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Effects of canopy-mediated abrasion and water flow on the early colonisation of turf-forming algae

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Abstract.

Canopies in both terrestrial and marine systems modify biotic and abiotic conditions, having a large effect on the understorey. In marine systems, algal canopies form predictable associations with the benthic understorey, and canopy-mediated processes may maintain these associations. Three canopy-mediated processes that are inherently linked are water flow through a canopy, abrasion of the substrate by the canopy, and light penetration. These processes were experimentally reduced to test the hypotheses that turf-forming algae would be positively affected by: (1) reduced abrasion by kelp canopies and (2) reduced water flow, and (3) negatively affected by shading. Biomass of turf-forming algae was greater when abrasion was reduced, but less when light was reduced. In contrast to predictions, however, reduced water flow had a negative effect on the percentage cover and biomass of turf-forming algae, rejecting the second hypothesis. It seems, however, that this negative effect was caused by an increase in shading associated with reduced canopy movement, not a reduction of water flow *per se*. None of the factors accounted for all of the change seen in understorey algae, indicating that it is important to study the interactive effects of physical processes.

Introduction

One of the most striking and consistent generalisations in ecology is that the presence of a canopy affects the composition of the understorey community, in part through modification of the physical environment (Belyea and Lancaster 1999). However, without understanding the processes by which this modification occurs, generalities cannot be identified, leading to a situation where every new system has to be studied without any prior knowledge (Levin 1992). Therefore, understanding the specific processes by which canopies alter the understorey may provide us with the ability to predict species associations and distributions (Wright and Jones 2004).

Predictable associations exist between algal canopies and the benthic understorey (Dayton *et al.* 1984; Kennelly and Underwood 1993; Bertness *et al.* 1999; Bruno 2000; Irving and Connell 2006b). These associations may be related to the ability of canopies to alter the physical environment, and can be both positive (Bertness *et al.* 1999; Irving *et al.* 2004a) and negative (Kennelly 1989; Connell 2003b; Irving and Connell 2006a). Regardless of the nature of this relationship, however, when canopy is removed a different set of taxa tends to dominate space (e.g. Dayton *et al.* 1992; Edwards 1998; Bulleri *et al.* 2002; Irving and Connell 2006b).

Numerous studies have demonstrated the effect of canopies on the understorey, but it is often difficult to separate the contribution of individual physical processes, possibly because many processes are linked (e.g. water movement, abrasion and shading). For example, in areas of greater water movement the canopy moves to a greater extent, subsequently causing both more abrasion of the substrate (Kennelly 1989; Toohey *et al.* 2004) and changes in light conditions. Therefore, it could be expected that in areas of less water movement, the effect of canopy abrasion may be less, but shading more, than in areas of greater water movement. Investigating the interactive effects of these factors may provide us with a better understanding of canopy-understorey relationships.

Algal canopies alter water flow across the benthos by creating a physical barrier to the water (Eckman *et al.* 1989). In doing so, the canopy itself is moved by the water, sweeping across the substrate and causing surface abrasion. This physical abrasion can alter the species composition of the understorey by directly excluding invertebrates (e.g. Duggins *et al.* 1990; Connell 2003b) and algae (Velimirov and Griffiths 1979; Kennelly 1989; Irving and Connell 2006a; Irving and Connell 2006b). Light penetration is also reduced under canopies (shading), and may have large effects on the benthic understorey (Reed and Foster 1984; Kennelly 1989; Edwards 1998; Connell 2005). Although the individual effects of these physical factors have been well demonstrated, their interactive effects are currently unknown.

In southern Australia, filamentous turf-forming algae dominate open space on hard, subtidal substrate in the absence of an algal canopy (Fowler-Walker and Connell 2002; Irving *et al.* 2004b), but are quickly lost from the benthos with the addition of a canopy (Melville and Connell 2001; Irving and Connell 2006a; Irving and Connell 2006b). I experimentally altered the amount of water flow through canopies, the amount of abrasion by canopies, and light intensity to test the hypotheses that turf-forming algae would be positively affected by: (1) reduced abrasion by kelp canopies and (2) reduced water flow, and (3) negatively affected by shading (reduced light).

Materials and methods

Study site

The study site (West Island, South Australia, 35°36’ S, 138°35’ E) consists of a sloping boulder reef that terminates in sand at ~ 5 m depth and supports diverse assemblages of algae (Shepherd and Womersley 1970), including the canopy alga *Ecklonia radiata* (C. Agardh) J. Agardh and the filamentous turf-forming algae *Feldmannia lebelli* Crouan and Crouan and *F. globifera* Kuetzig. Experimental units (see below) were attached to boulders on experimental reefs placed on sand at ~ 5 m depth (see Shepherd and Turner 1985 for a photograph of the experimental reefs).

Natural v. artificial abrasion

The first experiment had two aims: (1) to assess the extent to which artificial kelp mimicked natural abrasion by *E. radiata* and (2) assess the effects of abrasion on turf-forming algae. The effects of type of kelp (artificial *v*. natural) was tested in a crossed design with abrasion (present *v*. absent *v*. procedural control; *n* = 4 per treatment). The “abrasion present” treatment was open settlement plates (see below), “abrasion absent” was plates covered with a wire mesh cage (5 cm × 5 cm mesh size), and “procedural control” an incomplete cage that allowed abrasion but controlled for potential artefacts associated with the presence of a cage. Data were analysed using a two-factor Analysis of Variance (ANOVA), with both factors being fixed and orthogonal.

Each “artificial kelp” was a strip of nylon mesh shade cloth (~ 1 mm mesh, 70 % shade) 10 cm wide and 50 cm long, to mimic the laterals of kelp. Because shade cloth is slightly buoyant, each “kelp” blade was weighed down at the tip by a small lead weight (0.3 cm diameter), allowing the blade to scrape across the substrate in a similar manner to natural kelp in the presence of water flow. In the absence of water flow, the blades stayed erect, slightly above plates, like natural kelp. In treatments where artificial kelp was present, each settlement plate was surrounded by 12 artificial "kelp", so that the plate was covered, as they would be with natural *E. radiata*.

In all experiments, settlement plates were attached to boulders as a consistent substrate for the colonisation of algae. Plates (11 cm × 11 cm) were made from Hardiflex fibreboard. Plates were attached with the rough surface facing upwards, as filamentous turf-forming algae readily colonise this surface (Irving and Connell 2002). Plates were slightly larger than the sampled area (10 cm × 10 cm; see "Sampling" below) to avoid the possibility of edge effects altering experimental outcomes.

Effect of water flow and abrasion

The effects of canopy abrasion (present *v*. absent *v*. procedural control) and water flow (present *v*. reduced *v*. procedural control) on percentage cover and biomass of turf-forming algae were tested in a crossed design (*n* = 4 per treatment). Artificial "kelp" was used to simulate abrasion by natural kelp (as for "Natural *v*. Artificial abrasion" above), as it was not possible to reduce water flow around natural kelp.

Frames to limit water flow were cubic wire frames (each side 30 cm) surrounded by clear plastic on four sides, but open at the top and bottom. Frames that were only enclosed with plastic on two sides were used to test for artefacts of the frame (flow procedural control). Cages to limit abrasion were the same design as those used in experiments comparing natural and artificial abrasion (above). Data were analysed using a two-factor ANOVA, with factors of flow and abrasion. Both factors were considered to be fixed and orthogonal.

Effect of shade

To estimate the effect of reduced light intensity on turf-forming algae, light was reduced in a concurrent experiment (full sunlight *v*. shade *v*. procedural control; $n = 6$ per treatment). Settlement plates were shaded by attaching black Mylar® plastic roofs (20 cm × 20 cm) to wire frames (20 cm × 20 cm × 20 cm) for the "shade" treatment, while clear Mylar® roofs were used to test for artefacts of the presence of frames and roofs. Unshaded plates were attached to boulders without frames or roofs. The effect of shading on percentage cover and biomass of turf-forming algae was tested using a single-factor ANOVA.

Colonisation and removal of turf-forming algae

Turf-forming algae at the field site colonise to cover bare substratum outside canopies within 2 weeks (Russell and Connell 2005), but have very low abundance under canopies (< 5 % cover, Irving and Connell 2006a). Although longer periods are required to test hypotheses about the longer-term maintenance of assemblages beneath canopies (e.g. 300 days: Connell 2003a; Irving and Connell 2006b), previous experiments have shown that 100 % of filamentous turfs can be removed by kelp canopies in < 40 days (Irving and Connell 2002), so I considered 60 days sufficient time to observe the effect of canopies on algal turfs.

Canopies formed by kelp suppress the colonisation of turf-forming algae, but can also remove algae that have already colonised (e.g. encroaching from surrounding gaps in the canopy). To test the effects of kelp canopy on both the colonisation and removal of turfs, all experiments (Natural *v*. Artificial, Water Flow *v*. Abrasion, and Shade) were done twice, once for colonisation of turfs on bare settlement plates and once for the removal of algae that had already established on settlement plates. For colonisation experiments, bare plates were placed under experimental treatments and turf-forming algae allowed to grow for 60 days before sampling. Because no algae were present on plates at commencement of these experiments, the final percentage cover and biomass of algae were compared among treatments.

To test for the removal of algae by canopies, plates were attached to boulders on the natural reef for 45 days to allow turfs to establish prior to being randomly re-assigned to experimental treatments. The change in percentage cover was calculated for each individual plate, and compared among treatments. Change in biomass was calculated by subtracting the mean initial biomass (see “Sampling” below) from the final biomass of algae on each plate.

Sampling

Initial percentage cover of turf-forming algae was quantified for all settlement plates by placing a 10 cm × 10 cm grid containing 25 regularly spaced points over the plate and recording the number of points that had algae directly beneath them (Drummond and Connell 2005). However, initial biomass of individual plates could not be sampled because biomass sampling is destructive. To estimate the amount of biomass removed by canopies, mean initial biomass was calculated by destructively sampling four plates, which were not assigned to experimental treatments, at the start of the experiment.

At the completion of each experiment, the percentage cover of algae on each settlement plate was quantified (as above). Each plate was then placed in an individual bag and returned to the laboratory. All algae in the central 10 cm × 10 cm area of each plate were scraped off and dried in an oven at 70^{o} C for 48 hours, to constant weight, before being weighed to the nearest 0.1 g.

Tests for differences in light and flow conditions

To test for differences in light conditions among experimental treatments, light intensities were recorded for all experiments (n = 3 measurements per treatment). Light measurements were taken using an underwater quantum sensor (LI-192SA, Li-Cor, Lincoln, NE, USA) and surface meter (LI-250), with individual readings being the average of light intensity over 15 seconds. Measurements were taken at midday on a day when no cloud was present, so that light conditions were kept as constant as possible, and the sensor placed slightly above the upper surface of settlement plates. Data are presented as μmoles m^{-2} s^{-1} of light. Differences in light intensities in the flow *v*. abrasion experiment were analysed using a two-factor ANOVA, with the orthogonal factors of flow (three levels: present, reduced, procedural control) and abrasion (three levels: present, absent and procedural control). Single-factor ANOVAs were used to compare light levels between artificial and natural kelp (three levels: artificial kelp flow absent, artificial kelp flow present and natural kelp) and for the shading experiment (three levels: shade, open and procedural control).

To test for relative differences in flow among treatments, and to enable a relative comparison of water flow under artificial and natural kelp, plaster clods were attached to plates for the full experimental design. Clods were cylinders of casting plaster 4.5 cm diameter × 5 cm high. Before being deployed in the water, all clods were dried at 70^{o} C for two days and weighed to the nearest 0.1 g. For all experiments, clods were collected 7 days after being placed under experimental conditions and dried at 70^{o} C for 2 days before being weighed to the nearest 0.1 g. Percentage loss of clods was compared among treatments. All clods were made from a single batch of plaster, so dissolution rate should be consistent among all clods. To test for differences in flow among treatments, a two-factor ANOVA was used for the full flow *v.* abrasion experimental design. A single-factor ANOVA was also used to test for differences among artificial kelp, natural kelp and open reef (four levels: artificial kelp reduced flow, artificial kelp flow present, natural kelp, open reef).

Results

Natural v. artificial abrasion

No difference was detected between natural and artificial abrasion on the colonisation of turf-forming algae for either percentage cover or biomass (Figure 1a & b, Table 1). Abrasion had a significant negative effect on colonisation, reducing percentage cover. However, Student Newman Keuls (SNK) comparison of means showed that percentage covers were the same when abrasion was present or absent (Figure 1a, Table 1). Abrasion had a significant negative effect on the biomass of turf-forming algae (Figure 1b, Table 1).

For the removal of already established algae, there were no differences between natural and artificial abrasion for percentage cover or biomass of algae (Figure 2a, Table 2). When abrasion was absent, biomass of turf-forming algae continued to increase after being placed in experimental conditions, but decreased when abrasion was present and for the procedural control (Figure 2b, Table 2).

Effect of water flow and abrasion

There was an interactive effect of flow and abrasion on colonisation of algae with a significant negative effect of abrasion only in the absence of flow (Figure 3a, Table 3a & b). There was also a significant effect of the partial cage (abrasion procedural control) when flow was absent. In contrast to percentage cover, biomass of turf-forming algae was only affected by abrasion, and was less when abrasion was present than absent (Figure 3b, Table 3a).

A greater percentage cover of algae was removed from plates when water flow was absent than when flow was present (Figure 4a, Table 4). Both water flow and abrasion affected the removal of algal biomass. Biomass of turf-forming algae was reduced more when flow was absent than present (Figure 4b, Table 4) and reduced more when abrasion was present than absent (Figure 4b, Table 4).

Effect of shade

The percentage cover of algae that colonised settlement plates was not affected by shade (Figure 5a, Table 5). In contrast, shade had a large negative effect on biomass (Figure 5a, Table 5). For the removal of algae, the change in both percentage cover and biomass was affected by shade. In full light, both the percentage cover and biomass of algae increased, while under shade percentage cover and biomass decreased (Figure 5b, Table 6).

Tests for differences in light and flow conditions

Light intensity was much less under artificial canopies when water flow was absent than present (Figure 6a; $F_{2,18} = 89.23$, $P < 0.0001$). In the presence of water flow, light intensity was greater under artificial than natural kelp canopies, but was least under artificial canopies when water flow was absent (Figure 6a; $F_{2,6} = 45.88$, $P < 0.001$). This difference is possibly because when water flow was absent, the artificial canopy remained motionless above (but not touching) plates, but when water flow was present the artificial canopy would move on and off the plates in different directions, leaving the plate totally uncovered for short periods (B. Russell, pers. obs.). In contrast, even in high flow conditions, part of the natural canopy always seemed to be covering the settlement plates, leaving very little time that plates were totally uncovered.

Light intensity was less under shade roofs than under procedural control roofs or the open, which did not differ from each other (Figure 6b; $F_{2,6} = 26.80$, $P = 0.001$) . Light intensity under shade roofs was similar to light intensity in the absence of water flow and under natural kelp canopies.

Less mass was lost from plaster clods when water flow was absent (43.6 ± 0.6 %) than present (54.3 ± 0.6 %) or in the procedural control (51.7 ± 0.6 %; two-factor ANOVA flow × abrasion: $F_{2,18} = 100.89$, $P < 0.0001$). When water flow was present, a greater percentage of mass was lost from clods under artificial canopies (flow present: 55.7 ± 0.2 %) than under natural canopies (52.4 ± 0.8 %), but loss from under artificial canopies did not differ from clods in the open (55.8 ± 0.4 %; single-factor ANOVA: $F_{2,6} = 14.96$, $P < 0.005$). This result indicates that artificial canopies were not slowing water flow to the same degree as natural canopies.

Discussion

A key finding was that water flow had a large effect on the early colonisation of turf-forming algae under canopies. The effect of physical abrasion by kelp canopies on the benthos seems to increase with increasing water flow (Kennelly 1989), so it was expected that when flow was reduced, the movement of canopy across the surface of settlement plates would be less, thus reducing abrasion. However, in my experiments, the canopy removed a greater percentage cover and biomass of turf-forming algae when water flow was reduced. Thus, abrasion alone cannot account for this effect, reinforcing that algal canopies alter multiple physical factors. It is likely that other factors, such as light intensity or nutrient availability, were altered by a reduction in flow, and consequently caused the differences in algal growth.

Movement of algal canopies increases with water flow. This increased movement may allow greater light penetration (Leigh *et al.* 1987), and light can structure understorey assemblages (e.g. Reed and Foster 1984; Kennelly 1989; Duggins *et al.* 1990; Clark *et al.* 2004; Toohey *et al.* 2004). The amount of light under artificial kelp was an order of magnitude less when water flow was absent than present, and was similar to under the shade roofs. This reduced light could account for the reduction in the biomass and percentage cover of algae. There was, however, greater loss of percentage cover of turf-forming algae when water flow was reduced (~ 80 % loss) than under the shade roofs (~ 20 % loss). This difference suggests that a reduction in light intensity may only account for part of the loss seen when water flow is reduced, especially given that the treatments reduced light intensity to below levels seen under natural kelp canopies.

There was a decrease in biomass and percentage cover of turf-forming algae when water flow was reduced. Although reduced light intensities in the reduced flow treatment may account for some of this loss (see previous paragraph), it is possible that when water flow was reduced, nutrient depleted water was not moved away from the algae. The effect of water flow on nutrient uptake by macroalgae is not a simple relationship. In general, uptake of nutrients is limited at slower water velocities (Wheeler 1980; Hurd *et al.* 1996; Williams and Carpenter 1998; Ryder *et al.* 2004), because a boundary layer of nutrient depleted water rapidly forms around algae (Hurd 2000). Furthermore, filamentous turf-forming algae have a physiology that is suited to quick uptake of nutrients (Hein *et al.* 1995; Pedersen and Borum 1996), and are more likely to be affected by any boundary layer of water that is poor in nutrients (Hurd 2000). Therefore, it is possible that the turf-forming algae rapidly used the available nutrients, creating a nutrient poor boundary layer and reducing growth.

When abrasion was removed there was greater biomass of turfs on settlement plates for both natural and artificial abrasion. Physical abrasion by algal canopies is known to reduce the biomass of erect forms of benthic algae (Kennelly 1989; Kendrick 1991; Irving and Connell 2006a; but see Toohey et al. 2004). Kendrick (1991) found that artificial abrasion reduced percentage cover and biomass of turfs, but that there was a greater negative effect on biomass. The present study showed a similar result. It is possible, therefore, that biomass of turf-forming algae is quickly lost to canopy abrasion, but when the algal filaments are smaller than some critical vertical height no more is lost. If this is so, biomass could be lost without a corresponding reduction in percentage cover.

I did not detect any difference between the effects of abrasion by natural and artificial kelp, yet for the colonisation of algae both mean percentage cover and biomass appeared to be greater for artificial kelp. Water flow was reduced by natural kelp canopy but not artificial kelp (percentage of plaster clods lost), and light intensity was almost 4 times greater under artificial than natural kelp. Furthermore, density of kelp influences understorey composition (Kendrick *et al.* 1999), and my artificial kelp may have been more consistent with more sparse densities of kelp than used in this study. Therefore, even though no difference was detected between the effects different canopies, it is probable that greater water flow and greater light meant that the effect of artificial kelp was only between 50 % (biomass) and 80 % (percentage cover) of natural kelp. However, the greater light intensity and water flow are likely to make my interpretation of treatment effects more conservative, increasing the likelihood of accepting the null hypothesis.

When water flow was absent, there was greater shading under artificial than natural canopies. This difference in shading may create problems for interpreting the effects of water flow, because any observed effect may be a result of the greater shading rather than a reduction of water flow *per se*. Again, this demonstrates the difficulty in separating the effects of individual physical factors altered by canopies. The greater light intensity under artificial canopies, in the presence of water flow, also creates problems for comparing artificial and natural canopies, because the greater light intensity makes it less likely to detect an effect of canopy. Again, this leads to a more conservative experimental test and a greater likelihood of accepting the null hypothesis.

In the artificial kelp experiments, I detected artefacts associated with the cages used to remove abrasion. In general, the procedural controls had less turf-forming algae than when abrasion was present. This difference was probably caused by the kelp becoming caught in the partial cage (B. Russell pers. obs.), restricting movement and reducing abrasion. Furthermore, the procedural control plates generally had less algae than when abrasion was absent, suggesting that any effect of the cage was less than that of removing abrasion. However, the significant artefacts associated with cages suggest caution in interpreting the magnitude of effects in cage treatments.

It is widely acknowledged that canopies (both terrestrial and marine) have large effects on the structure of understorey assemblages. However, knowledge of the processes by which canopies alter the understorey will allow generalisations and prediction of canopy-understorey associations (Levin 1992; Wright and Jones 2004; Connell in press). This understanding may be important in view of the increasing loss of canopies, in favour of turf-forming algae (Jackson 2001; Eriksson *et al.* 2002). The experimental results presented here have increased knowledge how canopies alter these processes by showing that the amount of water flow through a canopy alters the intensity of abrasion and shading by canopies. Furthermore, I suggest that the reduction in abundance of turfs in reduced water flow may be partly caused by nutrient limitation, an area that requires further study.

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Table 1. Results of two-factor ANOVAs testing for the effects of type of canopy (natural *v.* artificial) and abrasion (present *v.* absent *v.* procedural control) on the colonisation of (i) percentage cover and (ii) biomass of turf-forming algae. Ln (X) transformation was used on (ii) to remove heterogeneity from the data. *df* degrees of freedom, *MS* mean square, *F*-ratio, *P* probability. *P* values in bold are significant.

Source	*df*	*MS*	*F*	*P*	*MS*	*F*	*P*
		(i) % cover			(ii) Biomass		
Canopy	1	486.00	0.47	0.500	0.723	1.17	0.294
Abrasion	2	4420.67	4.31	**0.029**	3.938	6.36	**0.008**
C × A	2	234.00	0.23	0.798	0.647	1.04	0.372
Residual	18	1025.56			0.647		

Table 2. Results of two-factor ANOVAs testing for the effects of type of canopy (natural *v.* artificial) and abrasion (present *v.* absent *v.* procedural control) on the removal of turf-forming algae, (i) change in percentage cover and (ii) biomass. Ln (X+1) transformation was used on (ii) to remove heterogeneity, but the data remained heterogeneous, so significance was judged at the more conservative α = 0.01 (Underwood 1997). *df* degrees of freedom, *MS* mean square, *F*-ratio, *P* probability. *P* values in bold are significant.

Source	*df*	*MS*	*F*	*P*	*MS*	*F*	*P*
		(i) % cover			(ii) Biomass		
Canopy	1	640.67	0.98	0.336	0.006	0.11	0.741
Abrasion	2	1608.67	2.46	0.114	0.404	7.49	**0.004**
C × A	2	964.67	1.47	0.255	0.011	0.21	0.815
Residual	18	654.44			0.054		

Table 3. (a) Results of two-factor ANOVAs testing for the effects of water flow (present *v.* absent *v.* procedural control) and abrasion by artificial canopy (present *v.* absent *v.* procedural control) on the colonisation of (i) percentage cover and (ii) biomass of turf-forming algae, (b) SNK comparison of means for the significant flow × abrasion interaction for percentage cover. *df* degrees of freedom, *MS* mean square, *F*-ratio, *P* probability. *P* values in bold are significant.

(a) Source	*df*	*MS*	*F*	*P*	*MS*	*F*	*P*
		(i) % cover			(ii) Biomass		
Flow	2	2907.11	3.18	0.057	0.035	1.35	0.276
Abrasion	2	2760.44	3.02	0.065	0.125	4.82	**0.016**
F × A	4	3591.11	3.93	**0.012**	0.047	1.81	0.156
Residual	27	913.19			0.026		

(b) Pairwise comparisons for percentage cover	
Flow	
Present	Abrasion present = Abrasion absent = Procedural control
Absent	Abrasion present << Abrasion absent = Procedural control
Abrasion	
Present	Flow absent < Flow present = Procedural control
Absent	Flow absent = Flow present = Procedural control

Table 4. Results of two-factor ANOVAs testing for the effects of water flow (present *v.* absent *v.* procedural control) and abrasion by artificial canopy (present *v.* absent *v.* procedural control) on the removal of turf-forming algae, (i) change in percentage cover and (ii) biomass. *df* degrees of freedom, *MS* mean square, *F*-ratio, *P* probability. *P* values in bold are significant.

Source	*df*	*MS*	*F*	*P*	*MS*	*F*	*P*
		(i) % cover			(ii) Biomass		
Flow	2	7744.00	8.83	**0.001**	3.993	5.42	**0.011**
Abrasion	2	185.33	0.21	0.811	2.495	3.39	**0.049**
F × A	4	565.33	0.64	0.635	0.152	0.21	0.932
Residual	27	877.33			0.734		

Table 5. Results of single-factor ANOVAs testing for the effects of reduction in light intensity (shade *v.* open *v.* procedural control) on the colonisation of (i) percentage cover and (ii) biomass of turf-forming algae. *df* degrees of freedom, *MS* mean square, *F*-ratio, *P* probability. *P* values in bold are significant.

Source	*df*	*MS*	*F*	*P*	*MS*	*F*	*P*
		(i) % cover			(ii) Biomass		
Shade	2	32.89	1.27	0.310	0.117	8.20	**0.004**
Residual	15	25.96			0.014		

Table 6. Results of single-factor ANOVAs testing for the effects of reduction in light intensity (shade *v.* open *v.* procedural control) on the removal of turf-forming algae, (i) change in percentage cover and (ii) biomass. Ln (X+1) transformation was used on (i) and (ii) to remove heterogeneity, but the data remained heterogeneous, so significance was judged at the more conservative α = 0.01 (Underwood 1997). *df* degrees of freedom, *MS* mean square, *F*-ratio, *P* probability. *P* values in bold are significant.

Source	*df*	*MS*	*F*	*P*	*MS*	*F*	*P*
		(i) % cover			(ii) Biomass		
Shade	2	896.89	8.02	**0.004**	0.309	7.18	**0.007**
Residual	15	111.82			0.043		

Fig. 1. The effect of natural abrasion (absent *v*. present *v*. procedural control) and artificial abrasion (absent *v*. present *v*. procedural control) on the colonisation of turf-forming algae on bare settlement plates for (a) percentage cover and (b) biomass of turf-forming algae.

Fig. 2. The effect of natural abrasion (absent *v*. present *v*. procedural control) and artificial abrasion (absent *v*. present *v*. procedural control) on the change in (a) percentage cover and (b) biomass of turf-forming algae. Treatments correspond to legend in Fig. 1.

Fig. 3. The effect of water flow (absent *v*. present *v*. procedural control) and canopy abrasion (absent *v*. present *v*. procedural control) on the colonisation of turf-forming algae on bare settlement plates. (a) percentage cover and (b) biomass of turf-forming algae. “0” indicates 0 % cover or 0 g biomass.

Fig. 4. The effect of water flow (absent *v*. present *v*. procedural control) and canopy abrasion (absent *v*. present *v*. procedural control) on the change in (a) percentage cover and (b) biomass of turf-forming algae. Treatments correspond to legend in Fig. 3.

Fig. 5. The effect of light (shade *v*. open *v*. procedural control) on (a) the colonisation of turf-forming algae, shown as percentage cover and biomass and (b) the change in percentage cover and biomass of turf-forming algae.

Fig. 6. Light intensity measured among (a) flow treatments (natural kelp *v*. absent *v*. present *v*. procedural control) and (b) shade treatments (shade *v*. open *v*. procedural control).

595 **Fig. 1.**

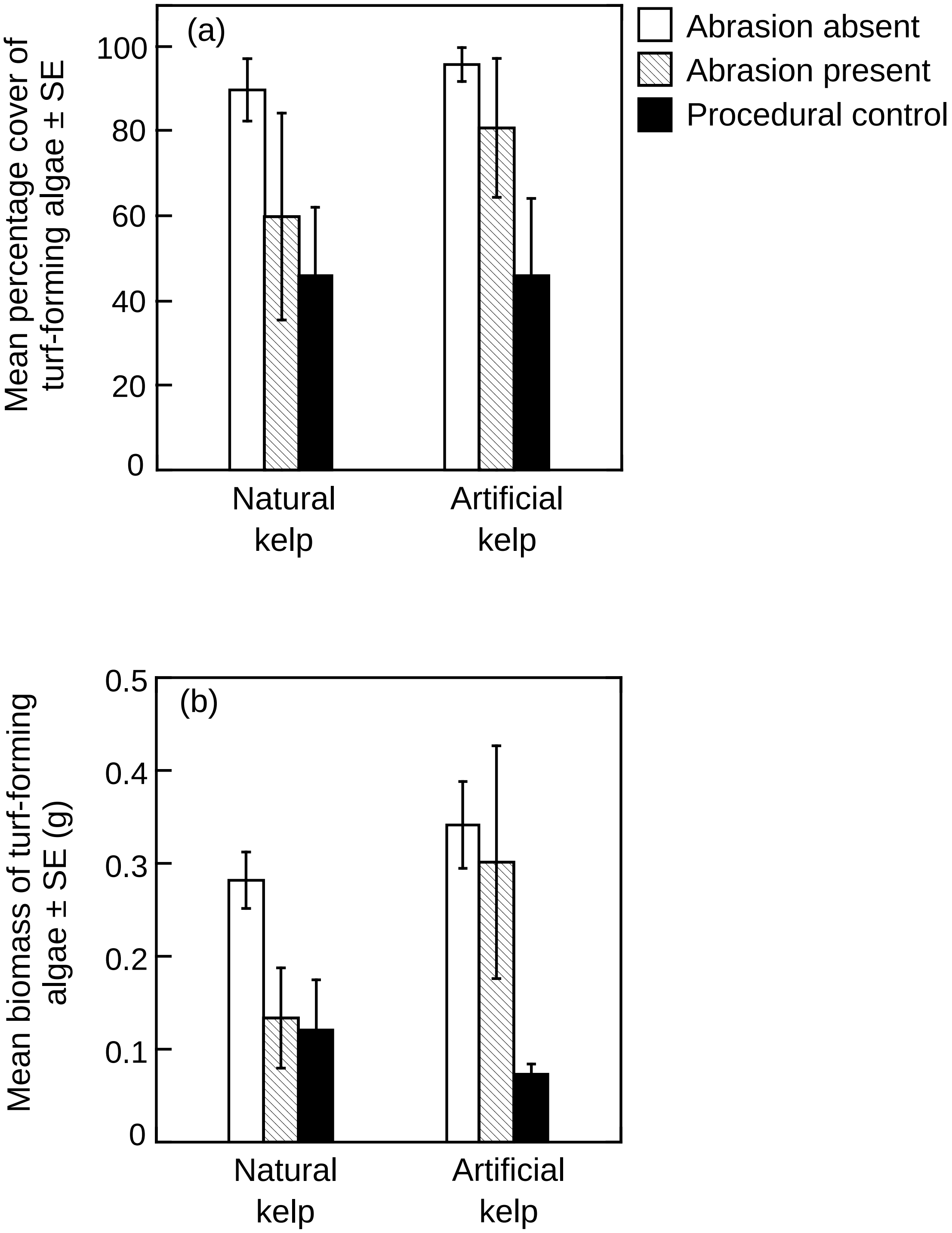

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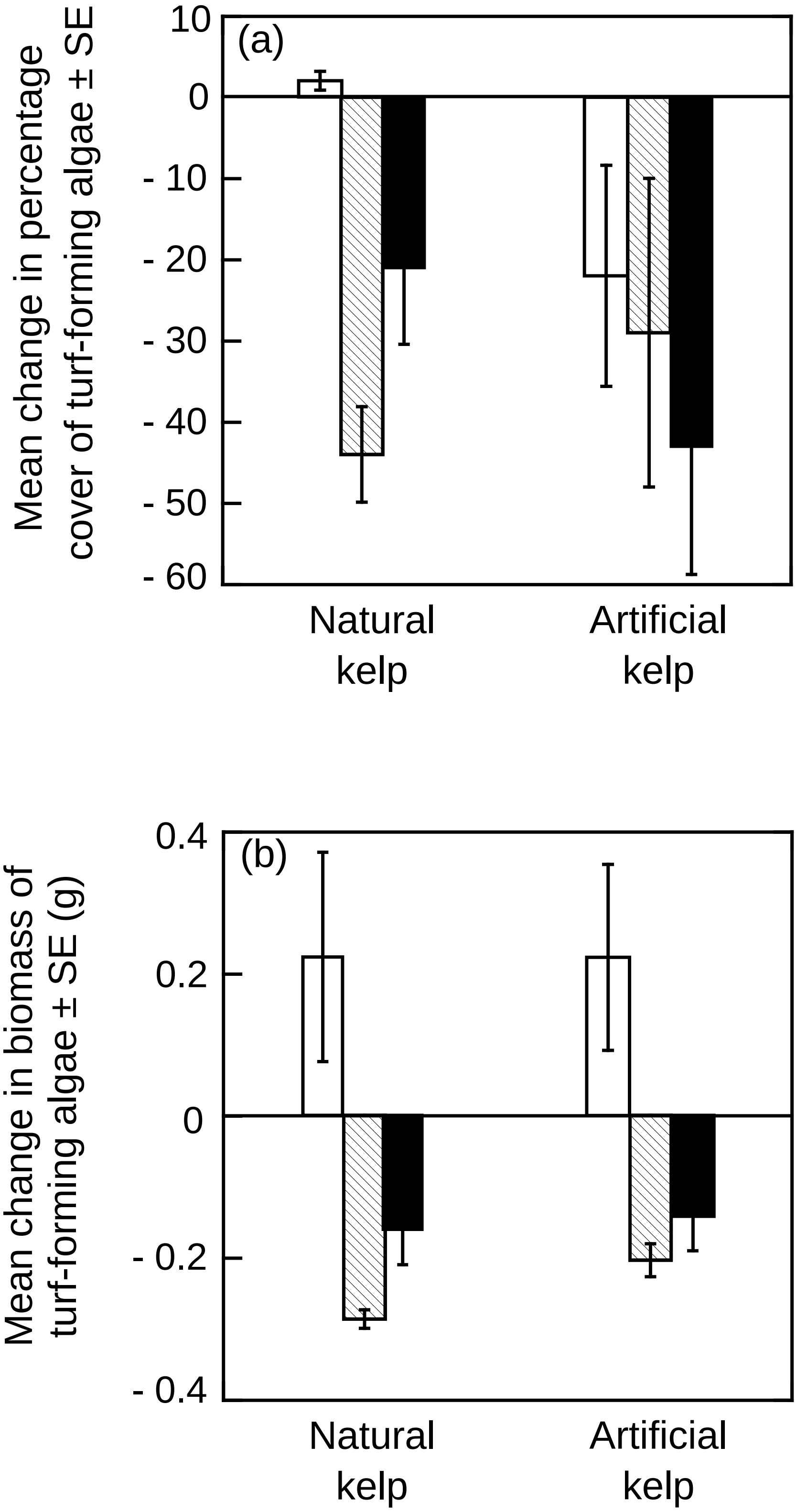
Fig. 2.



(a)
Mean change in percentage cover of turf-forming algae ± SE
10
0
- 10
- 20
- 30
- 40
- 50
- 60
Natural kelp
Artificial kelp
(b)
Mean change in biomass of turf-forming algae ± SE (g)
0.4
0.2
0
- 0.2
- 0.4
Natural kelp
Artificial kelp

Fig. 3.

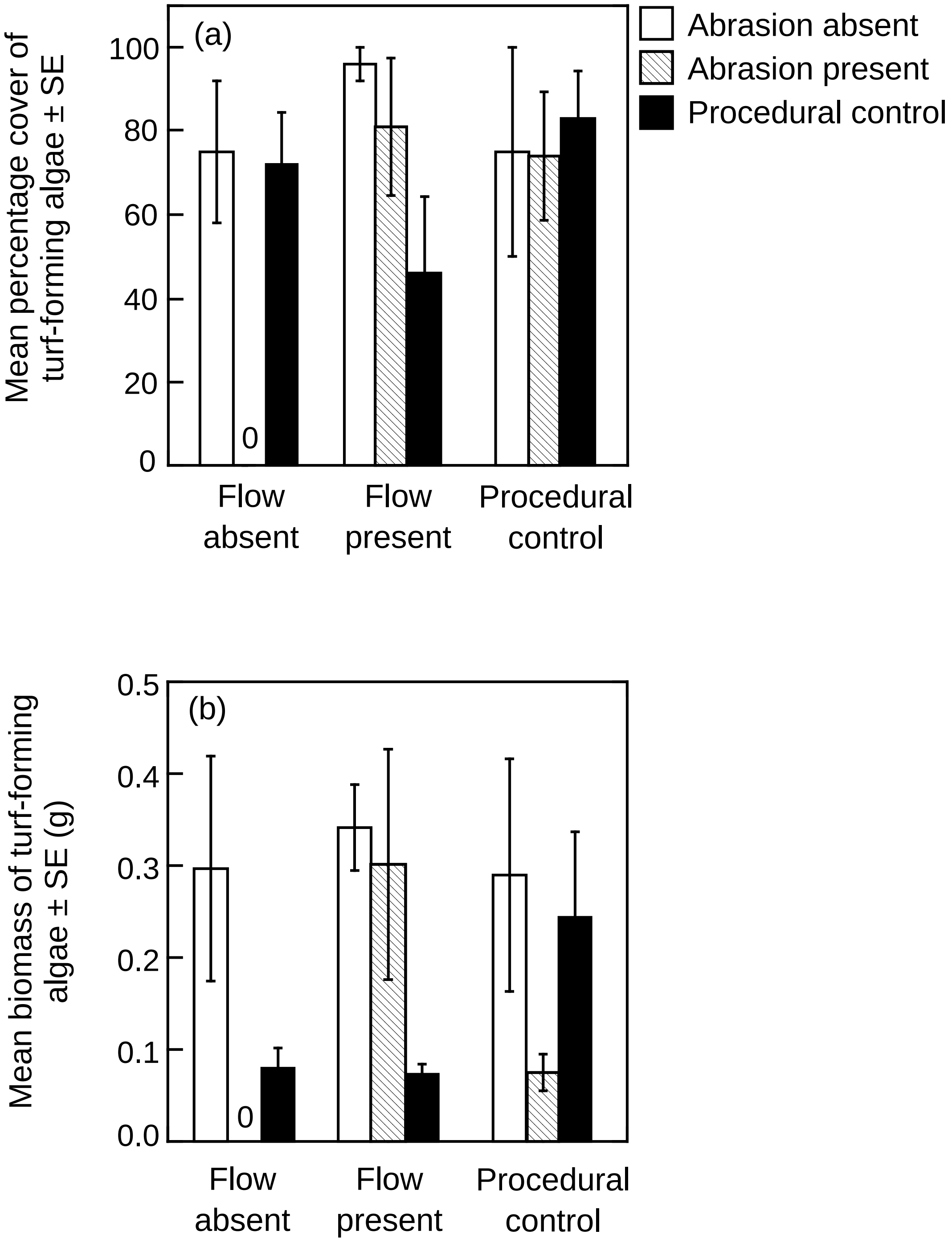

(a)
Mean percentage cover of turf-forming algae ± SE
0
20
40
60
80
100
0
Flow absent
Flow present
Procedural control
Abrasion absent
Abrasion present
Procedural control
(b)
Mean biomass of turf-forming algae ± SE (g)
0.0
0.1
0.2
0.3
0.4
0.5
0
Flow absent
Flow present
Procedural control

Fig. 4.

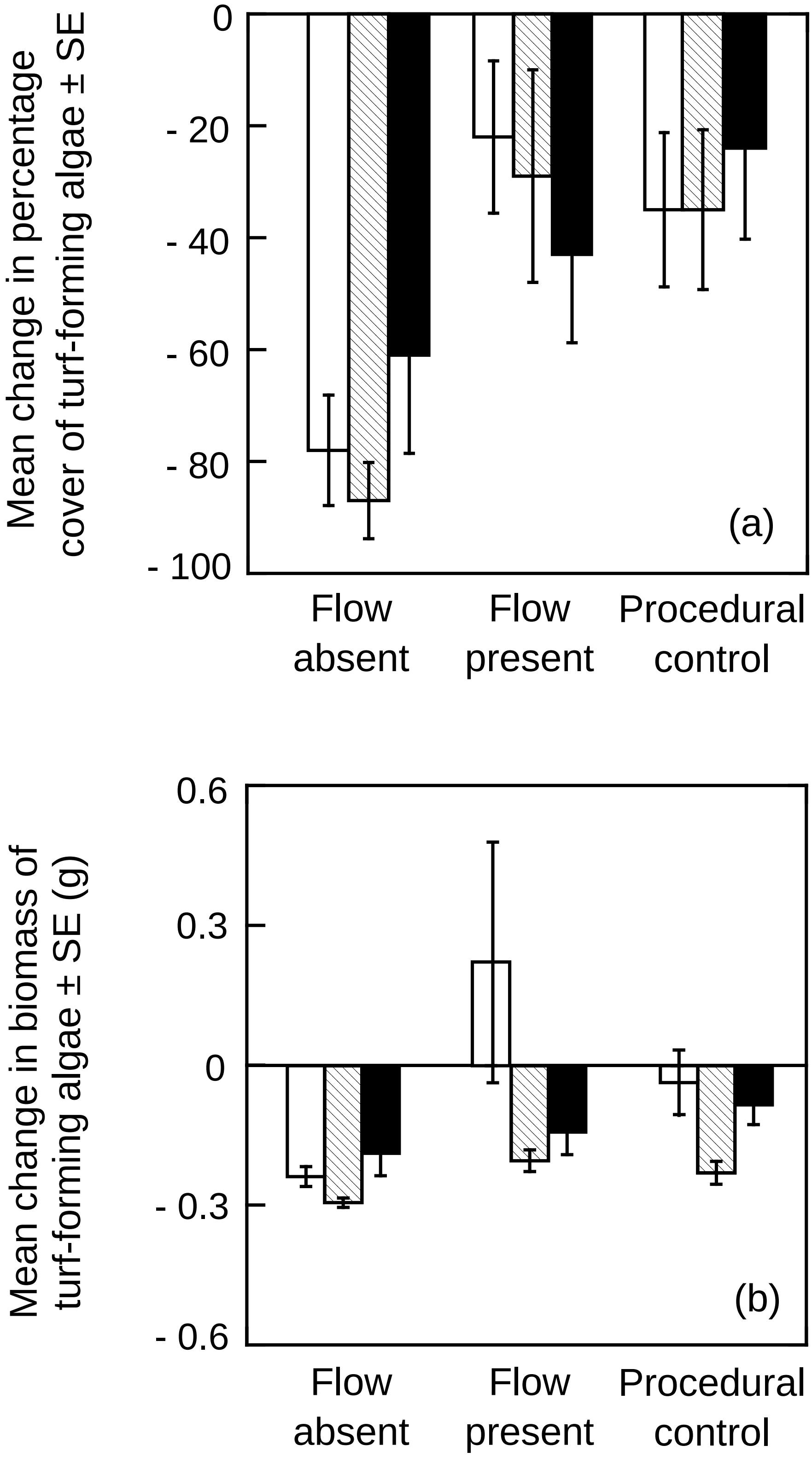

Mean change in percentage cover of turf-forming algae ± SE
0
- 20
- 40
- 60
- 80
- 100
(a)
Flow absent
Flow present
Procedural control
Mean change in biomass of turf-forming algae ± SE (g)
0.6
0.3
0
- 0.3
- 0.6
(b)
Flow absent
Flow present
Procedural control

Fig. 5.

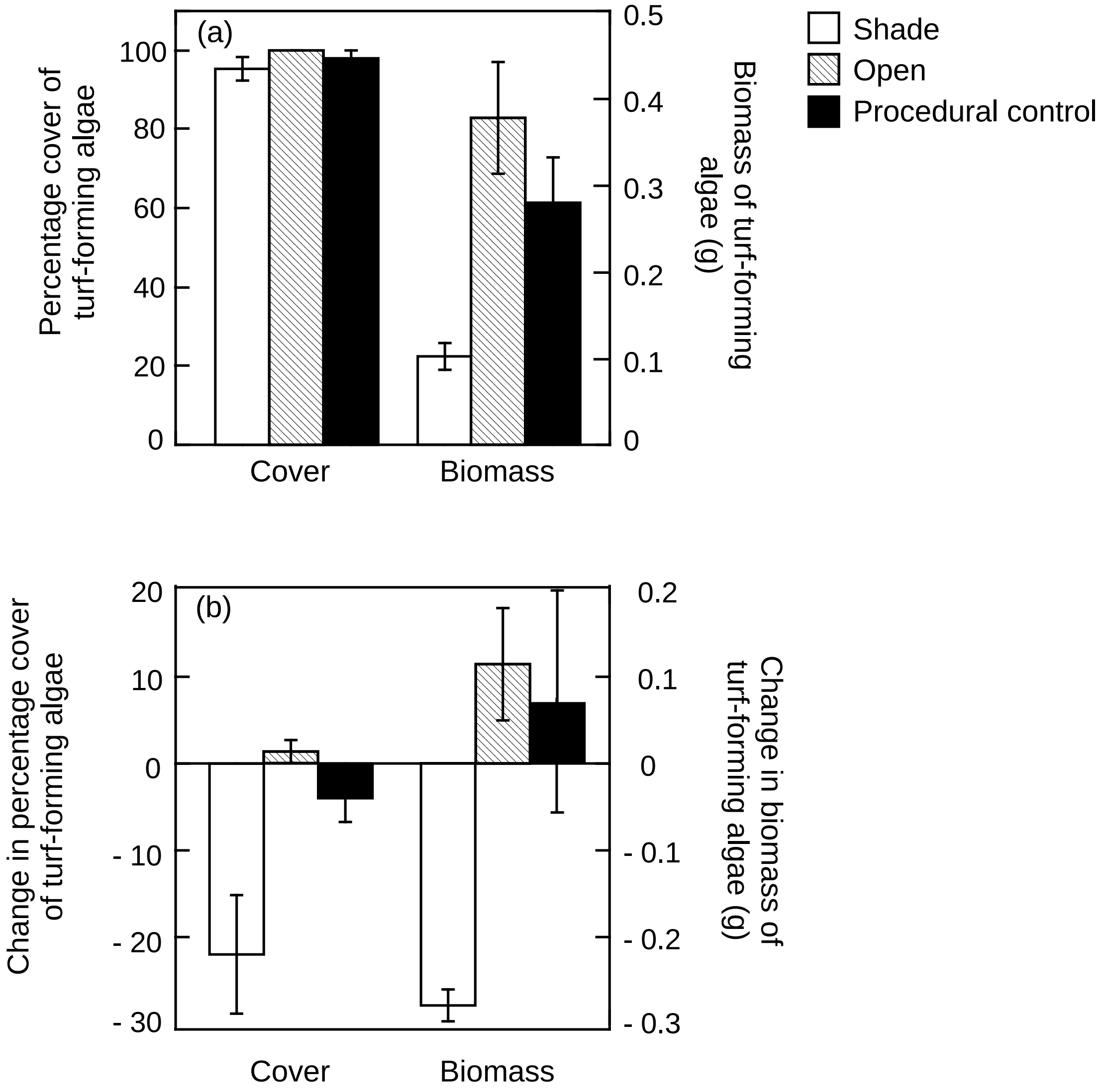
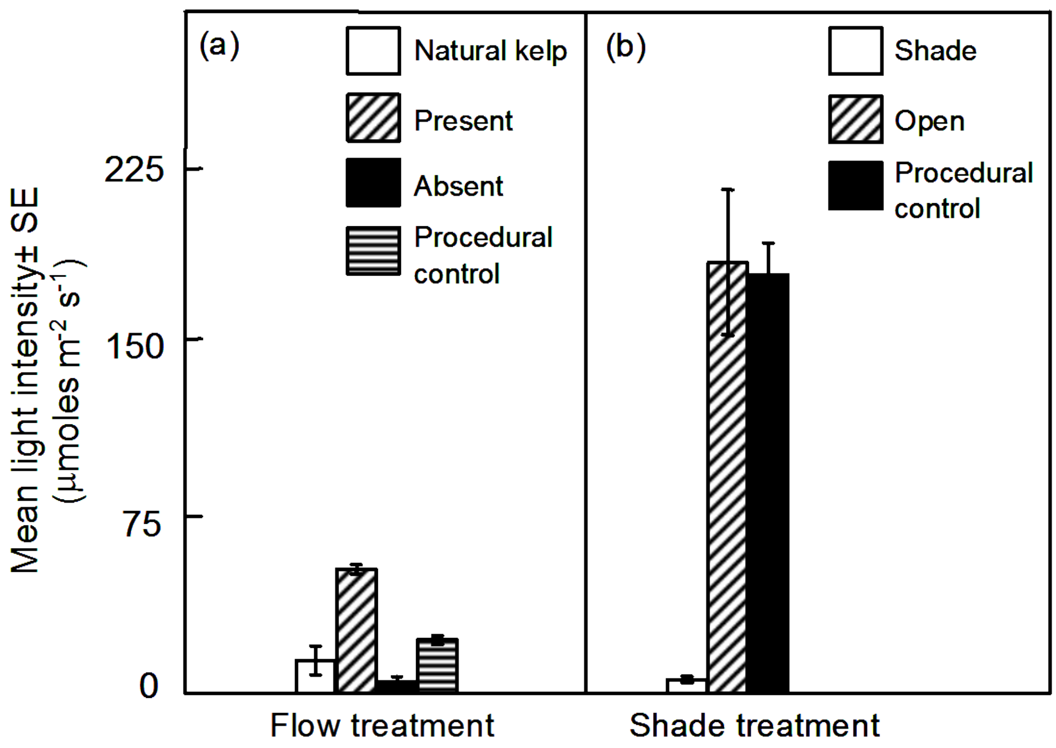

(a)
Percentage cover of turf-forming algae
0
20
40
60
80
100
Biomass of turf-forming algae (g)
0
0.1
0.2
0.3
0.4
0.5
Cover
Biomass
□ Shade
▨ Open
■ Procedural control
(b)
Change in percentage cover of turf-forming algae
20
10
0
- 10
- 20
- 30
Change in biomass of turf-forming algae (g)
0.2
0.1
0
- 0.1
- 0.2
- 0.3
Cover
Biomass

Fig. 6.


(a)
Natural kelp
Present
Absent
Procedural control
(b)
Shade
Open
Procedural control
Mean light intensity± SE (μmoles m^{-2} s^{-1})
225
150
75
0
Flow treatment
Shade treatment