Reef recovery and resilience: interpreting abiotic effects on critical early life stages of large brown algae

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ABSTRACT: Rocky reefs throughout the temperate zone are dominated by large brown algae, which are major foundation species and ecosystem engineers. There is usually an ecological bottleneck at the early life stage of such algae when they are vulnerable to a wide range of stressors. A large earthquake that affected the coastline of southern New Zealand highlighted the combined effects of sudden changes to multiple stressors on large algal assemblages. In particular, the regime of temperature, sediment and light suddenly changed as the coastal platform was lifted, and sediments from the catchment occluded the light environment of nearshore waters. Here we tested the effects of these stressors on early survival and growth of 3 formerly dominant species — the fucoids *Landsburgia quercifolia* and *Durvillaea antarctica* and the laminarian *Lessonia variegata* — over 100 d using a culture laboratory. After 42 d, interactive effects were found for growth of all species. Decreasing light and increasing temperature had the greatest negative effect on *L. variegata* and *D. antarctica* growth. Growth was minimal at the lowest light treatment (PAR: 16 µmol m^{-2} s^{-1}) for all species, but often least growth was found at the highest sediment treatment (PAR: 32 µmol m^{-2} s^{-1}). *L. quercifolia* was resilient to increasing temperature, whereas survival and growth decreased with increasing temperature for *D. antarctica* and *L. variegata.* These results are highly suggestive of the coincident influences of major stressors on the post-earthquake marine ecosystem. These results also highlight that recovery of large brown algae following disturbance events is likely to be slow due to an increase in coastal sedimentation and extreme water temperature.

KEY WORDS: Kelp · Fucoid · Juvenile macroalgae · Early life stage · Temperature · Sediment · Light · Earthquake · New Zealand

1. INTRODUCTION

Coastal ecosystem health and management of stressors have received increasing attention in the past few decades, in large part due to increased anthropogenic impacts affecting water quality and benthic habitat structure (Airoldi 2003, Wernberg et al. 2005, Fernandino et al. 2018, Magris et al. 2019, Smale et al. 2019). Multiple stressors including variations in light attenuation, sediment loading, water temperature and wave intensity can critically influence coastal ecosystem dynamics and are known to

be undergoing change (Airoldi 2003, Vaselli et al. 2008, Schiel et al. 2016, 2019, Smale et al. 2019, Thomsen et al. 2021). Increased sedimentation from riverine input and urban runoff can smother sessile organisms, increase turbidity and attenuate solar irradiance in coastal waters (Airoldi 2003, Isæus et al. 2004, Schiel et al. 2006, Alestra & Schiel 2015, Magris et al. 2019), with consequent effects on the depth distribution of key algal primary producers (Tait & Schiel 2011, 2018, Desmond et al. 2019). An increase in critical air temperatures and marine heatwaves can limit species distribution, decrease biodiversity

and enhance susceptibility to invasive species (Schiel et al. 2004, Yesson et al. 2015, Thomsen et al. 2019, Smale et al. 2019, Benedetti-Cecchi 2021).

Large brown, habitat-forming algae are among the organisms that are most vulnerable to an increase in coastal sedimentation and sea temperature (Schiel et al. 2016, Rindi et al. 2017, Smale et al. 2019, Tait 2019, Wernberg et al. 2019) as they are fixed in place on the reef platform and cannot migrate to reduce stress. They are also one of the more important members of a rocky reef community as they provide a foundation for and fill a variety of functional roles among temperate coastal ecosystems, such as providing substrate stability, acting as a food source and providing refuge to myriad species (Schiel & Foster 1986, Bertocci et al. 2015, Pérez-Matus et al. 2017, Wernberg et al. 2019).

Most large brown algae in temperate zones have seasonal reproduction which is synchronised with environmental cycles, especially light and temperature (Santelices 1990, Schiel & Foster 2006, Wernberg et al. 2019). There is a known bottleneck among the early life stages of large brown algae, where survival is often less than 0.001% of reproductive output (Schiel & Foster 2006). The already low survival of large brown algal recruitment can be further compromised by an increase in coastal sedimentation, which can smother and/or physically abrade zygotes, germlings and juveniles (Airoldi 2003, Irving et al. 2009, Alestra & Schiel 2015), as well as preclude propagule attachment to the substratum due to shifting substrate (Taylor & Schiel 2003, 2005, Schiel et al. 2006, Stevens et al. 2008, Taylor et al. 2010, Schiel & Gunn 2019). A reduction in subtidal solar irradiance caused by the suspension of sediments in the water column can also have a negative effect on large brown algal germlings and juveniles due to lower photosynthetic productivity (Airoldi 2003, Irving et al. 2009). Furthermore, warming sea temperature can negatively affect the survival and growth of the early life stage of large brown algae (Irving et al. 2009, Andrews et al. 2014, Alestra & Schiel 2015, Franco et al. 2018).

A combination of stressors such as an increase in coastal sedimentation, a reduction in water clarity, and an intensification of wave climate were brought to the forefront by a 7.8 Mw earthquake that struck southern New Zealand (herein, the Kaikōura coastline) in November 2016. The earthquake lifted the coastal platform by up to 6 m (Clark et al. 2017, Hamling et al. 2017) and caused massive mortality to intertidal and shallow subtidal organisms along 130 km of coastline (Schiel et al. 2019). The effects of the earthquake on these communities were accentuated by erosion of the sedimentary reef and boulders that became fully exposed (above the tidal line) following the uplift (Orchard et al. 2021). The earthquake uplift also resulted in extensive amounts of bare space in intertidal and shallow subtidal zones due to severe reductions in the abundance of several species of large brown algae, such as the southern bull kelps, *Durvillaea* spp. (a fucoid) and the shallow-living kelp, *Lessonia variegata* (a laminarian) (Schiel et al. 2019, 2021, Thomsen et al. 2019). One of the main large brown algal survivors in areas that were the most affected by the earthquake was the tough, shrub-like subtidal fucoid, *Landsburgia quercifolia.* Furthermore, lag effects of the earthquake such as the weathering/erosion of bare reef rock and an increase in riverine-related sedimentation from inland landslips continued to decrease nearshore water clarity and shift substrates (Orchard et al. 2021, Schiel et al. 2021). As a result, the settlement and survival of recruits were expected to be compromised by substrate erosion, sediment scour and smothering by sediments from damaged hills in the catchment (Airoldi 2003, Schiel et al. 2006, 2021). The highly turbid environment could also affect the survival and growth of juvenile macroalgae due to attenuation of light and effects of smothering (Airoldi 2003, Alestra & Schiel 2015, Magris et al. 2019). In fact, suspended sediments and the coastal light environment are inextricably linked in nearshore waters. For example, New Zealand generally has high sediment loads from catchments (Hicks et al. 2011), which reduce the penetration of light through the water column and affect spectral quality (Desmond et al. 2019, Tait 2019). Fine sediments often become resuspended in the water column and occlude solar irradiance, thereby affecting light delivery to algae (Airoldi 2003). There was also additional stress to this coastline from the 2017/2018 marine heatwave (Straub et al. 2019). This intense heatwave in combination with high air temperature and very low tides caused mass die-off of large brown intertidal algae along the Kaikōura coast and coast south of there (Thomsen et al. 2019).

Large brown algae are the dominant primary producers, space occupiers and habitat providers on the South Island of New Zealand in general and Kaikōura in particular (Schiel et al. 2019). The early life stages of these algae can be particularly susceptible to the effects of sediment, decreased light and increased temperatures. Here, under controlled laboratory conditions, we tested the individual and interactive effects of temperature and varying sedi-

ment/light regimes on early post-settlement survival and growth of key habitat-forming species of the low intertidal/shallow subtidal zone that existed in these zones before the earthquake. We hypothesised that the combination of warming seawater and decreasing light would have a negative effect on juvenile algal health. However, we suspected that warming seawater and increasing sediment would have a greater negative effect on algal health because the presence of sediment would not only decrease light but also stress algae through physical abrasion and smothering. Understanding these effects greatly aids an understanding of algal recovery to this coastal mega-event, as well as providing insights on how early post-settlement large brown algae may respond to changing reef conditions globally.

2. MATERIALS AND METHODS

2.1. Species and algal propagation

Three species of macroalgae were used in the experiments. These were the fucoids *Durvillaea antarctica* and *Landsburgia quercifolia* and the laminarian *Lessonia variegata. Durvillaea* spp. were the dominant macroalgae in the low intertidal/high subtidal zone along the Kaikōura coastline prior to the earthquake. They suffered high mortality and virtually disappeared at many sites post-earthquake. The species we used was almost certainly *D. antarctica*, but it can be difficult to distinguish from *D. poha. D. antarctica* species is dioecious and is only reproductive for a couple of months during austral winter. *L. quercifolia* is monoecious and occurs in the shallow subtidal zone along much of New Zealand, forming dense stands in many areas. *L. variegata* is a tough laminarian alga, often forming dense aggregations at the subtidal fringe on wave-exposed shores across much of New Zealand. These species were amenable to culturing and growth in laboratory conditions.

Algal cultures formed the basis of experiments. To settle propagules of each species, fertile reproductive portions of *L. quercifolia*, *D. antarctica* and *L. variegata* were collected from the Kaikōura coast in early July 2019. These were cleaned with autoclaved (121°C for 90 min) seawater and taken to an algal-culturing facility at the Cawthron Aquaculture Park (Glenduan, Nelson, New Zealand), a ca. 3 h journey from the collection site. Adult algal samples were stored in coolers (keeping species separate) while in transit from the collection site and then stored in a 4°C refrigerated room. Propagule release was instigated within 3 d of collection and propagules were settled onto 25 cm^2 Hardiflex™ (cement fibre) plates that were spread out in settlement tanks, and species were kept separate. To ensure that propagules were settled, attached and had survived initial lab conditions, all plates were cultivated in static tanks at 11°C seawater for 63 d before experimentation began. However, due to the alternative life history between fucoid (haploid egg or sperm to fertilised zygote to germling) and laminarian (germinating spores to gametophytes to fertilised zygote to germling) species, germlings used in the experiment were likely different ages when the experiment began. Static treatment tanks were cleaned, and the seawater was exchanged every 5 d prior to and during the experiment. Nutrients were maintained consistently by the addition of AlgalBoost F/2 media at every water change event (AlgaBoost™, D'Archino et al. 2019).

2.2. Experimental design

Three temperature treatments (factor 1) were crossed with 6 light/sediment treatments (factor 2) to test their effect on the health of each algal species (Table 1). The 6 different light/sediment levels were achieved by combining 4 light treatments with 2 sediment levels. Each plate (162 in total, consisting of 3 replicates of 3 species, and 18

Table 1. Experimental design. The 3 temperature treatments were crossed with the 6 light/sediment treatments ($3 \times 6 = 18$) Within each cross there were 3 replicates ($18 \times 3 = 54$). Photosynthetically active radiation (PAR) values and concentration of fine sediment solution (NTU) were set to ecologically equivalent levels and are listed in order respective to the light/sediment treatment

Treatment	Levels	Description
Temperature	3	11, 14, 17°C
Light/sediment	6	High light (HL), control (C), low sediment (T), single shade (S), high sediment (TT), double shade (SS) 105, 80, 50, 33, 32 or 16 µmol m^{-2} s^{-1} PAR; <3, <3, <3, ~250, <3, or ~700 NTU

treatment combinations) was placed in a clear, square 12.5 l Tellfresh© tank containing 10 l of UV-sterilised seawater and these tanks were spread across twelve 60 l flow-through water-bath trays (Fig. 1). For an ideal orthogonal balanced experimental design, 72 plates would have been required for each species (216 in total) and would have consisted of 3 replicates of 3 species, with 24 treatment combinations (temperature, 3 levels; light, 4 levels; sediment, 2 levels). However, we were unable to fully cross light and sediment due to inadequate number of settlement plates for each species and because of this low and high sediment treatments were only grown in ambient (control) light (Fig. 1). Individual treatment tanks were aerated with an air

stone (96 l min^{-1} from AirMac DBMX80 air pumps) while the surrounding water bath trays had flow-through water (at ca. 3.75 l min^{-1} flow rate) of the appropriate temperature (11, 14 and 17°C). The 11°C temperature treatment represents the average sea temperature on the Kaikōura coast during austral winter. Temperatures and light levels were monitored throughout the experiment using Onset HOBO pendant Temp/Light loggers, a YSI Pro Plus handheld multi-meter (for spot temperature measurements) and a LI-COR Underwater Quantum Sensor (LI-192). At every water exchange event all water bath trays were rotated to compensate for potential differences in LED light spectrum from one unit to another.
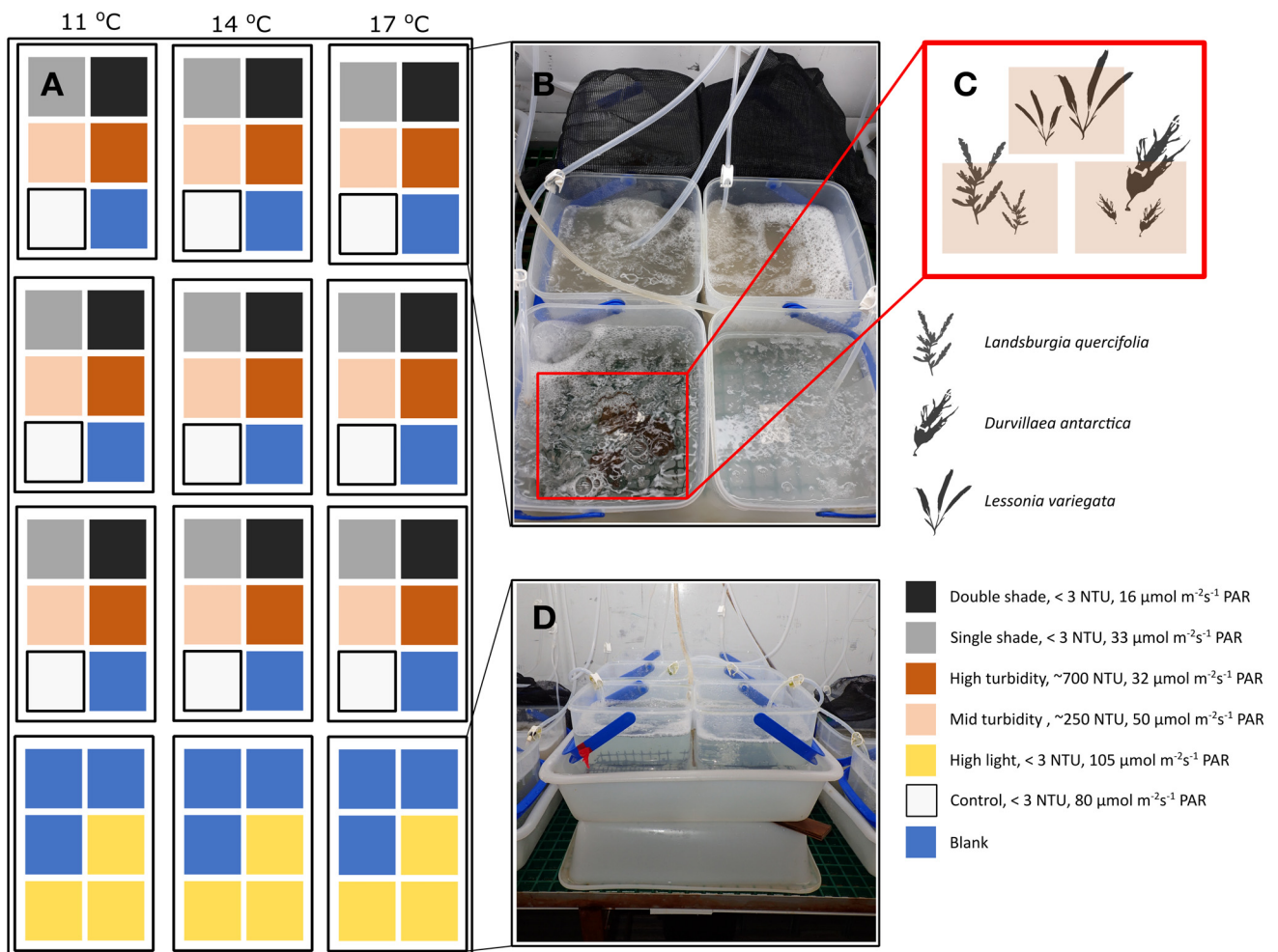

Fig. 1. Twelve 60 l temperature-controlled (flow-through) water-bath trays were used to hold 54 randomized static treatment tanks (A). A further 18 blank treatment tanks did not have any plates and were used to standardize design. Nine of the 12 water-bath trays contained control, shade and sediment static treatment tanks (B, and magnified in C). The remaining 3 water-bath trays contained static treatment tanks that were elevated to achieve higher light (D, with same mix of species as shown in C). Each temperature treatment (11, 14 and 17°C) had 3 'B' and 1 'D' tray/tank setups. Each treatment tank had a plate from each species (3 plates in total, as shown in C). Thus, each treatment had 3 replicate plates for analysis

2.3. Light and sediment treatments

Light was provided by an overhead array of full-spectrum LED lights (Thorn batten LEDs, 60 watt, 6500 K, 6000 lumens). Photosynthetic active radiation (PAR) quantities were chosen to represent ecologically relevant levels found *in situ* (Nelson 2005, Wernberg et al. 2005, Irving et al. 2009, Tait et al. 2014, Desmond et al. 2015, D'Archino et al. 2019, Layton et al. 2019). These were selected to represent the low and high ranges of light normally available to shallow subtidal species, particularly light levels found in the subcanopy, where a majority of early life stage alga are found. In 4 treatments, light levels were 105, 80, 33 or 16 µmol m^{-2} s^{-1} PAR. The highest light treatment (HL, 105 µmol $m^{-2}s^{-1}$) was achieved by elevation of tanks closer to the light source. The 2 lower light treatments were achieved by covering the tanks with a single layer (S, 33 µmol m^{-2} s^{-1}) or a double layer (SS, 16 µmol m^{-2} s^{-1}) of shade cloth, thereby physically restricting light intensity. The control treatments (C, 80 µmol m^{-2} s^{-1}) received ambient light (Fig. 1, Table 1). PAR measurements were collected by placing a LI-COR Underwater Quantum Sensor (LI-192) on the bottom of the treatment tanks and recording data with a LI-COR Light Senor Logger (LI-1500) (settings: inputs, 1 sensor [water]; sample rate, 1 Hz; range, auto; output, 1–5 s [averaging]).

A further 2 treatments used fine sediments both to lower the light available to cultures and test for any added effects of the sediments themselves. Fine sediment concentrations were set to ecologically equivalent levels (Geange et al. 2014) and were controlled by the careful daily addition of them to each independent, static unit. Sediment was kept in suspension by aerators that were placed in the bottom of the tanks. The different suspended sediment treatments were achieved by adding sediment to low (T) and high sediment (TT) treatment tanks to achieve ~250 nephelometric turbidity units (NTU) and ~700 NTU (Fig. 1, Table 1). NTU values were measured using a Hach 2100Q Turbidimeter. The different sediment treatments resulted in light levels of 32 µmol m^{-2} s^{-1} PAR (TT) and 50 µmol m^{-2} s^{-1} PAR (T). Sediment was collected as cement wash from a quarry located near the earthquake-affected coastline (for similar particle composition). It was filtered through a 65 µm plankton mesh to create a sediment solution and autoclaved at 121°C for 90 min to ensure sterility. The sediment solution was then pipetted into appropriate experimental tanks (0.28 g l^{-1} for T and 0.57 g l^{-1} for TT treat-ments). The sediment mostly remained in suspension during the 100 d experiment, but some did settle onto plates and most likely affected the growth of germlings. During water exchange events, plates were lightly brushed with a soft paintbrush to remove sediment from the plate surface. This was done for all light and sediment treatment plates to control for the effects of brushing.

2.4. Data collection/analysis

Individual blade counts and sizes of germlings were assessed by taking a close-up photograph of each plate, while still submerged, at 5 times: Days 0, 31, 42, 64 and 100. Each photo was analysed using Image J software (Rueden et al. 2017) to assess the number and size of individuals. Percent survival was determined based on the number of survivors at each time point per plate relative to the number of individuals per plate at Day 0. To calculate average size, a maximum of 20 individuals per plate were measured and then these measurements were averaged to achieve an average size per plate (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m710 p027_supp.pdf for details on how photographs of plants could be used for growth assessment). Blades were randomly selected from each plate.

To test for main effects (temperature, light/sediment) and their interactions on percent survival for each species, 2-way ANOVAs were run at Days 42 and 100. These times were chosen arbitrarily as approximately midway through the experiment and at the end, by which time many replicates had diminished numbers of germlings. A square root data transformation was used for all percent survival data and was applied because there were some instances where percent survival was 0. Two-way ANOVAs were used to test for main effects (temperature, light/sediment) and their interactions on blade length for each species at Days 42 and 100. All blade length data was transformed using log(average blade length (mm) +1). A log transformation was used because often a few individuals grow faster than others and can skew the data far to the right. Among models, each plate was treated as a sample for replication (i.e. 3 plates per treatment), and significance threshold (α) was 0.05. Tukey's HSD tests were performed for significant factors. All analyses were performed in Rstudio (R v.4.2.1). Model assumptions for variance homogeneity were checked by plotting residuals versus fitted values and also using normal Q–Q plots (Zuur & Ieno 2016).

3. RESULTS

3.1. Algal survival

There were no significant effects of temperature or light/sediment on the survival of *Landsburgia quercifolia* (Table 2). The survival of *L. quercifolia* was high in all temperature and light/sediment treatments (Fig. 2). Only temperature affected the survival of *Durvillaea antarctica*, with survivorship decreasing with increasing temperature, which resulted in nearly a 9-fold decrease in survivorship between the 11°C (28.6%) and the 17°C (3.3%) treatments at Day 42 (Fig. 3, Table 2).

Table 2. Results from 2-way ANOVA for temperature (11, 14, 17°C) × all light and sediment treatments on survival of algae. Samples include the sqrt(percent survival) for *Landsburgia quercifolia*, *Durvillaea antarctica* and *Lessonia variegata* at Days 42 and 100 of the trial. Note that there was very low survival of *D. antarctica* at Day 100. p-values are displayed in superscript parentheses next to significant *F*-values. Temp: temperature; light&sed: light/sediment

|	*L. quercifolia*			*D. antarctica*			*L. variegata*		
	df	MS	*F*	df	MS	*F*	df	MS	*F*
Day 42									
Temp	2	1.950	1.024	2	60.18	$18.27^{(p<0.001)}$	2	29.21	$10.10^{(p<0.001)}$
Light&sed	5	2.296	1.206	5	4.90	1.487	5	25.97	$8.983^{(p<0.001)}$
Temp × Light&sed	10	2.075	1.090	10	4.36	1.324	10	2.085	0.721
Residual	36	1.904		36	3.29		36	2.891	
Day 100									
Temp	2	1.802	0.914	2	9.177	$7.490^{(p=0.002)}$	2	85.89	$41.88^{(p<0.001)}$
Light&sed	5	2.458	1.247	5	0.326	0.266	5	12.63	$6.159^{(p<0.001)}$
Temp × Light&sed	10	2.122	1.077	10	0.251	0.205	10	4.42	$2.155^{(p=0.045)}$
Residual	36	1.970		36	1.225		36	2.05	
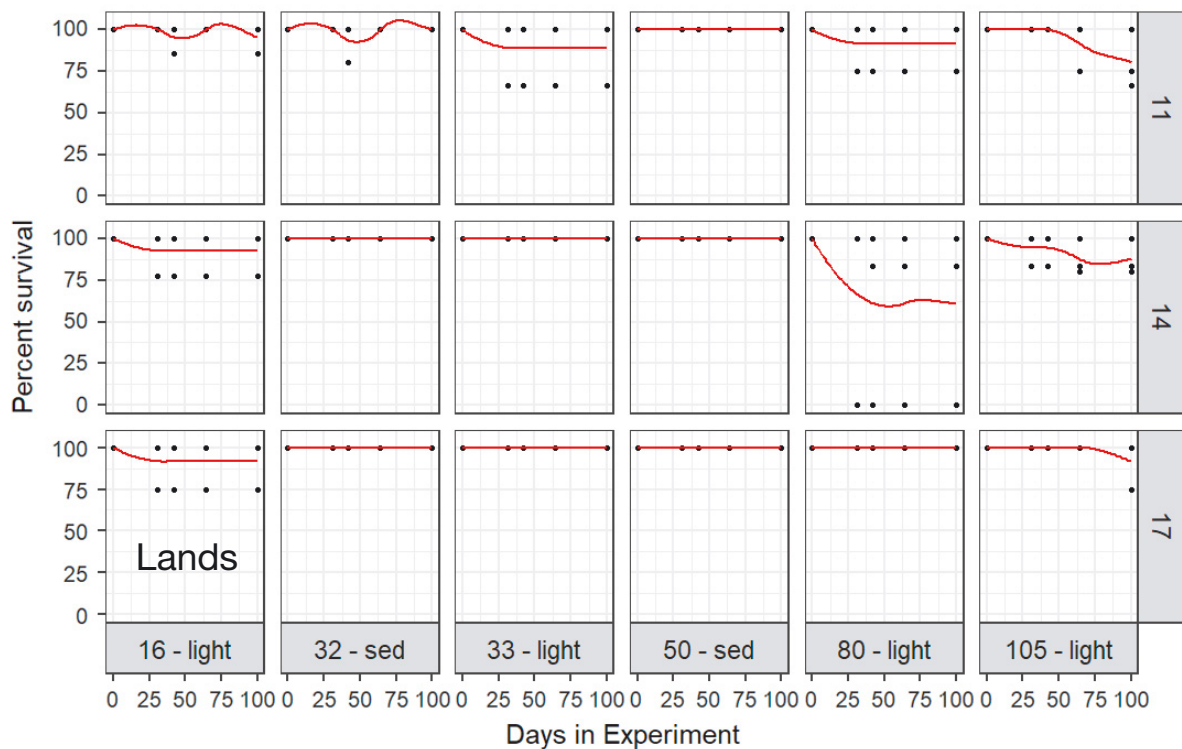
Fig. 2. Percent survival for *Landsburgia quercifolia*. Algae were 63 d old at the start of the experiment. Temperature is shown on the right *y*-axis (11°, 14° and 17°C). Age (in days of experimentation) is on the *x*-axis. In the grey boxes above 'Days in Experiment' is light intensity (in µmol m^{-2} s^{-1}), followed by treatment ('light' = light treatment and 'sed' = sediment treatment). Red line was fitted using the 'Smoother function' in Rstudio (using method = 'loess' and formula 'y ~ x')
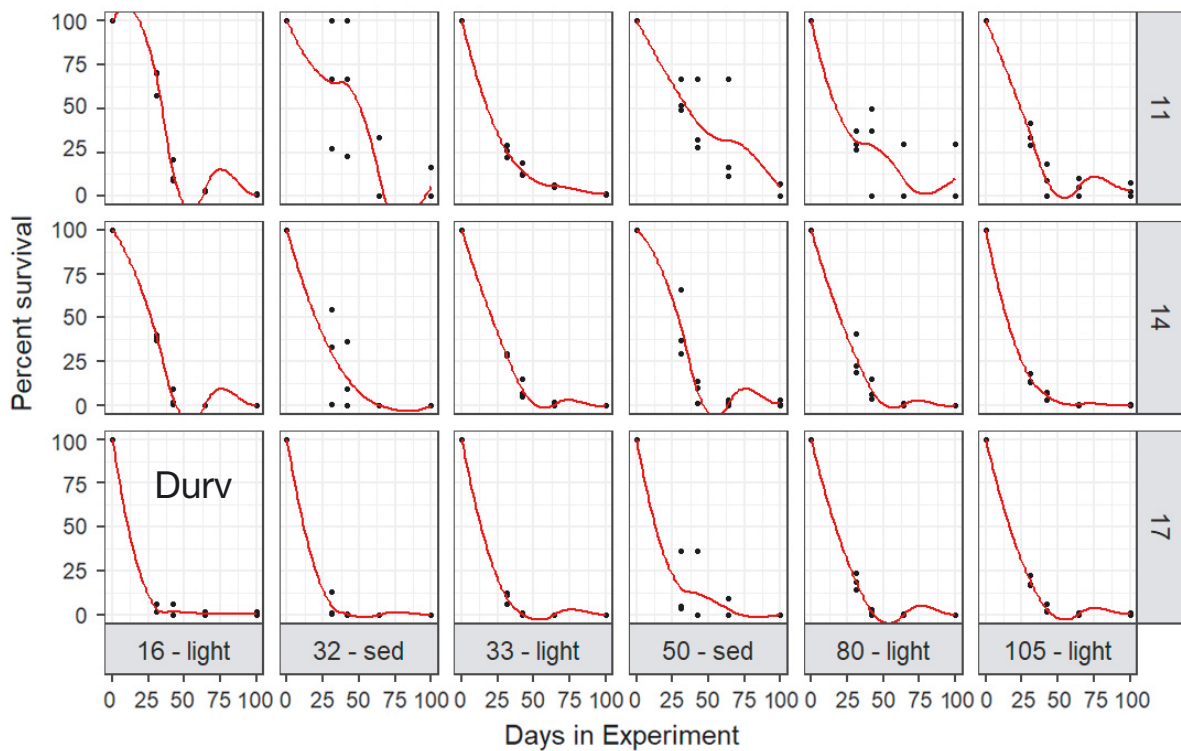
Fig. 3. Percent survival for *Durvillaea antarctica*. Details as in Fig. 2

Lessonia variegata was the only algal species where survival was significantly affected by the interaction of temperature and light/sediment, and this was only found on completion of the experiment after 100 d (Table 2). There was a general decrease in survival with increasing temperature after 42 d with ~50.1, ~38.5 and ~20.3% in the 11, 14 and 17°C treatments, respectively (Fig. 4, Table 2) and after 100 d with ~34.5, ~18.6 and ~2.38% in the 11, 14 and 17°C treatments, respectively (Fig. 4). However, because there were significant interactive effects after 100 d, we must disregard the significance of main effects (i.e. temperature). After 100 d, *L. variegata* had its poorest survival at 17°C but, interestingly, there was a significant negative interaction with increasing light on survival in the 11°C treatments. For example, there was significant greater survival in both sediment (T and TT) treatments at 11°C compared to C and HL treatments at the same temperature (Table S1: Tukey's HSD).

3.2. Algal growth

After 42 d, there were significant interactive effects of temperature and light/sediment on the growth of all species (Table 3). However, interactive effects were dissimilar between species. For example, the temperature at which *L. variegata* was grown had more of an effect on blade length than did the light treatments at Day 42 (Table 3, Fig. 5), although a decrease in light intensity resulted in a greater reduction of blade length at lower temperatures for *L. variegata* (Fig. 5). A decrease in light intensity also resulted in a greater reduction of blade length at lower temperatures for *D. antarctica* after 42 d (Fig. 5). Furthermore, an increase in temperature had a greater negative effect on growth within the sediment treatments for *L. variegata* (11.47 mm average blade length or 497% change from the beginning of the experiment at 11°C vs. 4.90 mm average blade length or 98.6% change at ~17°C) and *D. antarctica* (5.93 mm average blade length or 142% change from the beginning of the experiment at 11°C vs. 3.62 mm average blade length or 16.0% change at 17°C) but the opposite was true for *L. quercifolia*. After 42 d, *L. quercifolia* generally increased in blade length in the highest temperature treatment (17°C, 5.27 mm average blade length or 343% change compared to 4.86 mm average blade length or 280% change from the beginning of the experiment at 11°C, both sediment treatments pooled). However, significant interactions between temperature and light/sediment for *L. quercifolia* after 42 d did not
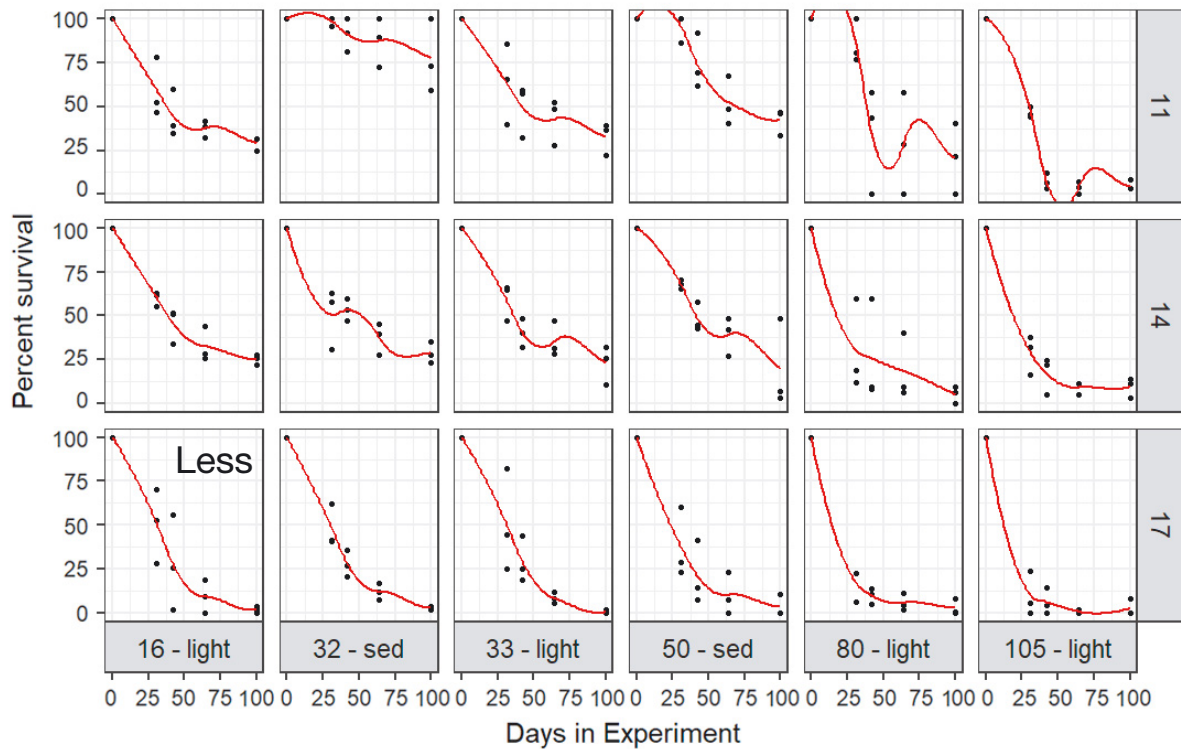
Fig. 4. Percent survival for *Lessonia variegata*. Details as in Fig. 2

Table 3. Results from 2-way ANOVA for temperature (11, 14, 17°C) × all light and sediment treatments for the average length of blades. Samples include an average of individual blades measured per plate (3 plates per treatment) for *Landsburgia quercifolia*, *Durvillaea antarctica* and *Lessonia variegata* at Days 42 and 100 of the trial. Log(blade length (mm) +1) transformation was performed on all data. Note that there was very low survival of *D. antarctica* at Day 100. p-values are displayed in superscript parentheses next to significant *F*-values. Temp: temperature; light&sed: light/sediment

	L. quercifolia			*D. antarctica*			*L. variegata*		
	df	MS	F	df	MS	F	df	MS	F
Day 42									
Temp	2	0.066	1.598	2	0.111	$3.281^{(p=0.055)}$	2	2.948	$54.68^{(p<0.001)}$
Light&sed	5	0.135	$3.273^{(p=0.016)}$	5	0.957	$28.25^{(p<0.001)}$	5	0.793	$14.71^{(p<0.001)}$
Temp × Light&sed	10	0.128	$3.117^{(p=0.006)}$	10	0.092	$2.717^{(p=0.022)}$	10	0.177	$3.285^{(p=0.004)}$
Residual	35	0.041		24	0.034		35	0.054	
Day 100									
Temp	2	0.0278	0.718	2	0.5536	$5.141^{(p=0.037)}$	2	7.806	$42.24^{(p<0.001)}$
Light&sed	5	0.5702	$14.72^{(p<0.001)}$	5	0.4761	$4.421^{(p=0.032)}$	5	1.839	$9.952^{(p<0.001)}$
Temp × Light&sed	10	0.0302	0.781	4	0.0454	0.421	10	0.323	1.746
Residual	35	0.0387		8	0.1077		25	0.185	

bring about any trends (Table S2). Interestingly, by Day 100, there were no significant interactions found between the treatments but there were significant main effects on each species (Table 3).

Species-specific trends were found between growth and temperature, which were accentuated from 42 to 100 d. *L. quercifolia* had longer blades, with an average of 6.24 mm (396% change in blade length from the beginning of the experiment) in the 17°C temperature treatment compared to an average of 5.78 mm (368% change in blade length) at 11°C, with all light and sediment treatments pooled after 42 d (Fig. 6). In contrast, *D. antarctica* had shorter blades in the highest (17°C) temperature treatment, with an average blade length of 6.15 mm (107% change in blade length from the beginning of the ex-
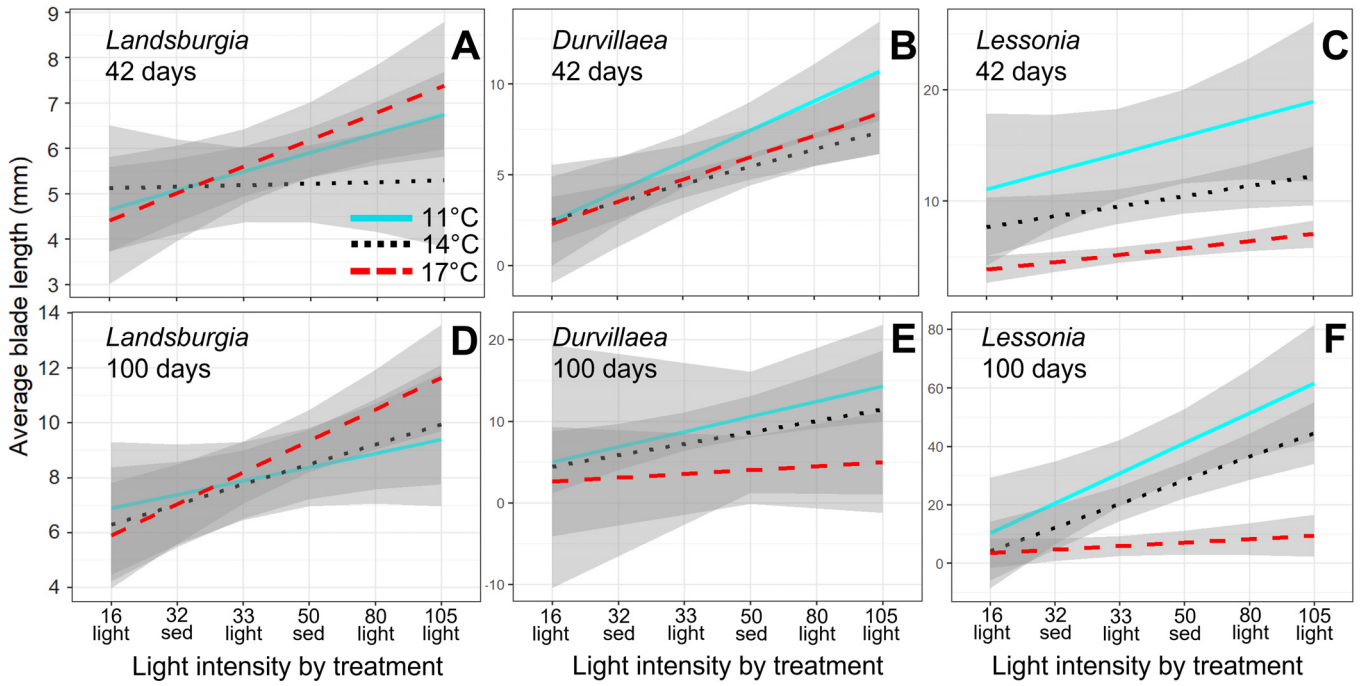
Fig. 5. Interaction plots of average length of blades (mm) per plate (n = 3 for each treatment) measured for *Landsburgia querci-folia*, (A, 42 d; D, 100 d); *Durvillaea antarctica*, (B, 42 d; E, 100 d); and *Lessonia variegata*, (C, 42 d; F, 100 d). Regression lines are based off the temperature treatment (see legend, A) and created using Smoother (method = lm) function in Rstudio. Light treatments are on the *x*-axis, increasing in light intensity (in µmol m^{-2} s^{-1}, 'light' = light treatment and 'sed' = sediment treatment). Shaded regions denote 95% confidence intervals. Note change in *y*-axis scale bar
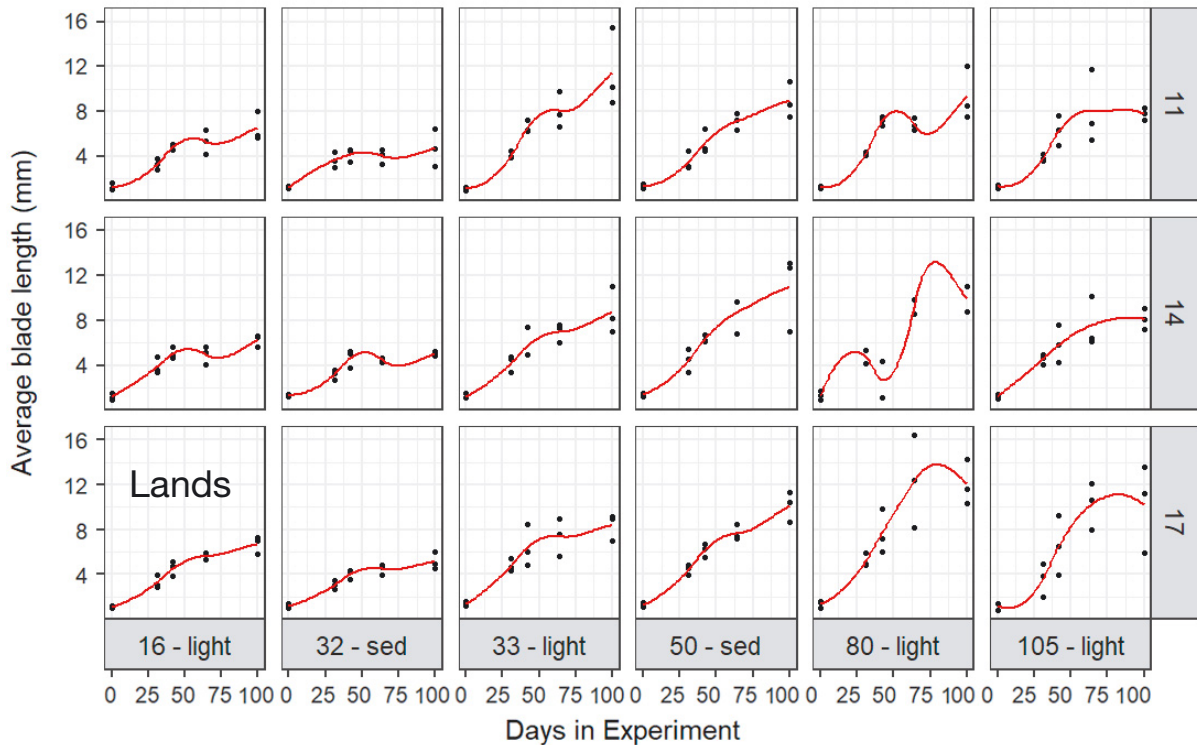
Fig. 6. Average blade length (mm) per plate for *Landsburgia quercifolia*. Details as in Fig. 2
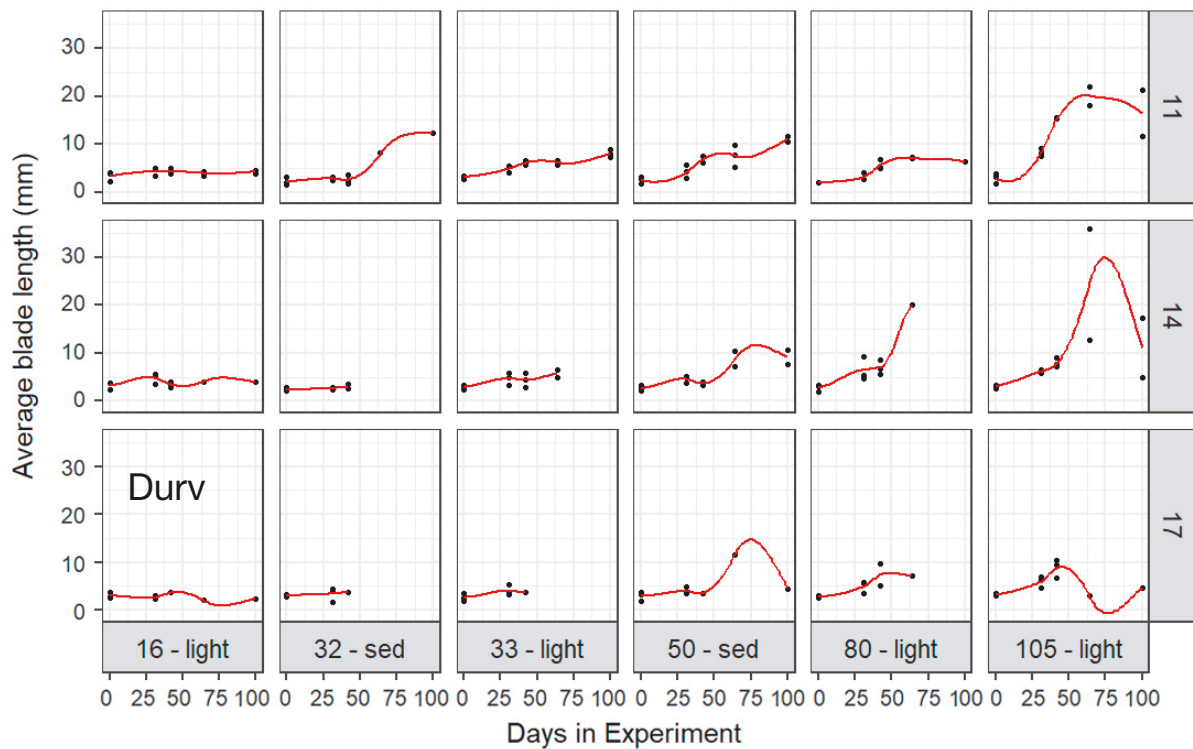
Fig. 7. Average blade length (mm) per plate for *Durvillaea antarctica*. Details as in Fig. 2

periment) at 17°C compared to an average blade length of 7.22 mm (150% change in blade length) at 11°C (Fig. 7, all light and sediment treatments pooled after 42 d). *L. variegata* had shorter blades in the highest (17°C) temperature treatment, with an average length of 5.49 mm (123% change from the beginning of the experiment) compared to an average blade length of 15.68 mm (500% change in blade length) at 11°C (Fig. 8, all light and sediment treatments pooled after 42 d). However, because there were significant interactive effects after 42 d, it would be illogical and misleading to report significance. After 100 d, *L. quercifolia* grown at 17°C still had longer blades than those at 11°C but this was not significant (Fig. 6, Table 3, all light/sediment treatments pooled). In contrast, *D. antarctica* had significantly shorter blades at 11°C compared to 17°C but there was low survival overall (all light/sediment treatments pooled Table 3, Table S2: Tukey's HSD). There were also significantly shorter blades of *L. variegata* in 17°C compared to 11°C after 100 d (all light/sediment treatments pooled Table 3, Table S2: Tukey's HSD).

In general, all species had lower growth in the lowest light and high sediment treatments (Figs. 6–8). Growth was either similar within species between these treatments or lowest growth was in the high sediment treatment, with the exception of *D. antarc-*

tica after 100 d and this is likely due to very low survival. This was despite the SS treatment having half the light intensity of the TT treatment (SS, 16 µmol m^{-2} s^{-1} vs. TT, 32 µmol m^{-2} s^{-1}, Figs. 6–8). Comparison of the TT and single shade S treatments further illustrated the negative impact of sediment. While the treatments had nearly the same light intensities (TT, 32 µmol m^{-2} s^{-1} and S, 33 µmol m^{-2} s^{-1}), *L. quercifolia* and *L. variegata* germlings in the SS treatment generally had shorter blades and this was often significant. For example, the average length of blades in the TT and S treatments for *L. quercifolia* was 4.30 mm (93.7% change from the beginning of the experiment) and 6.37 (136% change), respectively (Day 42; Table S2: Tukey HSD), and 4.91 mm (121% change from the beginning of the experiment), 8.96 mm (232% change), respectively (Day 100; Table S2: Tukey HSD). *L. variegata* had an average blade length of 5.05 mm in TT (132% change in blade length from the beginning of the experiment) and an average blade length of 12.23 mm in the S (318% change; Day 42; Table S2: Tukey HSD), and an average blade length of 12.01 mm in the TT (451% change) and 19.70 mm in the S (575% change; Day 100; Table S2: Tukey HSD). However, the impact of sediment on blade length was not always negative, with evidence of increased growth
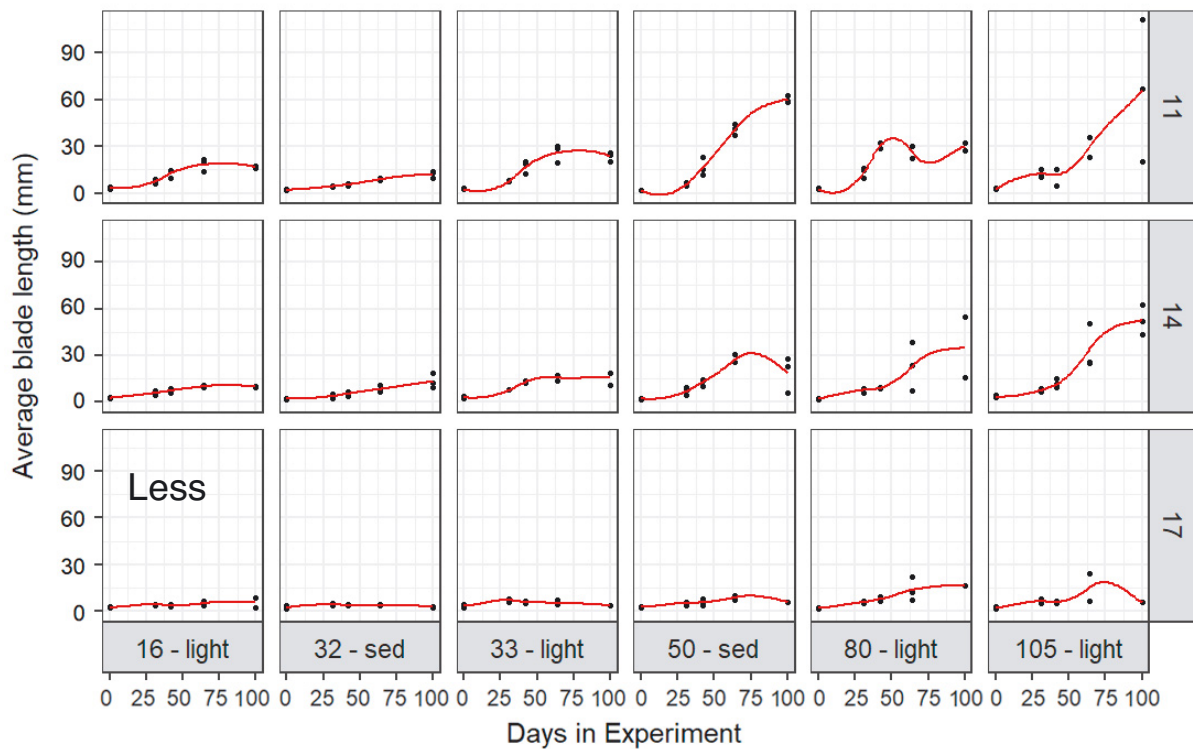
Fig. 8. Average blade length (mm) per plate for *Lessonia variegata*. Details as in Fig. 2

among the T (50 µmol m^{-2} s^{-1}) treatments compared to the C (80 µmol m^{-2} s^{-1}) treatments (Figs. 6–8). This was notable for *L. variegata* in the 11°C treatments, where at 100 d the average blade length was 60.25 mm (T, 3271 % in blade length from the beginning of the experiment) in the low sediment compared to an average blade length of 30.43 mm in the C (1014 % change in blade length, Fig. 8).

4. DISCUSSION

Understanding the response of the early life stages of large brown algae to different light and temperature regimes is critical to understanding the processes behind recovery of macroalgal habitats in altered shallow subtidal environments, such as those along the earthquake-affected Kaikōura coast of New Zealand. This information is also important for predicting how algal habitats will respond to altered conditions under climate change and other anthropogenic stressors. The results of this study indicate that there can be significant variability among species in their response to common stressors during the early life stage.

The age of algae matters. For example, there is an ecological bottleneck of large brown algae at the early life stage (Vadas et al. 1992, Schiel & Foster 2006). Yet, there are distinct differences between large brown algal orders and age classes among their early life stages, such as morphology and external fertilization time (Schiel & Foster 2006). Our results represent survival and growth metrics from an understudied macroscopic early life stage age group. Other laboratory studies have focused on germinating zoospores (e.g. Lüning & Neushul 1978, Lüning 1980, Reed 1990), gametophyte (e.g. Reed 1990, Nelson 2005, Layton et al. 2019), zygotes (e.g. Chapman 1984, Taylor et al. 2010, Schiel & Gunn 2019), developing sporophyte and young diploid individuals (e.g. Schiel 1985, Irving et al. 2009, Alestra & Schiel 2015). Each of these age groups is unique and short-lived compared to the mature adults. This also means there are particular vulnerabilities among each of these different age groups and thus it is important to understand thresholds to known stressors that plague coastal ecosystems such as warming seas and sedimentation (Schiel et al. 2006, Franco et al. 2017, Thomsen et al. 2019, Benedetti-Cecchi 2021).

We found different responses to light, sediment and temperature treatments in the early life stages of 3 species of habitat-forming large brown algae. While sediment in the water column and decreasing light levels generally had negative effects on the sur-

vival and growth of all 3 species, *Landsburgia quercifoila* was more adapted to the negative effects of these stressors in comparison to the other 2 species. Increasing temperature also had a negative effect on the survival and growth of *Durvillaea antarctica* and *Lessonia variegata*, but in contrast better growth was found at the highest temperature for *L. quercifolia*. Responses to interactions between temperature, sediment and light were also different according to the species, with *D. antarctica* and *L. variegata* more negatively affected than *L. quercifolia* by low light at high temperatures.

Rising sea temperatures are known to have a negative effect on many important habitat-forming large brown algae (Smale et al. 2019, Tait 2019, Thomsen et al. 2019). However, there are known species-specific survival and growth differences in thermal tolerance among the bottleneck early life stages (Nelson 2005, Irving et al. 2009, Andrews et al. 2014, Alestra & Schiel 2015, Wernberg et al. 2016). We found that *D. antarctica* had poor growth at the highest temperature treatment (3–5°C above ambient reproductive austral winter season). These results are in line with Alestra & Schiel (2015), who found less than 20% survival of juvenile *D. antarctica* after 2 wk in their high temperature treatments (14°C). In our study, less than 0.5% survival was documented in juvenile *D. antarctica* after 100 d in either the 14°C or 17°C temperature treatments, and only 8.52 and 3.28% survival after 42 d in 14 and 17°C temperature treatments, respectively. However, there was ~4% survival of juvenile *D. antarctica* in the 11°C treatments after 100 d and 28.6% survival after 42 d. As an intertidal species, *D. antarctica* must be resilient to extreme temperatures that may be found in the rocky reef environment at low-low tides. Nevertheless, there are thermal tipping points for this species during periods of reduced wave action and extreme heatwave events (Thomsen et al. 2019). *D. antarctica* is a winter-reproducing, fast-growing species that dominates exposed coastlines. By reproducing during winter, the early life stages avoid most of the marine heatwave events that take place in austral summer. An increase in marine heatwave events and/or changing seasonal weather patterns may therefore have dire consequences on critical *D. antarctica* early life stages.

We did expect to see a decrease in survival of *L. variegata* juveniles at higher temperatures as this laminarian species is mainly found in the subtidal zone and likely less adapted to thermal extremes than intertidal species. However, our results, which found a decrease in *L. variegata* survival and growth

at the highest temperature treatments, contrast with those found by Nelson (2005), who found that *L. variegata* gametophytes had faster growth and subsequent gametogenesis at the highest temperature treatment, and the greatest sporophyte development after 30 d. Our experiments did not even begin until *L. variegata* gametophytes had gone through gametogenesis, and sporophytes were macroscopic. Thus, although both ours and Nelson's (2005) studies experimented on the same species, it is likely that there are different thermal thresholds between these distinct age groups. Indeed, variable thermal thresholds have been found between the reproductive gametophyte stage and the vegetative sporophyte stage in many laminarian species (Lüning & Neushul 1978, Lüning 1980). Furthermore, there is evidence that the microscopic reproductive stage is more thermally tolerant than the macroscopic sporophyte stage within many large brown algae (Breeman 1988, Peters & Breeman, 1993).

There is also evidence of a variation in the amount of light necessary for growth among the different early life stages, which are often found in the light-limited subcanopy (Lüning & Neushul 1978, Lüning 1980, Reed & Foster 1984, tom Dieck 1993, Nelson 2005, Schiel & Foster 2006, Tait & Schiel 2018). Within the light-limited subcanopy on rocky reefs, there is evidence that photosynthetic efficiency is greater than at the light-saturated canopy level (Tait & Schiel 2018). However, our results demonstrated that the early life stage of all species grew significantly better with increasing light intensity. Although algal growth was enhanced with higher light, there was not a simple linear relationship between light and growth. For example, while the SS treatment had the lowest light level (16 µmol m^{-2} s^{-1}) and the S treatment had a similar light level to the TT treatment (33 µmol m^{-2} s^{-1} vs. 32 µmol m^{-2} s^{-1}, respectively), the least algal growth for all species usually occurred in the TT treatment. Thus, irradiance delivery or the difference in how light is attenuated (light spectrum disruption by modified, turbid vs. canopy, shade environment) may be more responsible for decreased photosynthetic efficiency (Desmond et al. 2019, Tait 2019). Here, again, the age of algae matters. There have been many studies on the microscopic early life stages of large brown algae that found an increase in growth with increasing light (Lüning & Neushul 1978, Lüning 1980, tom Dieck 1993, Nelson 2005, Tatsumi et al. 2021). However, the addition of sediment has an overwhelming negative effect on the survival of these microscopic gametophytes and zygotes (Chapman & Fletcher 2002, Irving et al. 2009, Alestra & Schiel 2015, Schiel

& Gunn 2019). These small organisms were smothered by sediment particles (Chapman & Fletcher 2002, Irving et al. 2009, Alestra & Schiel 2015) or propagules attached to sediment particles and therefore were unable to attach successfully to the substratum (Schiel & Gunn 2019). In our study, the older and larger macroscopic sporophytes were already attached to a substrate and were large enough to rise above the layer of fine sediment that settled from the water column. Still, there was often a thin layer of fine sediment that settled onto the algal blades (Fig. 9). This likely had a negative effect on the photosynthetic efficiency of these juvenile algae (Airoldi 2003, Tait 2019) by occluding photosynthetic surfaces of algae, so sediments likely had a greater effect than just the reduction in light in surrounding water (Airoldi 2003, Chapman & Fletcher 2002, Schiel et al. 2006).

There may be a threshold at which sediment concentration does not affect macroalgae growth, particularly if specimens are large enough to escape the potentially negative impacts of sediment burial. For example, juvenile *L. variegata* in this experiment had longer blades in the T treatment in comparison to those grown under ambient light (C) at 11°C, perhaps similar to the etiolation seen in crowded stands of terrestrial plants (Harper 1977) and marine algae (Schiel & Choat 1980, Schiel 1985). Larger (older) juvenile algae thus have a higher proportion of photosynthetic tissue above the smothering effect of sediment. This highlights the importance of competitive advantages

that provide morphological traits to escape sediment layers and/or opportunistic reproductive cycles at optimal seasons (such as when riverine sediment is low) (Airoldi & Cinelli 1997, Miller et al. 2009).

We found it interesting that the slowest-growing species, *L. quercifolia,* and fastest-growing species, *L. variegata*, in this experiment had the most, and least resilience to multiple stressors, respectively. This relationship is not novel (for examples see Tait et al. 2015 for *Cystophora torulosa* vs. *Undaria pinnatifida* and Blain & Shears 2020 for *Carpophyllum flexusosum* vs. *Ecklonia radiata*), but provides insight into how certain species resist and recover from disturbance events. For example, disturbance events that are short and intense (such as post-earthquake, an intense storm event or marine heatwave) will have a greater negative effect on early life stages of faster-growing species such as *L. variegata* because they are more vulnerable to the immediate effect of multiple stressors. In contrast, fast upward growth due to an increase in available irradiance does benefit the individual that can shade out (Reed & Foster 1984, Connell 2005) or abrade competitive neighbours through whiplash (Santelices 1990, Taylor & Schiel 2005). However, these same effects are likely to affect the survival and growth of nearby conspecific individuals. For instance, in this experiment *L. variegata* grew faster and bigger in the high-light treatments but also had low survival. Results from experiments over several months, such as this, are more likely to
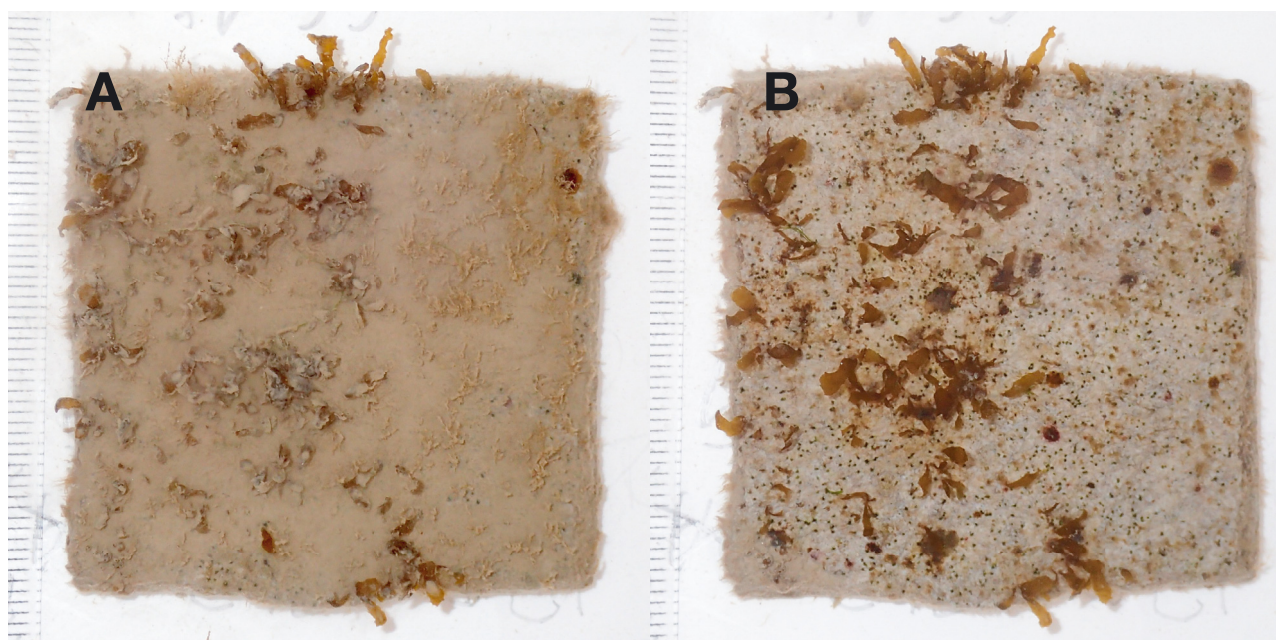

Fig. 9. Settled sediment on juvenile *Durvillaea antarctica* tissue in high sediment treatment, (A) before and (B) after brushing sediment

inform on these survival/growth dynamics, that also take place on the reef (Reed & Foster 1984, Santelices 1990, Connell 2005, Taylor & Schiel 2005). Furthermore, there is evidence that coastal stressors will be increasing in frequency, severity and duration (IPCC 2022) and because of this there is prudence in sustaining experiments as long as possible.

This study demonstrates that a negative effect of sediment on macroalgae survival and growth is much more complex than just compromised light dynamics and depends on critical ecological characteristics such as life stage and habitat where a species occurs along a zonational gradient. Importantly, the negative effects of sedimentation were also pronounced with increasing temperature, thereby accentuating how a combination of stressors can affect potential ecological tipping points. Although there are many interactive factors involved in algal growth on a reef, finding these results under controlled laboratory conditions provides confidence in how particular stressors such as temperature and sediment interact in early life history survival and growth.

These species-specific responses are important for understanding not only how areas around Kaikōura may recover (post-earthquake), but also how these species may respond to an altered environment. There is an increasing need for active management of coastal areas due to climate change threats. Appropriate actions to mitigate these threats, such as choosing native, thermally tolerant species for restoration, may be needed.

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