kelp during peak flow. *Mar. Biol.* 160:843–51.
- Denny, M. & Gaylord, B. 2002. The mechanics of wave-swept algae. *J. Exp. Biol.* 205:1355–62.
- Dudgeon, S. R. & Johnson, A. S. 1992. Thick vs. thin: thallus morphology and tissue mechanics influence differential drag and dislodgement of two co-dominant seaweeds. *J. Exp. Mar. Biol. Ecol.* 165:23–43.
- Duggins, D. O., Simenstad, C. A. & Estes, J. A. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science* 245:170–3.
- Fortes, M. D. & Lüning, K. 1980. Growth rates of North Sea macroalgae in relation to temperature, irradiance and photoperiod. *Helgoländer Meeresuntersuchungen* 34:15–29.
- Friedland, M. T. & Denny, M. W. 1995. Surviving hydrodynamic forces in a wave-swept environment: consequences of morphology in the feather boa kelp, *Egregia menziesii* (Turner). *J. Exp. Mar. Biol. Ecol.* 190:109–33.
- Gao, X., Endo, H., Taniguchi, K. & Agatsuma, Y. 2013a. Combined effects of seawater temperature and nutrient condition on growth and survival of juvenile sporophytes of the kelp *Undaria pinnatifida* (Laminariales; Phaeophyta) cultivated in northern Honshu. *Japan. J. Appl. Phycol.* 25:269–75.
- Gao, X., Endo, H., Taniguchi, K. & Agatsuma, Y. 2013b. Genetic differentiation of high-temperature tolerance in the kelp *Undaria pinnatifida* sporophytes from geographically separated populations along the Pacific coast of Japan. *J. Appl. Phycol.* 25:567–74.
- Gardner, N. L. & Setchell, W. A. 1925. *The marine algae of the Pacific coast of North America*. University of California Press, Berkeley, CA, USA, 624 pp.
- Gaylord, B. & Denny, M. W. 1997. Flow and flexibility I. Effects of size, shape and stiffness in determining wave forces on the stipitate kelps *Eisenia arborea* and *Pterygophora californica*. *J. Exp. Biol.* 200:3141–64.
- Gerard, V. A. 1987. Hydrodynamic streamlining of *Laminaria saccharina* Lamour. in response to mechanical stress. *J. Exp. Mar. Biol. Ecol.* 107:237–44.
- Gerard, V. A. 1997. The role of nitrogen nutrition in high-temperature tolerance of the kelp, *Laminaria saccharina* (Chromophyta). *J. Phycol.* 33:800–10.
- Hargrave, M. S., Foggo, A., Pessarrodona, A. & Smale, D. A. 2017. The effects of warming on the ecophysiology of two co-existing kelp species with contrasting distributions. *Oecologia* 183:531–43.
- Harley, C. D. G., Anderson, K. M., Demes, K. W., Jorve, J. P., Kordas, R. L., Coyle, T. A. & Graham, M. H. 2012. Effects of climate change on global seaweed communities. *J. Phycol.* 48:1064–78.
- Harley, C. D. G., Hughes, R. A., Hultgren, K. M., Miner, B. G., Sorte, C. J. B., Thornber, C. S., Rodriguez, L. F., Tomanek, L. & Williams, S. L. 2006. The impacts of climate change in coastal marine systems. *Ecol. Lett.* 9:228–41.
- Hepburn, C., Holborow, J., Wing, S., Frew, R. & Hurd, C. 2007. Exposure to waves enhances the growth rate and nitrogen status of the giant kelp *Macrocystis pyrifera*. *Mar. Ecol. Prog. Ser.* 339:99–108.
- Kain Jones, J. M. 1987. Patterns of relative growth in *Nereocystis luetkeana* (Phaeophyta). *J. Phycol.* 23:181–7.
- Kirkman, H. 1984. Standing stock and production of *Ecklonia radiata* (C.Ag.). *J. Exp. Mar. Biol. Ecol.* 76:119–30.
- Koehl, M. A. R., Silk, W. K., Liang, H. & Mahadevan, L. 2008. How kelp produce blade shapes suited to different flow regimes: a new wrinkle. *Integr. Comp. Biol.* 48:834–51.
- Koehl, M. A. R. & Wainwright, S. A. 1977. Mechanical adaptations of a giant kelp. *Limnol. Oceanogr.* 22:1067–71.
- Komazawa, I., Sakanishi, Y. & Tanaka, J. 2015. Temperature requirements for growth and maturation of the warm temperate kelp *Eckloniopsis radicata* (Laminariales, Phaeophyta). *Phycol. Res.* 63:64–71.
- Kraemer, G. P. & Chapman, D. J. 1991. Effects of tensile force and nutrient availability on carbon uptake and cell wall synthesis in blades of juvenile *Egregia menziesii* (Turn.) Aresch. (Phaeophyta). *J. Exp. Mar. Biol. Ecol.* 149:267–77.
- Kroeker, K. J., Kordas, R. L. & Harley, C. D. G. 2017. Embracing interactions in ocean acidification research: confronting multiple stressor scenarios and context dependence. *Biol. Lett.* 13:20160802.
- Krumhansl, K. A., Okamoto, D. K., Rassweiler, A., Novak, M., Bolton, J. J., Cavanaugh, K. C., Connell, S. D. et al. 2016. Global patterns of kelp forest change over the past half-century. *Proc. Natl. Acad. Sci. USA* 113:13785–90.
- Kuznetsova, A., Brockhoff, P. B. & Christensen, R. H. B. 2017. lmerTest package: tests in linear mixed effects models. *J. Stat. Softw.* 82:1–26.
- Lind, A. C. & Konar, B. 2017. Effects of abiotic stressors on kelp early life-history stages. *Algae*. 32:223–33.
- Lüning, K. & Freshwater, W. 1988. Temperature tolerance of Northeast Pacific marine algae. *J. Phycol.* 24:310–5.
- Mach, K. J., Hale, B. B., Denny, M. W. & Nelson, D. V. 2007. Death by small forces: a fracture and fatigue analysis of wave-swept macroalgae. *J. Exp. Biol.* 210:2231–43.
- Martone, P. T., Kost, L. & Boller, M. 2012. Drag reduction in wave-swept macroalgae: alternative strategies and new predictions. *Am. J. Bot.* 99:806–15.
- Nepper-Davidsen, J., Andersen, D. & Pedersen, M. 2019. Exposure to simulated heatwave scenarios causes long-term reductions in performance in *Saccharina latissima*. *Mar. Ecol. Prog. Ser.* 630:25–39.
- Pfister, C. A., Berry, H. D. & Mumford, T. 2018. The dynamics of kelp forests in the northeast Pacific Ocean and the relationship with environmental drivers. *J. Ecol.* 106:1520–33.
- Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., Brander, K. et al. 2013. Global imprint of climate change on marine life. *Nat. Clim. Change* 3:919–25.
- Pratt, M. C. & Johnson, A. S. 2002. Strength, drag, and dislodgement of two competing intertidal algae from two wave exposures and four seasons. *J. Exp. Mar. Biol. Ecol.* 272:71–101.
- R Core Team. 2019. *A Language and environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Reguero, B. G., Losada, I. J. & Méndez, F. J. 2019. A recent increase in global wave power as a consequence of oceanic warming. *Nat. Comm.* 10:1–14.
- Rogers-Bennett, L. & Catton, C. A. 2019. Marine heat wave and multiple stressors tip bull kelp forest to sea urchin barrens. *Sci. Rep.* 9:15050.
- Seymour, R. J., Tegner, M. J., Dayton, P. K. & Parnell, P. E. 1989. Storm wave induced mortality of giant kelp, *Macrocystis pyrifera*, in southern California. *Estuar. Coast. Shelf Sci.* 28:277–92.
- Simonson, E. J., Scheibling, R. E. & Metaxas, A. 2015. Kelp in hot water: I. Warming seawater temperature induces weakening and loss of kelp tissue. *Mar. Ecol. Prog. Ser.* 537:89–104.
- Smale, D. A., Burrows, M. T., Moore, P., O'Connor, N. & Hawkins, S. J. 2013. Threats and knowledge gaps for ecosystem services provided by kelp forests: a northeast Atlantic perspective. *Ecol. Evol.* 3:4016–38.

- Starko, S., Bailey, L. A., Creviston, E., James, K. A., Warren, A., Brophy, M. K., Danasel, A., Fass, M. P., Townsend, J. A. & Neufeld, C. J. 2019. Environmental heterogeneity mediates scale-dependent declines in kelp diversity on intertidal rocky shores. *PLoS ONE* 14:e0213191.
- Starko, S. & Martone, P. T. 2016. An empirical test of 'universal' biomass scaling relationships in kelps: evidence of convergence with seed plants. *New Phytol.* 212:719–29.
- Steneck, R. S., Graham, M. H., Bourque, B. J., Corbett, D., Erlandson, J. M., Estes, J. A. & Tegner, M. J. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ. Conserv.* 29:436–59.
- Teagle, H., Hawkins, S. J., Moore, P. J. & Smale, D. A. 2017. The role of kelp species as biogenic habitat formers in coastal marine ecosystems. *J. Exp. Mar. Bio. Ecol.* 492:81–98.
- Wernberg, T., Bennett, S., Babcock, R. C., De Bettignies, T., Cure, K., Depczynski, M., Dufois, F. et al. 2016a. Climate-driven regime shift of a temperate marine ecosystem. *Science* 353:169–72.
- Wernberg, T., de Bettignies, T., Joy, B. A. & Finnegan, P. M. 2016b. Physiological responses of habitat-forming seaweeds to increasing temperatures. *Limnol. Oceanogr.* 61:2180–90.
- Wernberg, T., Thomsen, M. S., Tuya, F., Kendrick, G. A., Staehr, P. A. & Toohey, B. D. 2010. Decreasing resilience of kelp beds along a latitudinal temperature gradient: potential implications for a warmer future. *Ecol. Lett.* 13:685–94.
- Yesson, C., Bush, L. E., Davies, A. J., Maggs, C. A. & Brodie, J. 2015. Large brown seaweeds of the British isles: evidence of changes in abundance over four decades. *Estuar. Coast. Shelf Sci.* 155:167–75.
- Young, I. R., Zieger, S., Vinoth, J. & Babanin, A. V. 2013. Global trends in extreme wind speed and wave height. *Proc. Int. Conf. Offshore Mech. Arct. Eng. – OMAE.* 2 A:451–5.