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# SYNERGISTIC EFFECTS OF CLIMATE CHANGE AND LOCAL STRESSORS: $CO_2$ AND NUTRIENT DRIVEN CHANGE IN SUBTIDAL ROCKY HABITATS

BAYDEN D. RUSSELL, JO-ANNE THOMPSON, LAURA J. FALKENBERG
and SEAN D. CONNELL*

*Southern Seas Ecology Laboratories,*
*School of Earth and Environmental Sciences,*
*University of Adelaide, South Australia, 5005, Australia*
Email: sean.connell@adelaide.edu.au
Phone: +61 8 8303 6125, Fax: +61 8 8303 6224
[*] Corresponding author

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## Abstract

Climate-driven change represents the cumulative effect of global through local scale conditions, and understanding their manifestation at local scales can empower local management. Change in the dominance of habitats is often the product of local nutrient pollution that occurs at relatively local scales (i.e. catchment-scale), a critical scale of management at which global impacts will manifest. We tested whether forecasted global-scale change (elevated $CO_2$ and subsequent ocean acidification) and local stressors (elevated nutrients) can combine to accelerate the expansion of filamentous turfs (kelp-inhibitors) at the expense of calcifying algae (kelp understorey). Our results not only support this model of future change, but also highlight the synergistic effects of future $CO_2$ and nutrient concentrations on the abundance of turfs. These results suggest that global and local stressors need to be assessed in meaningful combinations so that the anticipated effects of climate change do not create the false impression that, however complex, climate change will produce smaller effects than reality. These findings empower local managers because they show that policies of reducing local stressors (e.g. nutrient pollution) can reduce the effects of global stressors (e.g. ocean acidification) not under their governance. The connection between research and government policy provides an example whereby knowledge (and decision-making) across local through global scales provides solutions to some of the most vexing challenges for attaining social goals of sustainability, biological conservation and economic development.

## Introduction

Global climate as a driver of ecological patterns across local through biogeographic scales has long been of legitimate concern to ecology (Pianka, 1966). As climatologists forecast unprecedented increase to drivers of global climate change (e.g. $CO_2$ emissions: Raupach *et al.*, 2007), there becomes a pressing need to meaningfully incorporate cross-scale stressors into our theories on drivers of future ecological patterns. Whilst ecologists recognise that humans have come to dominate natural systems through a series of local modifications of species pools (i.e. composition of species via extraction and introductions; Hughes *et al.*, 2005), and the physical and chemical environment (e.g. biogeochemical cycles; Vitousek *et al.*, 1997), we have only recently incorporated global-scale changes to the physical and chemical environment as subjects of additional change (Root & Schneider, 2002). Whilst we understand that the pace and direction of human-driven change is unlikely to be independent of biogeography (Connell & Irving, 2008), we are often astonished by the capacity for small scale heterogeneity to modify the effects of climate (Helmuth *et al.*, 2002), suggesting that there remains a considerable need to identify how global stressors are modified by local conditions.

In the marine environment, it is possible that global change (e.g. increasing ocean acidification) will combine with local impacts (e.g. nutrient release) to accelerate ecological change across broader areas of coast. On temperate coasts, the most densely populated coasts of the globe, perennial canopies of algae (e.g. kelp forests) and their associated understorey have been replaced by mats of turf-forming algae near expanding human populations that discharge nutrients (Eriksson *et al.*, 2002; Airoldi & Beck, 2007; Connell *et al.*, 2008). We are concerned that when combined with increasing $CO_2$ concentrations, these normally ephemeral turfs may expand via: (1) the positive effects of $CO_2$ and nutrients on turfs; and (2) the negative effect of $CO_2$ on understorey habitat; i.e. acidification causing a reduction in calcification of coralline crusts (Harley *et al.*, 2006).

This model predicts that turfs would monopolise available space, break the facilitation between kelps and their understorey, and cause greater loss of canopies on human dominated coasts. Calcifying algae (crusts or encrusting coralline algae) are the most abundant and widespread organisms on subtidal rocky coasts of the polar-temperate-tropical world (Steneck, 1986). In temperate systems, recruitment of kelp is inhibited by turfs that overgrow encrusting corallines (Kennelly, 1987a). In turn, canopies of kelp inhibit turfs (Connell, 2003; Irving & Connell, 2006; Russell, 2007), facilitate crusts (Connell, 2003) and thereby maintain recruitment. Acidification, however, is likely to reduce calcification in coralline algae (Gao *et al.*, 1993; Leclercq *et al.*, 2000), while possibly enhancing abundance of turfs (Andersen & Andersen, 2006).

Knowledge of the potential effects of climate change in marine systems is, to date, primarily based on experiments that only assess global-scale stressors (e.g. ocean acidification in isolation). These stressors will not, however, act in isolation and experiments are needed to assess their potential synergistic effects (Harley *et al.*, 2006; Schlesinger, 2006). Therefore, the aim of this paper was to examine whether the combination of global ($CO_2$) and local (nutrients) perturbations has the potential to accelerate the currently observed change of temperate reefs from calcifying crusts (and kelp overstorey) to mats of turf (which inhibit kelp). We elevated $CO_2$ and nutrients separately and in combination to test the hypothesis that both nutrients and $CO_2$ cause the biomass and cover of turfs to increase, and the biomass of crusts to decrease, and that these changes would be greatest when future $CO_2$ and elevated nutrients are present in combination. If the results support this hypothesis, they would imply that global and local stressors need to be assessed in meaningful combinations so that the anticipated affects of climate change do not create the false impression that climate change, however complex, will produce smaller effects than is realistic.

## Materials and methods

### *Experimental design*

The effects of $CO_2$ and nutrients were tested on two groups of algae, coralline crusts (*Lithophyllum* sp.) and turf-forming algae (*Feldmannia* spp.), in a mesocosm experiment. Algae were exposed to combinations of $CO_2$ (current *v.* future) and nutrients (ambient *v.* elevated) in a crossed design. Two replicate mesocosms were used per combination of treatments, with replicate specimens of algae ($n = 5$ per algal type) in each mesocosm. Levels for $CO_2$ were based on the current ambient (current; 380 ppm) and IS92a model predictions for the year 2030 (future; 550 ppm). The current and predicted pH values for the Southern Ocean that correspond to these $CO_2$ concentrations are 8.1 (measured in this study) and 7.95 (model predictions by Meehl *et al.*, 2007), respectively. It is worth noting that the future concentration of $CO_2$ chosen for this experiment is likely to be conservative, as current $CO_2$ emissions are exceeding the worst-case predictions (model scenario A1F; Raupach *et al.*, 2007). The “elevated” concentration for nutrients was chosen to be similar to concentrations in waters off the coast of metropolitan Adelaide (Gorman *et al.*, in review), again, a conservative estimate of anthropogenic nutrient inputs.

The response of algae to experimental conditions was assessed using three response variables, dry mass, photosynthetic quantum yield and cover of algae recruiting to initially blank substrate. Dry mass of algae was measured at the completion of the experiment from a standard area (0.25 $cm^2$ for crusts; 6.25 $cm^2$ for turfs) by scraping algae off the substratum and weighing after having been dried to constant weight (i.e. 60°C for 48 hours). The percentage cover of algae growing on initially blank substrate (5 × 5 cm ceramic tiles) was used to assess the ability of algae to expand into unoccupied space and was quantified at the end of the experiment by visually estimating the percentage cover of algae ($n$ = 7 per mesocosm). Quantum yield of algae was calculated as the ratio of variable to maximum fluorescence ($F_v/F_m$) of dark adapted algae and was measured using a Pulse Amplitude Modulated (PAM) fluorometer (Walz, Germany). First, fluorescence of algae was measured by holding the fiberoptics of the PAM fluorometer in contact with the dark adapted alga (*in situ* in mesocosms) and exposing it to a pulsed measuring beam of red light (0.15 $\mu$mol $m^{-2}$ $s^{-1}$, 650 nm). This measurement was immediately followed by a pulse of saturating actinic light (0.8 s, 6000 $\mu$mol $m^{-2}s^{-1}$) to measure maximal fluorescence yield ($F_m$). Each yield value used in the analysis was a mean of three replicate measurements taken on different parts of the alga so that the yield was not underestimated due to recovery of the photosystems from repeated measurements.

Individual specimens of each type of algae were collected from a site known to have low ambient nutrient concentrations (West Island, South Australia, 35º 36’S 138 º 35’E; Russell & Connell, 2005) and were placed in holding mesocosms for two weeks to acclimate to laboratory conditions before the experiment was commenced. During acclimation, physical conditions in the mesocosms were similar to those at the collection site (i.e. 17ºC, low ambient nutrient concentrations). Following the acclimation period, algae were randomly re-assigned to mesocosms in which experimental conditions were gradually increased over a further 2 week period until they reached their pre-designated levels (see experimental design above). Response variables (above) were measured in algae 76 days after commencement of the experimental treatments.

Experiments were done in 40 L mesocosms, each recirculating in a closed loop with a 200 L reservoir tank. To ensure quality of the growing conditions in mesocosms, half of the water was removed from the reservoir tanks and replaced with fresh seawater once every two weeks. Lighting was supplied in a 12:12 light:dark cycle by pairs of fluorescent lights directly above the mesocosms, each pair containing one “grow light” which incorporated the UV spectrum (Sylvania® Gro-lux) and one “daylight” (Luxling® Daylight deluxe). The irradiance regime within mesocosms (33.96 ± 1.61 μmol $m^{-2}s^{-1}$) was similar to within algal canopies at the field site from which experimental algae were collected (Russell, 2007). Temperature within the mesocosms was kept at a constant 17ºC by controlling ambient air temperature.

### *$CO_2$ and nutrient addition*

All mesocosms were constantly aerated at 10 L $min^{-1}$, with the $CO_2$ concentration of the air altered depending on treatment. As the pH in seawater reduces with increasing concentration of $CO_2$ in a predictable manner, experimental conditions (see experimental design above) were maintained using pH probes and automatic solenoid controllers (Sera, Heinsberg, Germany) so that $CO_2$ was added to the mesocosms when required to maintain the experimental level. Probes were temperature compensated and calibrated using NBS calibration buffers to 0.01 pH units. Calibration of probes was checked on a daily basis, and recalibrated if necessary. As the regulation system constantly measured and maintained pH at the pre-set level, there was no daily fluctuation due to photosynthesis or respiration within mesocosms.

Nutrients were supplied as 3 g of Osmocote Plus® (Scotts, Australia) controlled release fertilizer per mesocosm. Osmocote is a pelletised fertilizer with an external coating that releases nutrients at a set rate over the life of the pellet (6 month release: 15, 5, 10 N-P-K). Specific tests have found that the nutrient concentration released into the water is directly proportional to the weight of fertilizer (Worm *et al.*, 2000) and has been successfully used to manipulate nutrient concentrations in this system (e.g. Gorgula & Connell, 2004; Russell & Connell, 2005). Pellets were placed in a nylon mesh bag (1 mm mesh size) and attached to the bottom of the mesocosm. Water samples were collected to confirm the concentration of nutrients being supplied and results presented here (see “Results” below) to allow the reader to place our experiment in their own regional context. Samples were collected using 25 ml sterile syringes, filtered (0.45 μm glass fibre) and immediately frozen. Samples were later analysed on a Lachat Quickchem 8200 Flow Injection Analyser for nitrate + nitrite ($NO_x$), ammonium and phosphate.

*Analyses*

The response of algae to experimental treatments was tested using three factor ANOVAs. Both factors ($CO_2$ *v*. Nutrient) were treated as fixed and orthogonal, with two levels in each factor ($CO_2$: current *v*. future; Nutrient: ambient *v*. elevated). Two replicate mesocosms were nested within both $CO_2$ and Nutrients. Where significant treatment effects were detected, Student-Newman-Keuls (SNK) post-hoc comparison of means were used to determine which factors differed.

## Results

### *Response of algae to experimental conditions*

Both elevated $CO_2$ and nutrient concentrations had negative effects on the biomass of coralline crusts (Fig. 1a). Dry mass of crusts was greatest under current conditions (i.e. current $CO_2$ and ambient nutrients) but was less under both elevated nutrients and future levels of $CO_2$ (Fig. 1a, Table 1a). Importantly, the mass of crusts was least when elevated nutrients and future $CO_2$ concentrations were present in combination (Fig. 1a). Future $CO_2$ concentrations also had a positive effect on the mass of turfs, while elevated nutrients had no effect (Fig. 1b, Table 1b).

At the beginning of the experiment, turfs covered 100 % of their substrate (rock) and were already at their maximum height, meaning that it was not possible to detect an increase in the cover of turfs during the experiment. However, turfs readily recruit to available space within 1-2 weeks (Russell & Connell, 2005). At ambient nutrient concentrations, the percentage cover of turfs on initially blank substrate did not differ between current and future $CO_2$ (Fig. 2, Table 2, SNK of significant $CO_2$ × Nutrient interaction). When nutrients were elevated, however, the percentage cover of turfs was greater in the presence of future than current $CO_2$ concentrations, and was greatest when future $CO_2$ and elevated nutrients were present in combination (Fig. 2, Table 2), the treatment which had the greatest negative impact on the mass of crusts. Importantly, under future $CO_2$ and elevated nutrient concentrations, turfs occupied 34 % more substratum than would be predicted by the independent effects of $CO_2$ and nutrients.

Future $CO_2$ concentrations had a negative effect on the photosynthetic yield of crusts (Fig. 3a, Table 3a) while elevated nutrients had no detectable effect. In contrast, both future $CO_2$ and elevated nutrients increased the yield of turfs, with the greatest increase when future $CO_2$ and elevated nutrients were present in combination (Fig. 3b, Table 3b). As with percentage cover of turfs, this represented a synergistic response where yield was 41 % greater than would be predicted by the independent effects of the experimental treatments.

### *Nutrient concentrations*

The concentration of $NO_x$ (nitrate + nitrite) was greater in the elevated (mean ± SE; 0.068 ± 0.017 mg $L^{-1}$) than ambient (0.004 ± 0.002 mg $L^{-1}$) nutrient treatments (ANOVA: $F_{1,2}$ = 53.28, $p$ = 0.018). The concentration of ammonia was greater in the elevated (0.018 ± 0.006 mg $L^{-1}$) than ambient (0.007 ± 0.002 mg $L^{-1}$) nutrient treatments (ANOVA: $F_{1,2}$ = 145.93, $p$ = 0.007), while phosphate did not differ between treatments (ambient, 0.022 ± 0.001 mg $L^{-1}$; elevated, 0.035 ± 0.003 mg $L^{-1}$; $F_{1,2}$ = 16.40, $p$ = 0.056).

## Discussion

Global stressors will manifest at local scales and consequently combine with local conditions to produce unexpected change to natural systems. We show that moderate forecasts of $CO_2$ concentration and current levels of nutrient elevation combine to accelerate an increase in turfs and decline in coralline crusts. We highlight the synergistic effect of combing these stressors, having a greater effect than predicted for either stressor in isolation (e.g. climate change predictions). Notwithstanding the increasing number and prevalence of local stressors, there is accumulating evidence that global and local stressors can combine to cause change that is greater than their sum (e.g. UV radiation, temperature & salinity; Przeslawski *et al.*, 2005). Yet, in the absence of knowledge of the synergistic effects of climate change and local conditions, we stand to experience an increasing number of “ecological surprises” (Paine *et al.*, 1998). Our results suggest that forecasts of climate change made in isolation of local stressors can underestimate their future effects, reinforcing increasing concern that multiple stressors combine to cause ecological regime shifts (Paine *et al.*, 1998; Bellwood *et al.*, 2004). While stressors are often studied in isolation, such studies cannot identify their synergistic effects from their isolated components and will underestimate the future effects of climate change.

In systems where space is fully occupied, such as rocky marine systems (Dayton, 1971), the creation of new space is a prerequisite for community change (Pickett & White, 1985; Airoldi, 1998). In kelp dominated systems, individuals are regularly lost through natural disturbance and the new space is necessary for regeneration of the canopy (Kennelly, 1987b). Any environmental condition which allows turfs to expand and dominate available space (e.g. human-derived nutrients; Gorgula & Connell, 2004) and inhibit the recruitment of kelp (Kennelly, 1987a) may lead to phase shifts from kelp to turf-dominated systems (e.g. Connell *et al.*, 2008). Here, nutrients and $CO_2$ combined to facilitate recruitment of turfs to occupy > 70 % more space than under current ambient conditions, a synergistic response which was 34 % greater than the sum of their individual effects. Therefore, the currently observed replacement of perennial canopies of algae and their associated understorey (e.g. crusts) by mats of turf-forming algae near expanding human populations (Eriksson *et al.*, 2002; Airoldi & Beck, 2007; Connell *et al.*, 2008) is likely to be exacerbated under future climates.

The decrease in pH associated with the uptake of anthropogenic $CO_2$ into the ocean reduces the ability of marine calcifying organisms to form their calcium carbonate structure (Feely *et al.*, 2004; Orr *et al.*, 2005). Reduced calcification has been noted in some calcifying algae (e.g. 1250 ppm, Gao *et al.*, 1993; 700 ppm, Leclercq *et al.*, 2000), and the reduced mass of crusts in our experiment shows this response holds for conservative projections of future $CO_2$

concentrations (i.e. 550 ppm). While some organisms may adapt to future $CO_2$ concentrations (e.g. by increasing photosynthesis), there is accumulating evidence that organisms cannot acclimate their rates of calcification to increased $CO_2$ concentrations (Langdon *et al.*, 2000). Therefore, any reduction in the abundance of crusts under future conditions is likely to continue while elevated $CO_2$ concentrations are maintained.

Elevated $CO_2$ concentrations in lakes can cause an increase in the abundance of filamentous algae (Andersen & Andersen, 2006), as we demonstrate for marine filamentous turfs. The progressive nitrogen limitation theory (PNL) predicts that elevated $CO_2$ concentrations cause nitrogen limitation in plants by enhancing photosynthesis (Schlesinger & Lichter, 2001; Gill *et al.*, 2002). Experiments in terrestrial systems have shown this to be the case (Bernhardt *et al.*, 2006; Finzi *et al.*, 2006; Gill *et al.*, 2006), yet there may be species specific responses in marine algae due to use of different photosynthetic mechanisms (Beardall *et al.*, 1998). In our experiment, elevated $CO_2$ caused an increase in the photosynthetic activity of turfs, but was greater still when in combination with increased nutrients. Yet, nutrient limitation is likely to vary across a number of spatial (and temporal) scales, depending on regional availability of nutrients and localised inputs of anthropogenic inputs (Connell & Irving, 2008). For example, the waters of South Australia are relatively oligotrophic (Rochford, 1980) and nutrient inputs have disproportionately large effects compared to more nutrient rich waters (Russell *et al.*, 2005, Connell *et al.*, unpubl. data). In this case, global change (i.e. increasing $CO_2$) may interact with regional ecology (e.g. oligotrophic *v.* eutrophic regions) or local impacts (e.g. anthropogenic nutrient inputs) to create regionally different responses.

While climate change is a global phenomenon, the impacts of this change (e.g. ocean acidification) manifest on local scales and it is change at these scales that needs to be incorporated into ecological forecasts of climate change (Osmond *et al.*, 2004). Here, we indicate that $CO_2$ would act as an additional stressor that not only enhances the growth of competitors (i.e. turfs), but also drives the accelerated decline of naturally abundant perennial species (i.e. coralline crusts). Our findings on nutrient and $CO_2$ driven synergies empower local managers because they show that policy taken to reduce the effects of local stressors (e.g. nutrient pollution) can reduce the effects of global stressors (e.g. ocean acidification) which are not under their governance. Indeed, efforts to reduce the compounding influence of multiple stressors may reduce the frequency and extent to which ecological systems change to unexpected states (Paine *et al.*, 1998; Scheffer & Carpenter, 2003). If multiple perturbations reduce the resilience of a system, then local management may be effective in reducing the effects of climate change (Hughes *et al.*, 2007).

While there is increasing attention being directed towards ways to mitigate climate change, such as reducing multiple stressors, there is little evidence on the effectiveness of proposed actions. We show that elevated nutrients will enhance the effect of climate change on both crusts (negatively affected) and turfs (positively affected). However, this result can only show that the consequences of climate change may be alleviated if reduced concentrations of nutrients are achieved or maintained in the near future (i.e. before $CO_2$ concentrations increase substantially). What we are yet to identify is whether local mitigation measures are likely to be more effective when implemented before forecasted climates arrive (Mignone *et al.*, 2008). Recognition of this uncertainty, in combination with the greater attention paid to the anticipation and prevention of socially-unacceptable regime shifts, has lead to more proactive management of local stressors in some regions. In South Australia, local government has encouraged research into the processes that support or weaken resilience, and of the socio-economic drivers and governance that regulate modification of the physical environment (e.g. water quality) and their biota (e.g. fisheries). South Australian managers now recognise global-local connections of future change, recently implementing long-term policy solutions for the sea (policy on reducing wastewater discharge) that also act as solutions for the land (policy on establishing new sources of water that do not rely entirely on rainfall). Upgrades to wastewater treatment plants, to produce recycled water for residential and industrial use, not only reduces reliance rainfall for fresh water supplies, but also reduces the nutrient rich discharge that has primarily contributed to phase shifts on metropolitan reefs from kelp to turf-dominated (Connell *et al.*, 2008).

In conclusion, change to systems at local scales represents the cumulative effect of global through local scale conditions, and we need to understand the manifestation of climate change in local settings. Recent motivation for system-wide management (ecosystem management) relies on a process of decision-making at local through regional scales and provides some of the most vexing challenges for attaining social goals of sustainability, biological conservation and economic development. We demonstrate that understanding how global ($CO_2$) and local (nutrients) stressors combine to bring change at local scales (i.e. change in the relative abundance of algal species) may provide insights into understanding not only the potential impacts of climate change, but also the potential roles of local policy and management of local stressors in the face of global climate change.

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**Table 1**. The combined effects of $CO_2$ (current *v*. future) and Nutrients (ambient *v*. elevated) on the dry mass of (a) coralline crusts and (b) turfs, as determined by two-factor ANOVAs. No effect of mesocosm was detected, so pooled analyses are presented here. ns, $p > 0.05$; ∗, $p < 0.05$; ∗∗, $p < 0.01$; ∗∗∗, $p < 0.005$.

| Source | *df* | *MS* | *F* | *P* |
|---|---|---|---|---|
| **(a) Crusts** | | | | |
| $CO_2$ | 1 | 0.0019 | 19.00 | ∗∗∗ |
| Nutrient | 1 | 0.0005 | 5.00 | ∗ |
| $CO_2$ × Nutrient | 1 | 0.0000 | 0.00 | ns |
| Residual | 36 | 0.0001 | | |
| **(b) Turfs** | | | | |
| $CO_2$ | 1 | 3.29 | 8.27 | ** |
| Nutrient | 1 | 0.15 | 0.37 | ns |
| $CO_2$ × Nutrient | 1 | 0.38 | 0.69 | ns |
| Residual | 36 | 0.39 | | |

SNK tests on significant terms in (a):

$CO_2$: Current $CO_2$ > Future $CO_2$

Nutrients: Ambient nutrients > Elevated nutrients

SNK tests on significant terms in (b):

$CO_2$: Current $CO_2$ < Future $CO_2$

**Table 2**. The combined effects of $CO_2$ (current *v*. future) and Nutrients (ambient *v*. elevated) on the percentage cover of turfs on unoccupied substrate, as determined by a two-factor ANOVA. No effect of mesocosm was detected, so pooled analyses are presented here. ns, $p > 0.05$; ∗∗, $p < 0.01$; ∗∗∗, $p < 0.005$.

| Source | *df* | *MS* | *F* | *P* |
|---|---|---|---|---|
| $CO_2$ | 1 | 105.63 | 0.90 | ns |
| Nutrient | 1 | 11730.63 | 100.25 | ∗∗∗ |
| $CO_2$ × Nutrient | 1 | 950.63 | 8.12 | ∗∗ |
| Residual | 36 | 117.01 | | |

SNK tests on significant $CO_2$ × Nutrient term:

Ambient nutrients: Current $CO_2$ = Future $CO_2$

Elevated nutrients: Current $CO_2$ < Future $CO_2$

Current $CO_2$: Ambient nutrients < Elevated nutrients

Future $CO_2$: Ambient nutrients < Elevated nutrients

**Table 3**. The combined effects of $CO_2$ (current *v*. future) and Nutrients (ambient *v*. elevated) on the fluorescent yield of dark adapted (a) coralline crusts and (b) turfs, as determined by two-factor ANOVAs. No effect of mesocosm was detected, so pooled analyses are presented here. ns, $p > 0.05$; ∗, $p < 0.05$; ∗∗, $p < 0.01$; ∗∗∗, $p < 0.005$.

| Source | *df* | *MS* | *F* | *P* |
|---|---|---|---|---|
| **(a) Crusts** | | | | |
| $CO_2$ | 1 | 0.0108 | 6.75 | ∗ |
| Nutrient | 1 | 0.0035 | 2.19 | ns |
| $CO_2$ × Nutrient | 1 | 0.0001 | 0.06 | ns |
| Residual | 36 | 0.0016 | | |
| **(b) Turfs** | | | | |
| $CO_2$ | 1 | 0.0080 | 8.00 | ∗∗ |
| Nutrient | 1 | 0.0245 | 24.50 | ∗∗∗ |
| $CO_2$ × Nutrient | 1 | 0.0026 | 2.60 | ns |
| Residual | 36 | 0.0010 | | |

SNK tests on significant terms in (a):

$CO_2$: Current $CO_2$ > Future $CO_2$

SNK tests on significant terms in (b):

$CO_2$: Current $CO_2$ < Future $CO_2$

Nutrients: Ambient nutrients < Elevated nutrients

## Figure Legends

**Fig. 1.** The dry mass (mg ± SE) of (a) coralline crusts and (b) turfs exposed to different concentrations of $CO_2$ (current *v*. future) and Nutrients (ambient *v*. elevated).

**Fig. 2.** The percentage cover (± SE) of turfs that recruited to unoccupied substrate exposed to different concentrations of $CO_2$ (current *v*. future) and Nutrients (ambient *v*. elevated).

**Fig. 3.** The fluorescence yield of dark adapted (a) coralline crusts and (b) turfs exposed to different concentrations of $CO_2$ (current *v*. future) and Nutrients (ambient *v*. elevated).

**Fig. 1**

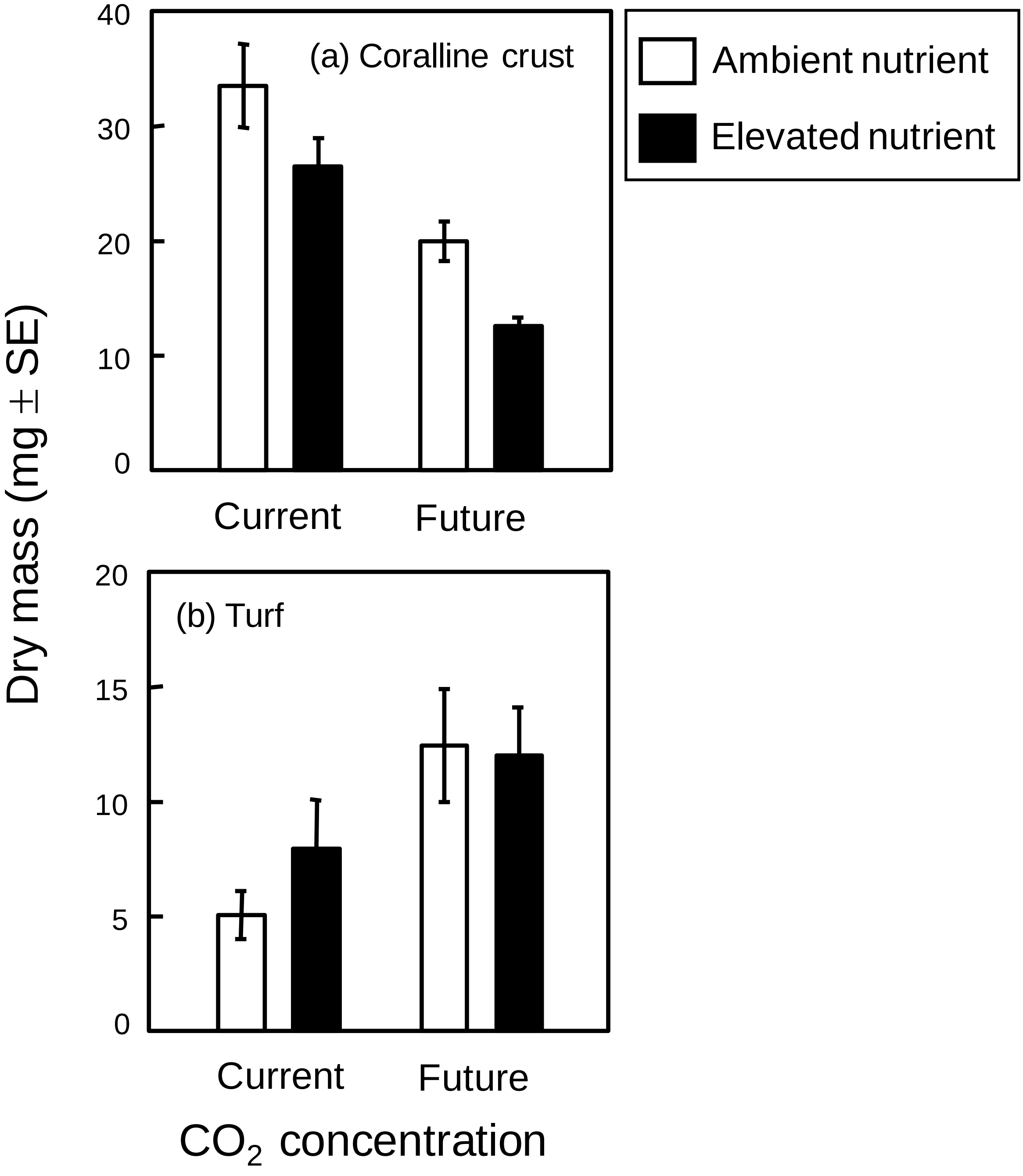

40
30
20
10
0
(a) Coralline crust
Current
Future
Ambient nutrient
Elevated nutrient
Dry mass (mg ± SE)
20
15
10
5
0
(b) Turf
Current
Future
CO2 concentration

**Fig. 2**

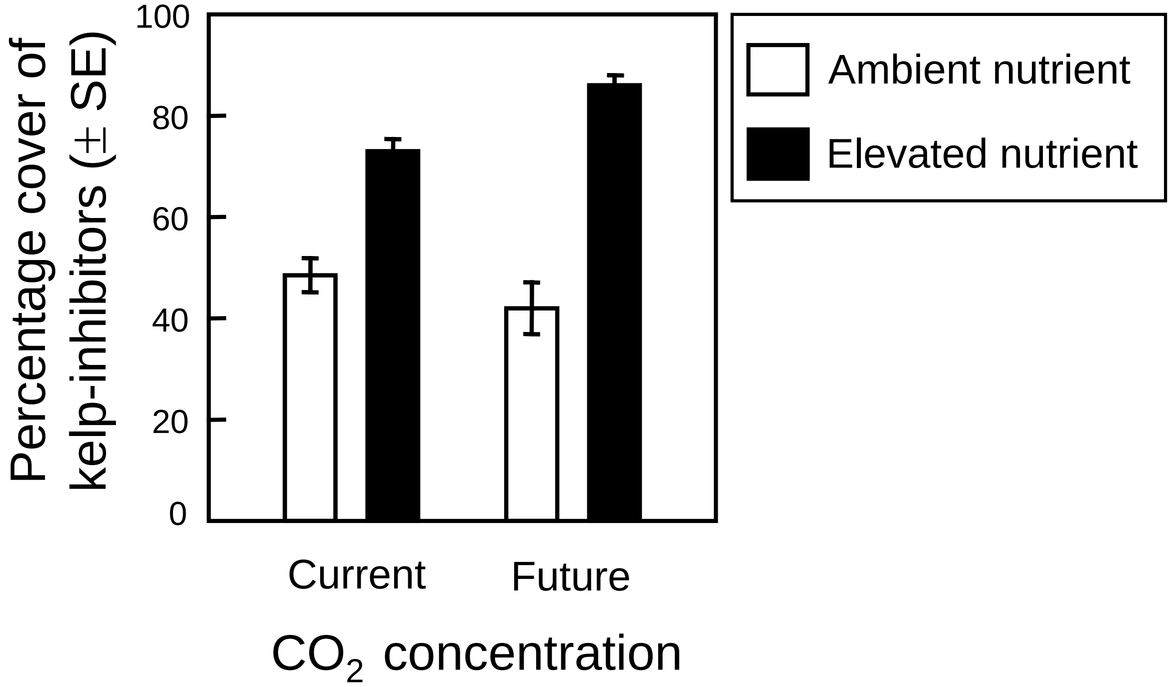
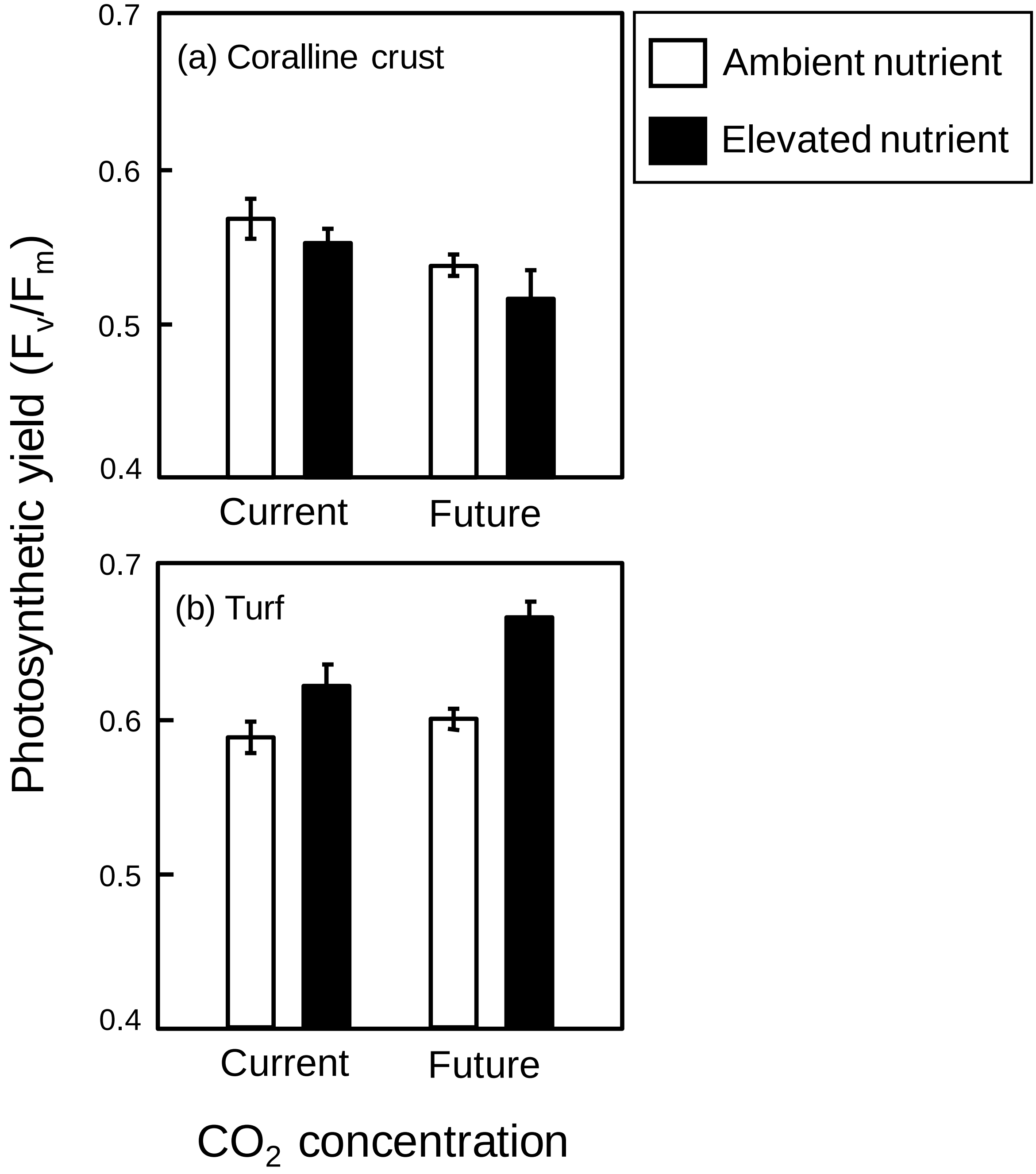

Percentage cover of kelp-inhibitors (± SE)
100
80
60
40
20
0
Ambient nutrient
Elevated nutrient
Current
Future
$CO_2$ concentration

**Fig. 3**


(a) Coralline crust
(b) Turf
Ambient nutrient
Elevated nutrient
0.7
0.6
0.5
0.4
Photosynthetic yield ($F_v/F_m$)
Current
Future
$CO_2$ concentration