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**Alistair G. B. Poore, Lars Gutow, José
F. Pantoja, Fadia Tala, David Jofré
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Oecologia

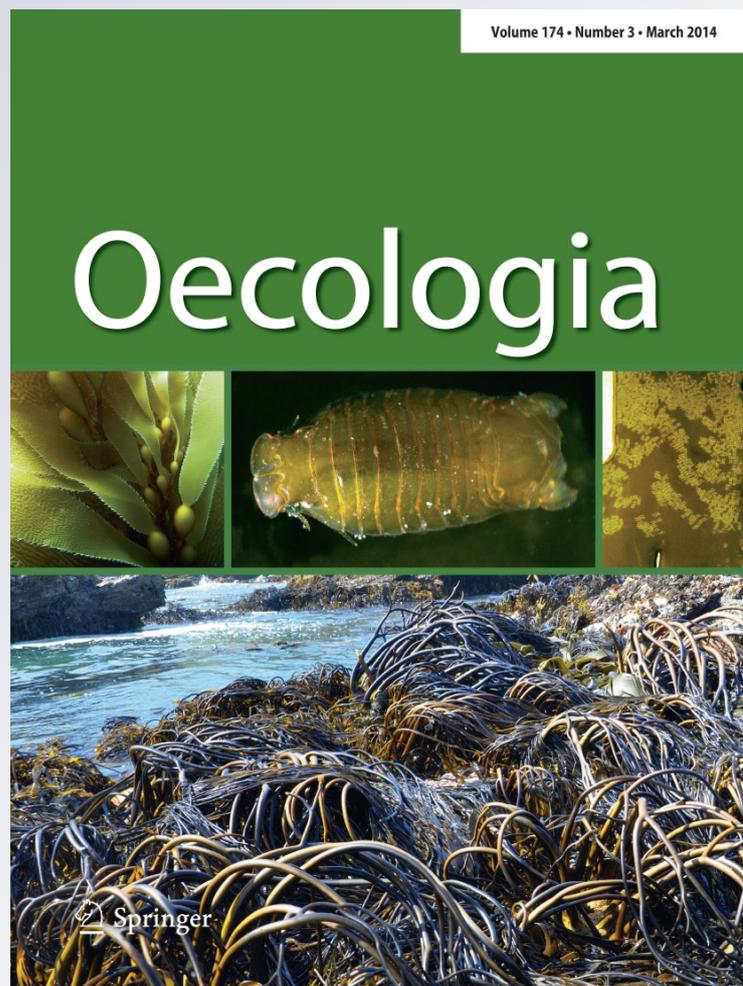
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Major consequences of minor damage: impacts of small grazers on fast-growing kelps

Alistair G. B. Poore · Lars Gutow · José F. Pantoja · Fadia Tala · David Jofré Madariaga · Martin Thiel

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Abstract Damage by small herbivores can have disproportionately large effects on the fitness of individual plants if damage is concentrated on valuable tissues or on select individuals within a population. In marine systems, the impact of tissue loss on the growth rates of habitat-forming algae is poorly understood. We quantified the grazing damage by an isopod *Amphoroidea typa* on two species of large kelps, *Lessonia spicata* and *Macrocystis pyrifera*, in temperate Chile to test whether non-lethal grazing damage could reduce kelp growth rates and photosynthetic efficiency. For *L. spicata*, grazing damage was widespread

in the field, unevenly distributed on several spatial scales (among individuals and among tissue types) and negatively correlated with blade growth rates. In field experiments, feeding by *A. typa* reduced the concentration of photosynthetic pigments and led to large reductions (~80 %) in blade growth rates despite limited loss of kelp biomass (0.5 % per day). For *M. pyrifera*, rates of damage in the field were lower and high densities of grazers were unable to reduce growth rates in field experiments. These results demonstrate that even low per capita grazing rates can result in large reductions in the growth of a kelp, due to the spatial clustering of herbivores in the field and the selective removal of photosynthetically active tissues. The impacts of small herbivores on plant performance are thus not easily predicted from consumption rates or abundance in the field, and vary with plant species due to variation in their ability to compensate for damage.

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Introduction

Damage by herbivores can profoundly affect the fitness of individual plants (Morris et al. 2007) and the composition and productivity of plant communities worldwide (Cyr and Pace 1993; Poore et al. 2012). While herbivores usually reduce the fitness of the plants they eat, the consequences of damage to an individual plant are not always easily predicted by the amount of tissue consumed or average grazer abundance. Herbivore damage is usually unevenly distributed among plant parts that vary in their contribution to growth, survival or reproductive output (Marquis 1996).

The feeding specificity of small herbivores, in particular, can lead to disproportionate effects of low levels of damage when grazing is concentrated on highly valuable tissues. For example, insect damage resulting in the loss of 8–12 % of leaf area can cause a 50–78 % reduction in seed output in oaks (Crawley 1985). Grazing damage may also be unevenly distributed among individuals within a population (Underwood et al. 2005). Consequently, predicting the fitness consequences of tissue loss to individual plants depends on understanding both the mean rates of damage at the population level and the variation around that mean (i.e. whether damage is clustered on certain individuals).

Disproportionate effects of low levels of damage on plant fitness can arise when meristems or flowers are lost (Doak 1992; Krupnick and Weis 1999), when structural damage results in branch loss (Marquis 1996), increased feeding by other herbivores (Hammons et al. 2009) or access to pathogens (Stout et al. 2006), or if damage to one tissue type interacts in a non-additive fashion with damage to other parts (e.g. leaves and inflorescences; Puentes and Ågren 2012). The ability of plants to compensate for tissue loss by increasing net photosynthesis, activating dormant meristems or reallocating stored resources further contributes to variation in the relationship between damage and fitness (Stowe et al. 2000; Tiffin 2000), where plant tolerance is described by the slope of this relationship (Strauss and Agrawal 1999). Predicting the consequences of grazing is thus dependent on the distribution of damage on several spatial scales (within and among individual plants).

In marine ecosystems, the abundance of primary producers can be strongly controlled by herbivores (Poore et al. 2012), but relatively few studies have considered the non-lethal effects of tissue loss on growth rates, photosynthesis or reproduction of individual producers. In a recent meta-analysis of over 600 marine herbivore exclusion experiments (Poore et al. 2012), the vast majority of studies recorded percent cover or biomass as response variables, with only 1.4 % being measures of algal or seagrass growth. Furthermore, few studies have examined compensatory growth of marine primary producers in response to damage (e.g., in macroalgae, Cerda et al. 2009; Hay et al. 2011; in seagrasses, Prado et al. 2011; Vergés et al. 2008) despite the potential for such growth to mask the impacts of grazer damage. Consequently, we have a limited understanding of how producers tolerate damage, and of how levels of non-lethal damage affect individual fitness.

In this study, we tested how the growth and photosynthesis of two species of fast-growing kelps are affected by localised damage by a grazing isopod. Kelps form extensive, highly productive habitats along temperate coastlines (Steneck et al. 2002), and their canopies can support high densities of mesograzers (including isopods, amphipods and small gastropods) whose impacts on their hosts are

poorly understood compared to large grazers (particularly urchins). There is evidence that amphipod grazing is associated with declines in the biomass of *Macrocystis pyrifera* in California from field observations (Tegner and Dayton 1987; Graham 2002) and from experiments where fish predation has been experimentally reduced (Davenport and Anderson 2007). These examples, and increasing evidence from mesocosm experiments in other regions (Duffy and Hay 2000; Newcombe and Taylor 2010), indicate the potential for mesograzers to affect the abundance of large brown algae. Very few field experiments, however, have quantified mesograzer impacts on kelps at natural densities (see Toth et al. 2007) resulting in a poor understanding of whether individual fitness is likely to be reduced by their feeding activities. As with insects feeding on terrestrial plants, the uneven spatial distributions of mesograzers (Brawley 1992) and their tissue specificity give rise to the potential for disproportionate effects on algal fitness. Preferential feeding on meristems (e.g. Poore 1994) or reproductive tissues (e.g. Pansch et al. 2008) is known, and structural damage to stipes can increase the likelihood of losing entire blades to wave action (Muñoz and Santelices 1989; Duggins et al. 2001; Krumhansl and Scheibling 2011). Damage may also facilitate feeding by other grazers (Molis et al. 2010) or the spread of diseases (Campbell et al. 2013). Furthermore, the ability of kelps to translocate nutrients within the thallus gives rise to the possibility of compensatory growth, making it more difficult to reveal the relationships between damage and fitness (Cerda et al. 2009).

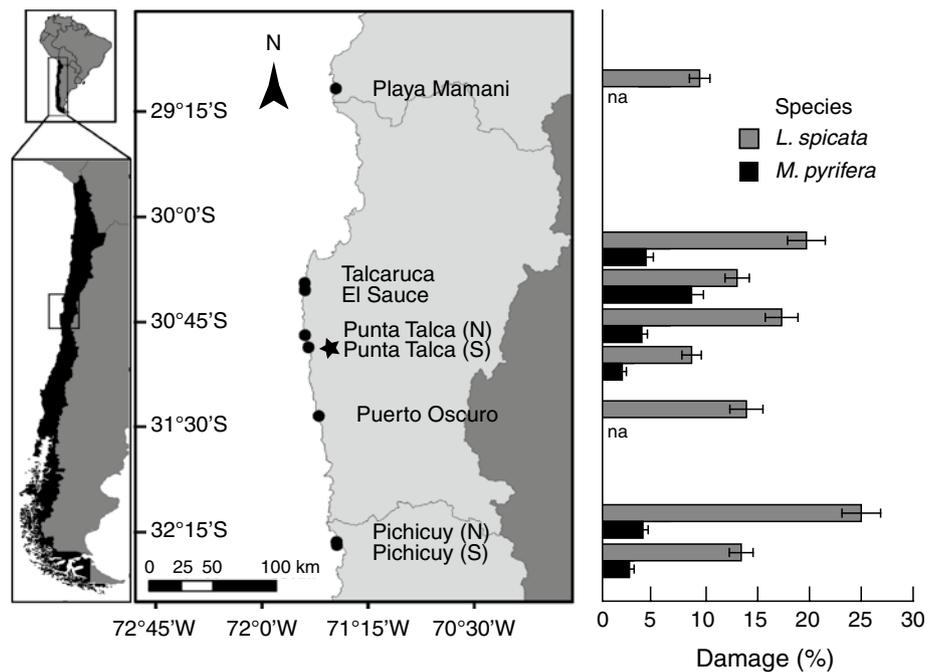
To predict the impact of tissue loss on kelp performance, we quantified the spatial distribution of grazing damage by the isopod *Amphoroidea tyra* on the large, fast-growing kelps *Lessonia spicata* and *Macrocystis pyrifera* at several spatial scales in the field (among tissue types, among individuals, and among sites in northern-central Chile). Furthermore, we determined the relationship between the observed levels of damage and parameters that contribute to individual fitness. In laboratory experiments, we measured the rate at which isopods are able to damage kelp tissues and then, in field experiments, tested the hypothesis that increasing damage results in reduced algal growth and photosynthesis.

Materials and methods

Study organisms and sites

Amphoroidea tyra H. Milne-Edwards (Crustacea: Isopoda: Sphaeromatidae) is an abundant herbivorous isopod, up to 22 mm in length, in intertidal and shallow subtidal kelp forests along the coast of Chile (Thiel and Vásquez 2000; Hinojosa et al. 2007). *Lessonia spicata* (Suhr) Santelices

Fig. 1 Study sites and damage to blades of *L. spicata* and *M. pyrifera* from a large-scale survey of eight sites in northern-central Chile. Data are mean \pm SE of visual damage estimates (%) ($n = 100$ blades per site). *M. pyrifera* was not present at Playa Mamani and Puerto Oscuro. Experiments were run at Punta Talca (south), marked with a star



(previously *L. nigrescens*, González et al. 2012) and *M. pyrifera* (Linnaeus) C. Agardh (Phaeophyta: Laminariales) are the dominant habitat-forming algae in the low intertidal zone between 29 and 41 °S in northern-central Chile (González et al. 2012). Both kelp species are ecologically and economically important resources in the region (Vásquez 2008). In order to determine whether isopod grazing is widespread throughout the kelp habitat, damage to *L. spicata* and *M. pyrifera* blades was quantified at eight rocky shore sites along a 370-km stretch of the Chilean coast (Fig. 1). Further surveys of blade damage and isopod abundance were conducted at Punta Talca (30°55'52"S, 71°40'14.50"W) and organisms from this site were used for all experiments.

Large scale survey of damage to kelp blades

Damage to *L. spicata* was quantified at all eight study sites (Fig. 1) from 100 haphazardly collected blades, and, for *M. pyrifera*, from six of the eight sites (this species did not occur at Playa Mamani and Puerto Oscuro). Blades were collected from a 50-m stretch of the shoreline between 16 December 2012 and 13 January 2013 with no more than one blade collected from each holdfast. Visual estimates of the damage to the surface of each blade (to the nearest 10 %) were obtained by lighting the blades from behind and distinguishing between the darkly pigmented epidermal layers and paler regions scraped by isopod feeding (Fig. S2, Appendix 2 in Online Resource). This measure equates to the percentage of the projected area of the blade damaged and not to the percentage of surface area, due to

the inability to determine, with blades lit from behind, if a damaged section also had corresponding damage on the alternate side. Damage scores were contrasted among species and sites with analysis of variance (ANOVA) in SYSTAT 13 with species as a fixed factor and site as a random factor (excluding the two sites that lacked *M. pyrifera*).

Distribution of damage among and within kelp individuals

At Punta Talca (south) on 29 November 2012, we quantified the distribution of damage on *L. spicata* and *M. pyrifera* in a spatially hierarchical sampling design (among tissue types within a blade, among blades within a holdfast, and among holdfasts) and simultaneously recorded the abundance of *A. tya*. For *L. spicata*, we sampled 40 holdfasts, five stipes per holdfast, and five blades from the apical sections of each stipe (each approximately 50 cm long). For the larger *M. pyrifera*, we sampled 30 independent stipes and five blades per stipe. In both species, we recorded the percent damage and biomass of the sampled blades, damage to the adjacent stipe and, for *M. pyrifera*, the damage to the pneumatocyst adjacent to each blade. Further measurements quantified the patterns of damage with tissue age within a blade (i.e. distance from the blade meristem) (detailed methods in Appendix 1, Online Resource 1).

For *L. spicata*, the percent damage to blades was contrasted among holdfasts with ANOVA with holdfast as a random factor, stipe as random factor nested within holdfast and blade biomass as covariate. Percent damage to stipes was analysed with ANOVA with holdfast as

a random factor and stipe as random factor nested within holdfast. For *M. pyrifera*, percent damage to blades was contrasted among stipes with ANOVA with stipe as a random factor and blade biomass as a covariate. Analyses of variance and the % of variation attributable to each factor (derived from least squares estimates of variance components) were calculated using the PERMANOVA routine of Primer V6 (note that this was used to produce univariate ANOVA, given we were analysing a single dependent variable and using Euclidean distance as the distance measure; Anderson et al. 2006).

The relationship between isopod abundance on *L. spicata* and blade damage was analysed with quantile regression using the *quantreg* package in R (available at <http://cran.r-project.org/web/packages/quantreg/index.html>). We quantified the degree of spatial clumping in isopod abundance on *L. spicata* at the holdfast and stipe scale by calculating the coefficient of dispersion (*CD*), where *CD* is the ratio of the variance to the mean (s^2/\bar{x}). This coefficient is equal to one if counts per sample are randomly dispersed, >1 if clumped, and <1 if regularly spaced. Deviation from a random distribution is tested by contrasting *I*, where $I = s^2/\bar{x}(n - 1)$, against the χ^2 distribution with $n - 1$ degrees of freedom (Krebs 1999).

Impacts of *A. tupa* grazing on kelp growth and photosynthesis

We grew *L. spicata* and *M. pyrifera* in the presence and absence of grazing isopods to test the hypothesis that high levels of surface damage by *A. tupa* affects their growth and photosynthesis. For both species, ten stipes from separate holdfasts were allocated to each grazing treatment (mean \pm SE initial biomass = 58.2 ± 1.9 g for *L. spicata*; 64.4 ± 3.0 g for *M. pyrifera*). For *L. spicata*, isopods were collected from this alga and added to the grazer treatment at a density of 20 individuals per 100 g wet weight, representative of a high density cluster of isopods occurring at this site (see Fig. 3). For *M. pyrifera*, we used ten individuals per 100 g wet weight, higher than the density observed in our surveys at Punta Talca (south), but resulting in levels of blade damage (~20 %) evident from our field surveys.

The growth of five blades haphazardly chosen per stipe was measured using the methods of Tala and Edding (2005). Briefly, a 5-mm hole was punched 5 cm from the stipe–blade junction in *L. spicata* and 5 cm above the pneumatocyst–blade junction in *M. pyrifera*, and the distance moved by this hole over time represented the blade elongation rate. All stipes were placed individually in large mesh bags (30 cm wide and 80 cm long, 1 mm mesh opening) and randomly allocated to positions along a rope between two buoys in the ocean adjacent to the Universidad Católica del Norte in Coquimbo (Bahía La Herradura, 29°58'S,

71°21'W). After 3 days, we measured total stipe biomass, blade growth and damage, and replaced the few isopods (3 % of all individuals) that were lost. After 6 days, these measures were repeated with the addition of total biomass, and the photosynthetic efficiency and concentrations of photosynthetic (Chl *a*) and accessory pigments (Chl *c* and total carotenoids) for three blades per stipe. Photochemical efficiency, i.e. the maximal quantum yield (F_v/F_m), was calculated with a portable pulse modulation fluorometer (PAM 2500; Walz, Effeltrich, Germany) from the meristematic and distal zone of blades following dark incubation for 20 min. Pigment concentrations were based on extraction of meristematic and distal zones with N,N-dimethylformamide for 24 h at 4 °C in darkness and extinctions in a scanning UV/Vis 1601 spectrophotometer (Rayleigh, China), following the methods of Gómez et al. (2005), and the dichromatic equations of Inskeep and Bloom (1985) for Chl *a* and Henley and Dunton (1995) for Chl *c* and total carotenoids.

Change in biomass (% per day) was contrasted among grazer treatments using ANOVA with grazer treatment (isopod vs. control) as a fixed factor, and day (3 and 6) as a repeated measure. Blade elongation (mm per day) was analysed with grazer treatment as fixed factor, stipe as random factor nested within treatment and day as a repeated measure. Maximum quantum yield (F_v/F_m), and pigment concentrations were contrasted among treatments using ANOVA with grazer treatment as fixed factor and stipe as random factor nested within treatment and blade region (meristematic vs. distal regions) as a blocked factor.

Further feeding experiments were run to quantify the rate at which an individual of *A. tupa* could damage the surface of *L. spicata* and *M. pyrifera*, and, for *L. spicata*, whether *A. tupa* displayed any preference for previously damaged tissues (detailed methods in Appendix 2, Online Resource 1).

Consequences of blade damage to kelp growth in the field

The relationship between damage and growth rates of *L. spicata* was quantified in situ by marking three blades from each of 30 stipes chosen to encompass the range of blade damage (0–100 %) observed at Punta Talca (south) in November 2012. The blades were hole-punched and, after 6 days, blades were collected and we measured blade elongation, biomass, percent damage, F_v/F_m and the concentrations of pigments (methods as described above). This experiment was run with *L. spicata* only due to the much lower levels of damage to *M. pyrifera* in the field, and the absence of grazer effects on giant kelp growth in our experiments. The relationship between growth of *L. spicata* and blade damage was analysed with quantile regression, with blade elongation (mm day⁻¹) as the dependent variable and

percent damage as the independent variable. The relationships between growth and F_v/F_m and each of the pigment concentrations ($\text{mg g wet weight}^{-1}$) were tested with linear mixed models in the PROC MIXED procedure in SAS 9.2 with blade elongation (mm day^{-1}) as the dependent variable, percent damage as the independent variable, and stipe as a random factor.

Results

Large-scale survey of damage to kelp blades

Grazing damage to the blades of *L. spicata* and *M. pyrifera* was evident at all sites sampled (Fig. 1), with a high proportion (85 % in *L. spicata*, 37 % in *M. pyrifera*) of blades with at least some damage. The damage to blades of *L. spicata* (site means of 9.2–25.0 %) was higher than to *M. pyrifera* (1.9–8.6 %) ($F_{1,5} = 46.8, P = 0.002$), with significant variation among sites sampled ($F_{5,1188} = 20.6, P = 0.001$) and the magnitude of the difference between species varying with site (a significant interaction between site and species, $F_{5,1188} = 12.9, P = 0.001$).

Distribution of damage among and within kelp individuals

At Punta Talca (south), the damage to *L. spicata* blades was unevenly distributed at each of the spatial scales sampled: among blades (Fig. 2; the residual variation comprising 39.4 % of the total variation; Table 1), among stipes within a holdfast (31.9 % of the total variation), and among holdfasts (28.7 % of the total variation). Grazing damage was also present on the stipes of *L. spicata* (mean \pm SE = 7.3 ± 0.9 % damage) but at lower levels than the blades (15.3 ± 0.9 %, $F_{1,39} = 33.6, P < 0.001$). Damage to stipes was also unevenly distributed at the each of the spatial scales sampled (Table 1). In *M. pyrifera*, damage to blades was unevenly distributed among the stipes sampled (Table 1) and higher than that present on stipes (0.8 ± 0.2 %, $F_{1,29} = 13.5, P < 0.001$) and adjacent pneumatocysts (paired *t* test, $t_{59} = 1.32, P = 0.006$). The damage to blades of *L. spicata* did not vary with the age of tissues within a blade (Fig. S1 and Appendix 1, Online Resource 1). In *M. pyrifera*, blade damage varied with distance from the blade meristem, but not consistently with tissue age within a blade (Fig. S1 and Appendix 1, Online Resource 1).

Fig. 2 The frequency distribution of damage to blades of **a** *Lessonia spicata* ($n = 975$ blades) and **b** *Macrocystis pyrifera* ($n = 148$) at Punta Talca (south)

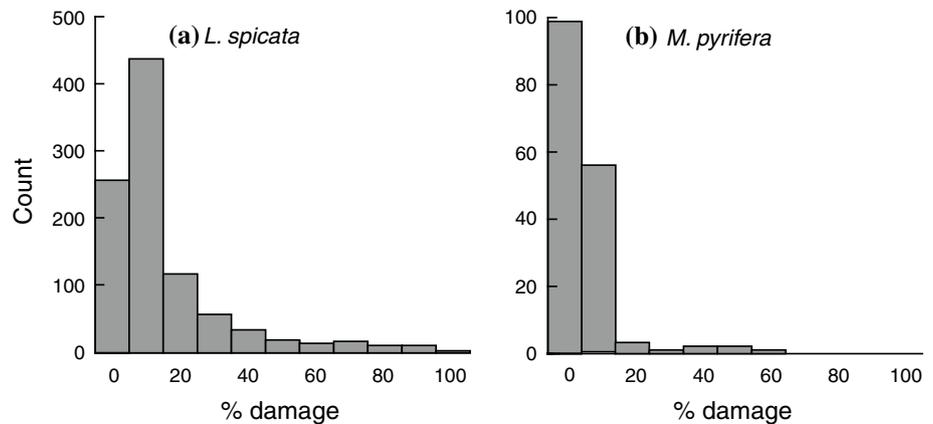


Table 1 Analyses of variance of damage to blades and the stipe adjacent to sampled blades in *Lessonia spicata* and *Macrocystis pyrifera* sampled from Punta Talca (south)

Holdfast was a random factor, Stipe a random factor nested within holdfast, and blade biomass a covariate. The % of variation is derived from least squares estimates of variance components from ANOVA
* Significant effect ($P < 0.05$)

| Source | df | Blade damage | | | | Stipe damage | | | |
|--------------------|-----|--------------|------|---------|-------|--------------|------|--------|-------|
| | | MS | F | P | % var | MS | F | P | % var |
| <i>L. spicata</i> | | | | | | | | | |
| Holdfast | 39 | 2,724.8 | 4.03 | <0.001* | 28.7 | 1,307.4 | 2.22 | 0.001* | 20.6 |
| Stipe (holdfast) | 160 | 672.7 | 4.19 | <0.001* | 31.9 | 584.2 | 4.05 | 0.001* | 36.0 |
| Biomass | 1 | 350.5 | 0.23 | 0.63 | 0 | 179.8 | 0.42 | 0.51 | 0 |
| Error | 774 | 160.5 | | | 39.4 | 144.1 | | | 45.4 |
| <i>M. pyrifera</i> | | | | | | | | | |
| Stipe | 29 | 234.7 | 3.95 | <0.001* | 39.8 | 12.09 | 1.88 | 0.01* | 29.1 |
| Biomass | 1 | 491.7 | 2.61 | 0.11 | 9.4 | 0.38 | 0.04 | 0.84 | 70.1 |
| Error | 117 | 59.389 | | | 50.8 | | | | |

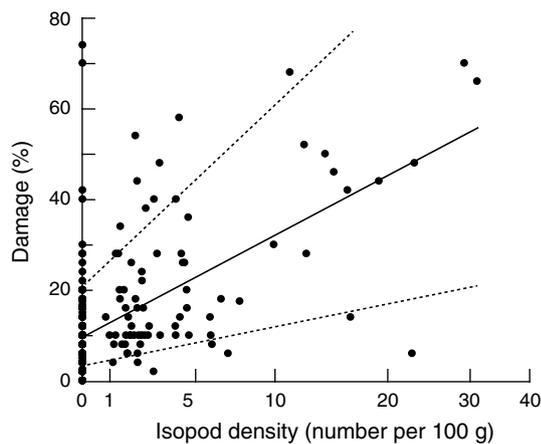


Fig. 3 The relationship between isopod abundance and blade damage to *L. spicata*. Data are the average damage of five blades per stipe and isopod density (individuals per 100 g wet weight) ($n = 200$). The lines are the 90th, 50th and 10th quantiles, with a significant positive relationship for the 90th ($t = 3.9$, $P < 0.001$) and 50th ($t = 5.3$, $P < 0.001$) quantiles, but not the 10th ($t = 1.5$, $P = 0.13$)

The mean density of *A. tya* on *L. spicata* was 2.05 ± 0.33 individuals per 100 g wet weight, but highly variable, ranging from 0 to 21 individuals per stipe (0–31 individuals per 100 g). Their spatial distribution was highly aggregated at both the scale of holdfasts (coefficient of dispersion, $CD = 10.39$, $P < 0.001$) and the scale of stipes within holdfasts ($CD = 7.4$, $P < 0.001$). Higher densities of isopods were associated with increasing, and more variable, rates of damage to individual blades (Fig. 3). Isopod density on *M. pyrifera* was very low with 0–3 individuals per stipe (0.48 ± 0.17 individuals per 100 g wet weight).

Impacts of *A. tya* grazing on kelp growth and photosynthesis

Grazing by *A. tya* in experimental conditions resulted in mean \pm SE blade damage of 54 ± 2 % after 3 days, and 70 ± 2 % after 6 days. After 6 days, the ungrazed stipes had increased in mass by 0.13 ± 0.03 % per day, while those grown in the presence of grazing isopods decreased in mass by 0.43 ± 0.06 % per day (Fig. 4a; Table 2). After 6 days, the growth rate of the grazed blades was significantly (80 %) lower than the rates of the ungrazed blades (Fig. 4c; Table 2). Grazed blades had significantly lower concentrations (27–60 % reductions) of Chl *a*, Chl *c* and total carotenoids than the ungrazed blades (Fig. 5a; Table S1, Online Resource 1). Maximum quantum yield (F_v/F_m) of blades did not differ significantly between grazed and ungrazed blades (Fig. 5c; Table S1, Online Resource 1).

In *M. pyrifera*, high densities of isopods in experimental conditions resulted in damage to blades of 20 ± 1 and 22 ± 1 % after 3 and 6 days, respectively. After 6 days,

stipes had increased in mass by 12 ± 1 % (Fig. 4b), and elongated by 3.2 ± 1.9 cm (Fig. 4d), with the effects of grazing dependent on the day measured (a significant day \times grazer interaction; Table 2). There were no significant effects of the grazing treatment on the concentration of photosynthetic pigments or F_v/F_m (Fig. 5b, c; Table S1, Online Resource 1).

In feeding experiments, individual isopods could rapidly damage the blades of *L. spicata* (to a mean \pm SE of 56 ± 7 % damage in 3 days) and *M. pyrifera* (to 25 ± 5 %) (Fig. S3, Online Resource 1). The feeding rates of *A. tya* did not differ between undamaged and previously damaged blades of *L. spicata*, and they displayed no habitat preference for either blade type (Appendix S2, Online Resource 1).

Consequences of blade damage to kelp growth in the field

In the field, blade growth rates of *L. spicata* were highly variable with low levels of damage, but consistently low with high levels of damage (Fig. 6a). There were significant negative relationships between blade damage and the concentration of Chl *a* ($F_{1,69} = 19.2$, $P < 0.001$), Chl *c* ($F_{1,70} = 16.9$, $P < 0.001$) and total carotenoids ($F_{1,72} = 12.0$, $P < 0.001$) (Fig. 6b). There was no significant relationship between damage and maximum quantum yield (F_v/F_m) of blades ($F_{1,50} = 0.01$, $P = 0.94$).

Discussion

We determined that minor grazing damage by a small herbivore can have disproportionately large effects on the growth rate of a highly productive kelp. Grazing isopods consumed less than 0.5 % of *L. spicata* biomass per day in our field experiment, but reduced the concentration of pigments by up to 60 % and blade growth rate by almost 80 %. Despite low average abundances of isopods, individual *L. spicata* can face extensive surface damage due to the spatial aggregation of grazers, with damage associated with reduced growth in the field. These results from *L. spicata* contrast with the expectation that the adult stages of kelps are rarely impacted by canopy-dwelling mesograzers (e.g. Graham et al. 2007), and with our findings on the giant kelp *M. pyrifera* which displayed high growth rates unaffected by isopod grazing.

Grazing impacts on kelp individuals

The distribution and abundance of kelp is frequently controlled by large invertebrates (particularly urchins) that graze the substratum and prevent the recruitment of kelps from their early life-history stages (e.g. Dean et al. 1984;

Fig. 4 The impact of *A. tya* grazing on kelp **a, b** biomass and **c, d** blade elongation in the grazing experiment with *L. spicata* and *M. pyrifera*. Data are mean \pm SE of change to stipe biomass (% g wet weight day⁻¹) after 3 and 6 days of each tissue type, blade elongation (mm day⁻¹) in the grazed treatment with isopods and the control lacking isopods ($n = 10$ stipes per treatment (**a, b**), 50 blades per treatment (**c, d**))

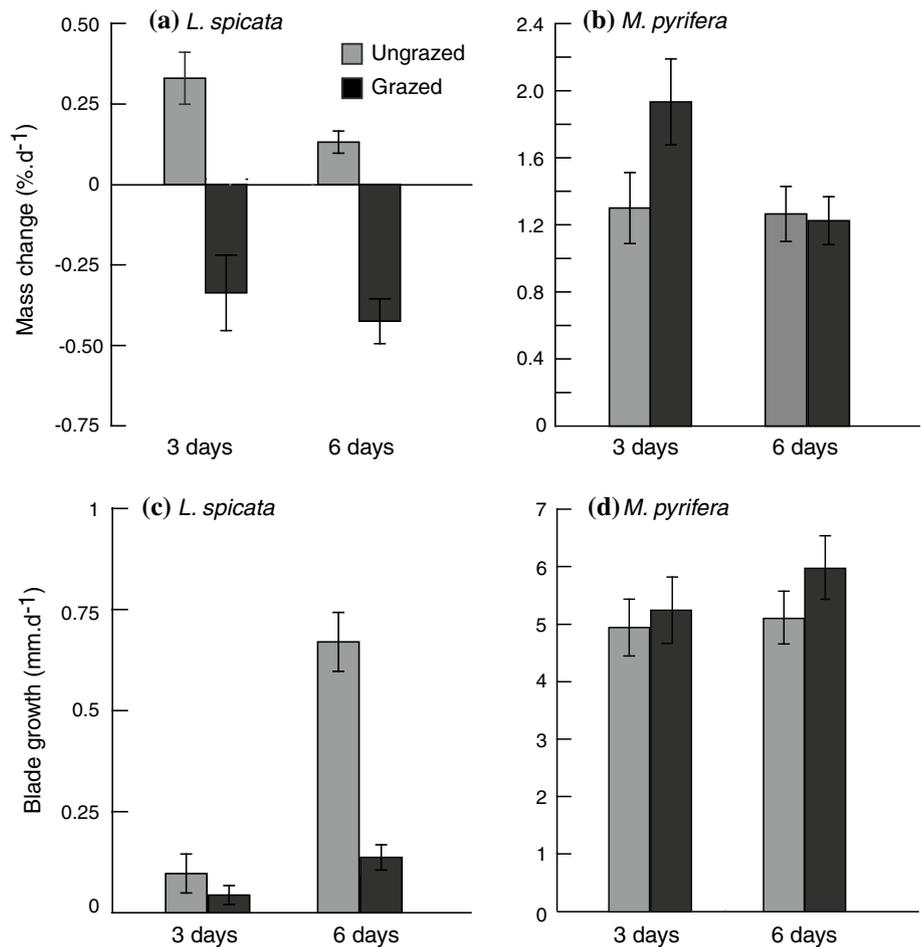


Table 2 Analyses of variance of mass loss (% per day), blade elongation (mm day⁻¹) of *L. spicata* and *M. pyrifera* in experimental conditions with and without grazing isopods

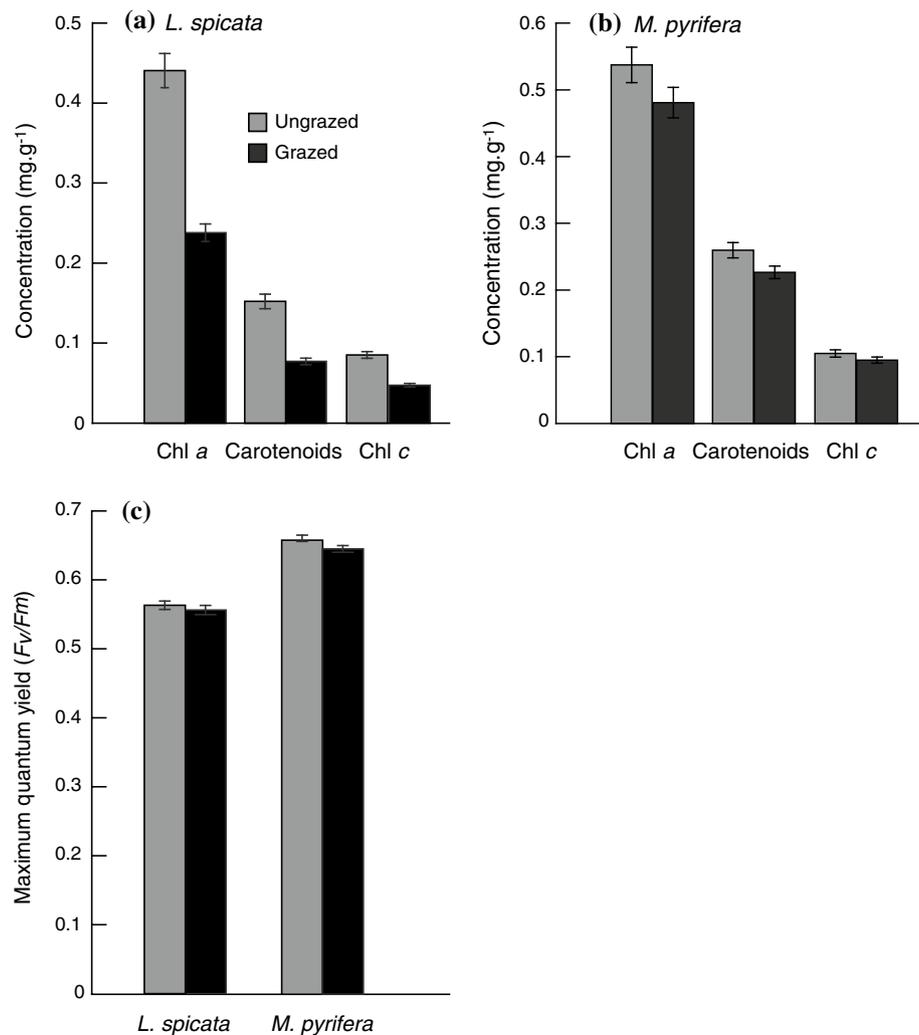
| Source | df | <i>L. spicata</i> | | | <i>M. pyrifera</i> | | |
|-----------------------------|----|-------------------|-------|---------|--------------------|------|---------|
| | | MS | F | P | MS | F | P |
| Mass loss | | | | | | | |
| Grazer | 1 | 3.74 | 39.06 | <0.001* | 0.88 | 1.63 | 0.21 |
| Day | 1 | 7.57 | 9.61 | 0.007* | 1.38 | 8.46 | 0.009* |
| Stipe (grazer) | 18 | 1.0 | 4.48 | 0.001* | 0.54 | 3.30 | 0.006* |
| Grazer \times day | 1 | 0.03 | 1.41 | 0.26 | 1.13 | 6.94 | 0.02* |
| Error | 18 | 0.02 | | | 0.16 | | |
| Blade elongation | | | | | | | |
| Grazer | 1 | 5.12 | 9.00 | 0.001* | 5.44 | 0.07 | 0.78 |
| Day | 1 | 3.47 | 14.78 | 0.007* | 1.47 | 0.67 | 0.42 |
| Stipe (grazer) | 18 | 0.57 | 2.21 | 0.005* | 80.65 | 6.43 | <0.001* |
| Grazer \times day | 1 | 2.28 | 9.70 | 0.004* | 0.21 | 0.09 | 0.76 |
| Blade (stipe) | 80 | 0.26 | 2.73 | 0.005* | 12.55 | 9.52 | <0.001* |
| Day \times stipe (grazer) | 18 | 0.23 | 2.48 | 0.003* | 2.33 | 1.77 | 0.045* |
| Error | 80 | | | | 1.32 | | |

Grazer (present vs. absent) was a fixed factor, Day a repeated measure, Stipe a random factor nested within the grazer treatment, and Blade a random factor nested within Stipe
* Significant effect ($P < 0.05$)

Henríquez et al. 2011). The experimental exclusion of macrograzers from kelp forests usually results in large, predictable increases in kelp biomass (Poore et al. 2012).

Once established, kelp biomass predominantly enters detrital pathways (Krumhansl and Scheibling 2012), but is impacted by occasional outbreaks of macrograzers

Fig. 5 The impact of *A. tya* grazing on **a, b** pigment concentrations and **c** maximum quantum yield in the grazing experiment with *L. spicata* and *M. pyrifera*. Data are mean \pm SE of the concentrations of chlorophyll *a*, chlorophyll *c* and total carotenoids (mg per g wet weight) and maximum quantum yield (F_v/F_m) in the grazed treatment with isopods and the control lacking isopods ($n = 30$ blades per treatment)



(Uthicke et al. 2009). Grazing by small herbivores that inhabit the kelp blades is assumed to have limited impact except in periods of population explosions due to release from predators (Graham et al. 2007). Here, we showed that the production of biomass in the kelp *L. spicata* can be strongly reduced by the grazing activities of a small herbivore, the isopod *A. tya*. Grazing damage due to isopod feeding was frequent at all sites visited in our large-scale survey along the northern-central coast of Chile, and the negative impact of this damage on the growth of *L. spicata* was evident from our field experiment. The reduced growth rate as a consequence of damage was also consistent with the negative correlation between blade damage and growth rate we observed in the field, although without experimental evidence we could not exclude the possibility that this correlation resulted from isopods in the field preferring to feed on slow-growing blades, or that faster-growing blades were simply less likely to be encountered by herbivores. With a characteristic pattern of surface damage and no other mesograzers observed on the blades of *L. spicata*, it

was evident that *A. tya* was the dominant grazer of blade tissue at our study sites; the limpet *Scurria scurra*, which can cause extensive stipe loss in *Lessonia* spp. (Muñoz and Santelices 1989), excavated holdfast and stipe tissues at some sites.

Very few studies have examined the relationship between mesograzers damage and the growth rates of kelps or other large brown macroalgae. Johnson and Mann (1986) demonstrated similar disproportionate effects on the kelp *Saccharina longicruris* due to grazing by the gastropod *Lacuna vincta*. These gastropods removed only 0.05 % of the available biomass, but caused a reduction in algal growth by 75 % over 3 weeks. With simulated grazing to *S. longicruris*, Krumhansl and Scheibling (2011) also demonstrated that damage of only 1 % of blade area could greatly accelerate kelp tissue losses. In contrast to our study, however, the impacts on canopy area in those studies were largely due to grazers facilitating tissue loss rather than reducing blade elongation rates. For *M. pyrifera*, Davenport and Anderson (2007) demonstrated that

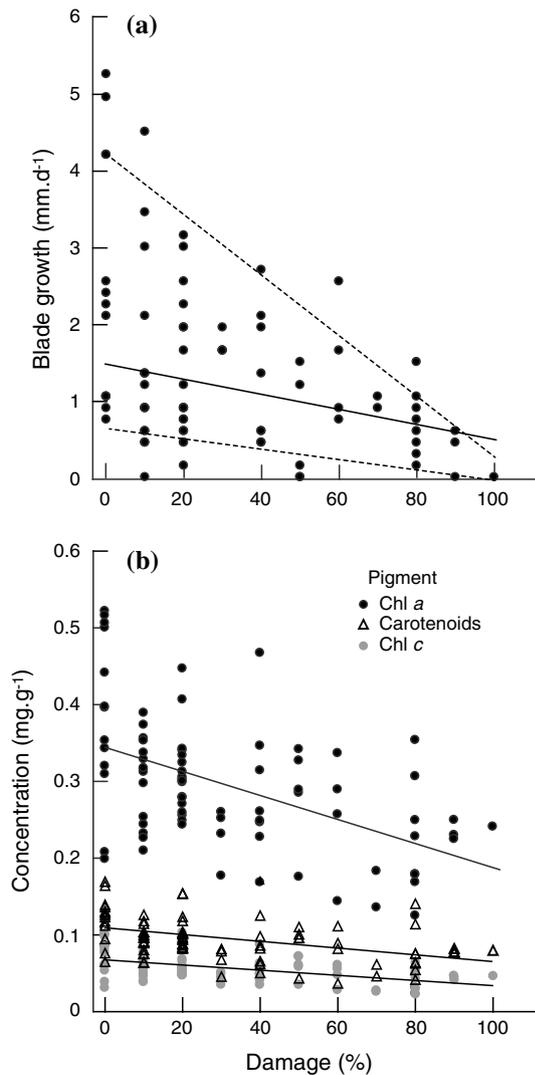


Fig. 6 The relationships between blade damage to *L. spicata* and **a** growth and **b** photosynthetic pigment concentrations in the field. Data are the blade elongation (cm) after 6 days, and the concentrations of chlorophyll *a*, chlorophyll *c* and total carotenoids (mg g wet weight⁻¹) ($n = 90$ blades). In **(a)** the lines are the 90th, 50th and 10th quantiles, with significant negative relationships for each quantile (90th, $t = 4.9$, $P < 0.001$; 50th, $t = 2.5$, $P = 0.01$; 10th, $t = 3.8$, $P < 0.001$)

damage by the amphipod *Peramphithoe humeralis* resulted in kelp individuals producing fewer fronds and meristems, but blade growth did not differ significantly between grazer treatments. With exclusion experiments, Toth et al. (2007) clearly established that three species of the gastropod *Littorina* can reduce the growth of the furoid *Ascophyllum nodosum* at natural densities in the field. Given that algal fitness is often strongly coupled with size (Pavia et al. 2002), and that reproduction in *L. spicata* is dependent on standing stock (Tala et al. 2004), these reductions in growth due to mesograzer damage are expected to have longer

term consequences on the reproductive success of individuals. For *L. spicata*, further research is needed to link growth rates to reproductive output, including the likelihood of damaged photosynthetic tissue recovering.

In contrast to *L. spicata*, isopod grazing on *M. pyrifera* was low and did not reduce blade growth rates even at levels of damage higher than regularly observed in our field surveys. The lower abundance of isopods on *M. pyrifera* could arise from increased exposure of mesograzers to fish predation on this subtidal species, in contrast to the intertidal *L. spicata* (see Gutow et al. 2011 for amphipod susceptibility to predation in *M. pyrifera* at sites in northern-central Chile). It seems unlikely to be due to low palatability, as *M. pyrifera* was consumed by *A. tya* at higher rates (per biomass) than *L. spicata* in our feeding experiments, and *L. spicata* is generally of low palatability to other crustacean mesograzers in the system (Rothäusler and Thiel 2006). The difference in the effects of damage on growth in the two species could be explained by differences in the amount of blade tissue that was damaged in our experiments (lower in *M. pyrifera* than in *L. spicata*) or differences in the ability of the two kelps to compensate for tissue damage. Our results with *M. pyrifera* are consistent with the ability of this species to tolerate damage by other mesograzers (Cerdeira et al. 2009) and with studies on other kelp species where meristematic growth rates were uncoupled from damage to other tissues. In *Ecklonia radiata*, for example, as much as 50 % biomass loss due to the canopy-dwelling urchin *Holpneustes purpurascens* did not affect blade elongation rates even when consumption ultimately resulted in death of the individual (Steinberg 1995).

Spatial distribution of damage

Amphoroidea tya was highly aggregated at the scale of stipes and holdfasts, and the distribution of their grazing damage was highly skewed at each of the spatial scales we examined (among holdfasts, among stipes within holdfasts, among blades and within blades). Consequently, some kelp individuals, and some parts of individuals, received much higher damage than the population-level averages, with the associated declines in biomass production. The often aggregated spatial distribution of small herbivores (including other mesograzers on kelps; Johnson and Mann 1986; Graham 2002), and their feeding specificity among plant parts, ensures that their impact on the fitness of individual plants is not easily predicted from population-level averages of consumption rates. An understanding of how selection by herbivores may affect plant traits is dependent on the distribution of damage among and within individuals, with concentrated damage often having larger impacts than dispersed damage (Marquis 1996). Our field experiment with *L. spicata* used isopod densities representative of the

grazer aggregations observed in our field surveys, and thus represents the likely upper bounds of grazer impacts. The decline in blade growth rate with damage in the field, however, was evident across the entire range of damage levels, and thus not limited to cases of extreme damage.

The clumped distribution of isopods in the field, associated with more highly damaged blades, was not explained by any preference to select or consume tissues of *L. spicata* that were already damaged (Appendix 2). The spatial variation in the quality of kelp tissues, however, could still explain isopod distributions if food qualities (e.g. nutritional value, phlorotannin levels or tissue toughness) were themselves unevenly distributed. Alternatively, the clumped distributions could arise from small-scale variation in water motion in this high-energy environment (known to affect mesograzers; Duggins et al. 2001), isopod behaviour with respect to conspecifics (e.g. mating opportunities) or limited dispersal of juveniles post-hatching (considered unlikely because isopods move on the scales of 10s of centimetres during a swimming bout; personal observation).

Within kelp individuals, the grazing damage to *L. spicata* and *M. pyrifera* was concentrated on the highly pigmented epidermis tissue of the blades and stipes, with even single isopods being able to remove a large proportion of the surface tissue within a few days. We found no evidence that the photosynthetic efficiency of blade tissue differed between damaged and undamaged tissues, and thus the impacts of isopod grazing on the blade growth of *L. spicata* are most likely to result from the large reductions in the concentration of photosynthetic pigments per blade area. With lower pigment concentrations, damaged tissues seem to produce less energy for growth, and potential translocation of resources from undamaged regions of the blade is unable to compensate for this loss in *L. spicata*. In *M. pyrifera*, neither the concentration of photosynthetic pigments nor the photosynthetic efficiency was affected by grazing damage, even at levels of damage rarely seen in field populations. *Macrocystis pyrifera* may be unaffected by isopod damage due to the levels of damage never reaching thresholds that would reduce growth, or because this kelp has a higher potential to compensate for tissue losses due to reallocation of resources (Cerda et al. 2009).

More generally, the responses of individual plants to damage commonly vary between photosynthetic tissues that produce resources and tissues that function as resource sinks such as reproductive organs (Stowe et al. 2000), and with the timing of damage with respect to resource availability (e.g. early season vs. late season leaves; young vs. old plants; Boege and Marquis 2005). Our experiments were conducted in late spring–early summer which is the annual period of maximum growth of *Lessonia* spp. in central Chile (Tala and Edding 2005). Seasonal variations of isopod abundances have not yet been investigated in the

local *L. spicata* beds. However, if the isopod abundances remain constant throughout the year, the impact on *L. spicata* might be even higher in other seasons when the growth of the algae is lower.

In addition to damage to photosynthetically active tissues, any concentration of damage on other valuable tissues such as meristems or reproductive tissues could lead to disproportionate impacts of tissue loss on plant fitness. In *L. spicata*, new tissues within each blade were damaged at similar levels as older tissues more distant from the blade meristem. Given that the older tissues had been exposed to grazers for a longer period of time, this indicates that new growth is more likely to be damaged by isopods (if damage was unrelated to age, older tissues should accumulate damage with time). Damage to meristematic tissue is likely to contribute strongly to the reduced blade growth rates. In *M. pyrifera*, damage varied with distance from the blade meristem, but not consistently with tissue age. Grazing damage by other species of mesograzers consuming brown algae can be concentrated on meristems (e.g. Poore 1994), reducing the ability of macroalgae to produce new branches (Hay et al. 2011).

Damage from *A. typa* was concentrated on kelp blades, but also occurred to a lower degree on stipes of both species and the pneumatocysts (float structures) in *M. pyrifera*. While we have not addressed the long-term consequences of damage to these supportive structures, several studies have suggested that tissue losses due to breakage following grazing are likely to greatly outweigh losses due to consumption (Johnson and Mann 1986; Krumhansl and Scheibling 2012; de Bettignies et al. 2012). Relative to blades, the lower rates of damage to stipes, and the higher concentrations of potentially deterrent phlorotannins in Pansch et al. (2008), is consistent with an optimal allocation of defences by kelps to the valuable stipe tissues. Damage to either blade or stipe structures may also facilitate damage by other species (e.g. Molis et al. 2010), induce higher levels of physical or chemical defences that could alter feeding rates by other herbivores (Toth and Pavia 2007) or provide access for disease (Campbell et al. 2013). Alternatively, loss of blades due to grazing can reduce the likelihood of wave action dislodging entire holdfasts (Black 1976; Santelices et al. 1980; de Bettignies et al. 2012). Despite efforts to predict the impacts of mesograzers on kelps from their abundance and per capita consumption rates (e.g. Sala and Graham 2002), these possible indirect effects, and the uneven distribution of damage among plant parts, makes it difficult to predict impacts without an experimental approach.

Mesograzer impacts on marine primary producers

Evidence for impacts of crustacean grazing on kelp forests have been limited to exceptional observations of

extensive damage in the field (e.g. Chess 1993), often during unusual conditions of low fish abundance (e.g. Tegner and Dayton 1987; Graham 2002). We provide the first experimental and observational evidence that crustacean mesograzers can affect the growth rate of kelps under typical environmental conditions. Our experiments demonstrate that even low densities of small grazers can negatively affect kelp performance and that their impacts are not simply predicted by the amount of biomass consumed. This adds to the emerging body of experimental evidence of the top-down impacts of small grazing crustaceans on marine primary producers. The manipulation of mesograzer abundance in mesocosm settings (Duffy and Hay 2000; Newcombe and Taylor 2010), directly in the field (Cook et al. 2011; Whalen et al. 2013) or by the removal of predatory fish (Davenport and Anderson 2007) have all demonstrated that mesograzers can control the abundance of some marine primary producers. The strength of top-down control, however, is variable among experiments (Poore et al. 2009), among seasons (Whalen et al. 2013), among producer types (Poore et al. 2012), and with the presence and identity of predators (Pérez-Matus and Shima 2010).

Understanding how primary producers are impacted by mesograzers is essential for understanding their suggested role as intermediate links in trophic cascades (Duffy et al. 2005). With direct consumption of the host, as in this study, increased abundance of mesograzers following predator removals are likely to decrease host performance (as shown in the *M. pyrifera* beds of California, Tegner and Dayton 1987; or recently for the seagrass *Zostera marina* in California, Lewis and Anderson 2012). Alternatively, hosts can benefit from higher mesograzer abundance if they consume epiphytes rather than host tissue (also demonstrated for *Z. marina*, in Virginia; Whalen et al. 2013). Mesograzers clearly have the potential to alter benthic community structure, and the challenge remains to predict when and where this is likely given the variation in their feeding behaviour, and the uneven distribution of their grazing damage among and within producer species.

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