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The direct effects of increasing CO_2 and temperature on non-calcifying organisms: increasing the potential for phase-shifts in kelp forests

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Summary

Predications about the ecological consequences of oceanic uptake of CO_2 have been preoccupied with the effects of ocean acidification on calcifying organisms, particularly those critical to the formation of habitats (e.g. coral reefs) or their maintenance (e.g. grazing echinoderms). This focus overlooks the direct effects of CO_2 on non-calcareous taxa, particularly those that play critical roles in ecosystem-shifts. We used two experiments to investigate whether increased CO_2 could exacerbate kelp loss by facilitating non-calcareous alga that we hypothesised: (1) inhibit the recovery of kelp forests on an urbanised coast; and (2) form more extensive covers and greater biomass under moderate future CO_2 and associated temperature increases. Our experimental removal of turfs from a phase-shifted system (i.e. kelp to turf-dominated), revealed that the number of kelp recruits increased, thereby indicating that turfs can inhibit kelp recruitment. Future CO_2 and temperature interacted synergistically to have a positive effect on the abundance of algal turfs, whereby they had twice the biomass and occupied over four times more available space than under current conditions. We suggest that the current preoccupation with the negative effects of ocean acidification on marine calcifiers overlooks potentially profound effects of increasing CO_2 and temperature on non-calcifying organisms.

1. INTRODUCTION

A vexing challenge to ecological research is to identify the perturbations that cause systems undergo shifts from one state to another (Scheffer *et al.* 2001). Shifts in systems often occur quite suddenly because their drivers can be insidious and combine to alter interactions or competitive relationships between key species (Suding & Hobbs 2009). Factors that subtly undermine the resilience of systems are generally unrecognised (Scheffer *et al.* 2001) and we have an incomplete understanding of the effects of long-term perturbations (e.g. marine eutrophication and switches in algal dominance; Smith & Schindler 2009). Nonetheless, ecosystems continue to change, and the need to understand how future conditions (e.g. climate) may contribute to this change has become a fundamental area of ecological research.

The role of global environmental change in driving habitat shifts in marine ecosystems has received heightened attention (e.g. Hoegh-Guldberg *et al.* 2007; Hughes *et al.* 2007). Marine waters currently absorb approximately 30 % of the anthropogenic derived CO_2 from the earth's atmosphere and the resulting ocean acidification has been predicted to have drastic effects over the next 100 years (Feely *et al.* 2004; Orr *et al.* 2005). Unsurprisingly, research on the effects of climate change has a disproportionate focus on the effects of ocean acidification on calcareous organisms that form habitats (i.e. coral reefs', Hoegh-Guldberg *et al.* 2007; Anthony *et al.* 2008; Kuffner *et al.* 2008) or maintain habitats (e.g. grazers Fabry *et al.* 2008; Byrne *et al.* 2009). However, research into the role of the changing climate in the loss of marine habitats has been largely restricted to tropical waters (i.e. coral reefs) while in temperate systems the focus has centred on individual organisms (e.g. Dupont *et al.* 2008; Parker *et al.* 2009). This focus has, to date, overlooked historical and continuing deforestation of algal canopies across the world's temperate coastline (Eriksson *et al.* 2002; Airoldi & Beck 2007; Connell *et al.* 2008).

Kelp forests occur along the majority of the world's temperate coastlines and are among the most phyletically diverse and productive systems in the ocean (Mann 1973). On many coasts where humans have altered chemical and biological conditions, however, canopies of algae (e.g. kelp forests) have been replaced by mats of turf-forming algae (Eriksson *et al.* 2002; Airoldi & Beck 2007; Connell *et al.* 2008). While kelp canopies inhibit turfs (Irving & Connell 2006; Russell 2007), developing theory explains shifts from canopy to turf-domination as a function of reduced water quality that enables the cover of turf to expand spatially and persist beyond its seasonal limits (Gorman *et al.* 2009), subsequently inhibiting the recruitment of kelp and regeneration of kelp forests. Unlike kelps, many turf-forming species are ephemeral and require increased resource availability to enable their physiology and life history to be competitively superior to perennial species (Airoldi *et al.* 2008). It is critical, therefore, to identify future conditions that would have positive effects on turfs, thereby exacerbating the loss of algal canopies.

Although recent studies have identified the effects of anticipated levels of acidification on calcareous temperate algae (e.g. Martin & Gattuso 2009; Russell *et al.* 2009), none has examined the effects of elevated CO_2 and temperature on non-calcareous species such as algal turfs. Therefore, the purpose of our study was two-fold, to determine; (1) if turfs do in fact inhibit the recruitment of kelp under human mediated conditions (i.e. on a metropolitan coast), and if so; (2) to determine if future conditions could exacerbate the currently observed shift from kelp to turf-dominated reefs. We tested the hypotheses that (1) the removal of turfs on a metropolitan coast would cause greater recruitment of kelp, and (2) the abundance of turfs would increase under combined future conditions (i.e. elevated CO_2 and temperature).

2. METHODS

(a) *Ability of turfs to inhibit kelp recruitment*

We first tested the prediction that the removal of algal turfs from turf-dominated ecosystems (i.e. degraded systems; Connell *et al.* 2008) would enable recruitment of kelp (*Ecklonia radiata*) to increase. Algal turf and associated sediment were removed from 12 replicate 1 m^2 plots to expose the underlying substrate. These plots and 12 replicate controls (1 m^2 untouched plots) were positioned within 5 m of remnant patches of canopy, which acted as a source of recruits. This procedure was repeated at three sites (separated by > 1 km) that were associated with both extensive covers of turfs and remnant patches of canopy on the Fleurieu Peninsula, South Australia. The number of kelp recruits in plots was quantified in April 2008, ~12 months after turfs were removed.

(b) *Effect of future conditions on turfs*

Algal turfs were exposed to current and predicted future concentrations of CO_2 (380 ppm and 550 ppm, respectively) in crossed combination with ambient and elevated temperatures (17ºC and 20ºC, respectively) in a mesocosm experiment over 14 weeks from March – June 2008. Both future CO_2 and temperatures were based on IS92a model predictions for the year 2050 (Meehl *et al.* 2007), with the ambient temperature being the summer maxima at the algal collection site. There were two replicate mesocosms per combination of treatments (n = 5 replicate turf specimens per mesocosm).

The response of turfs to experimental conditions was assessed using three response variables; percentage cover and dry mass of algae recruiting to initially unoccupied substrate (5 × 5 cm fibreboard tiles), and effective quantum yield of algae on the original rock substrate. The percentage cover of algae was visually estimated to the nearest 5 % at the end of the experiment (n = 5 tiles per mesocosm) as suggested by Drummond and Connell (2005). Dry mass of algae was measured by carefully scraping all algae from a standard area on each tile (6.25 cm^2) into a pre-weighed aluminium tray, which was then rinsed with fresh water to remove excess salt and dried at 60°C for 48 hours. Fibreboard tiles were used as unoccupied substrate to remove confounding by any differences in either percentage cover or mass of algal samples that were placed into the experiments. Further, the tiles were placed into mesocosms with the rough side uppermost as turfs readily recruit to this surface (Irving & Connell 2002), which has similar roughness to basalt rock at the collection site.

Chlorophyll fluorescence, a relative measure of the photochemistry of Photosystem II (Genty *et al.* 1989), was measured under the experimental light conditions using a Pulse Amplitude Modulated (PAM) fluorometer (Walz, Germany). Effective quantum yield (Y) was calculated using the equation $Y = (F'_m - F)/F'_m$ (Genty *et al.* 1989), where F'_m is the maximal fluorescence, and F the minimal fluorescence, under illuminated conditions (van Kooten & Snel 1990). F was measured by holding the fiberoptics of the PAM fluorometer in contact with the algal sample (*in situ* in mesocosms) and exposing it to a pulsed measuring beam of weak red light (0.15 μmol m^{-2} s^{-1}, 650 nm) followed immediately by a pulse of saturating actinic light (0.8 s, 6000 μmol $m^{-2}s^{-1}$) to measure F'_m (Beer *et al.* 1998). Each yield value used in the analyses was a mean of three replicate measurements taken on different parts of each algal sample so that yield was not underestimated due to recovery of the photosystems from repeated saturating light pulses.

Turf specimens used in experiments were collected from a rocky reef at Victor Harbour, South Australia (35.57126ºS 138.61221ºE) at 2 m – 4 m depth. The turf assemblages used were comprised mainly of *Feldmannia* spp., which form densely packed mats of filaments up to 2 cm in height. Turfs were collected still attached to their rocky substrate (approximately the same size; ~ 5 cm × 5 cm) and allowed to acclimate in holding mesocosms for two weeks before the experiment commenced. During acclimation, physical conditions in the mesocosms were similar to those at the collection site (i.e. 17ºC and current atmospheric CO_2 concentrations). Algae were then randomly re-assigned to mecosms in which experimental conditions were gradually increased over a further 2 week period until they reached their pre-designated levels. All mesocosms were aerated at 10 L min^{-1}, with either current atmospheric air or air enriched with CO_2. Future concentrations of CO_2 in water were maintained at 550 ppm CO_2 (pH 7.95, based on the IS92a model for 2050; Meehl *et al.* 2007) using pH probes attached to automatic solenoids (Sera, Heinsberg, Germany) and CO_2 regulators. Probes were temperature compensated and calibrated using NBS calibration buffers on a daily basis. Elevated temperature was achieved by using heaters in the 20ºC treatment mesocoms. Total alkalinity (TA) of the seawater in mesocosms was measured on a weekly basis to monitor CO_2 and bicarbonate (HCO_3^-) concentrations (see online supplementary material for more detail).

Each mesocosm system consisted of a 40 L experimental aquarium connected to a 200 L reservoir tank with water recirculated in a closed loop, ensuring that all replicate mesocosms were independent of each other. To ensure quality of the growing conditions in mesocosms, one-third of the water was removed from reservoir tanks and replaced with fresh seawater weekly (see Russell *et al.* 2009). Lighting was supplied in a 12:12 light:dark cycle by pairs of fluorescent lights directly above each mesocosm (see online supplementary material for more detail).

(c) *Statistical analyses*

The effect of turf on kelp recruitment was analysed using a two-factor ANOVA, with factors of turf (turf present *v*. turf removed) and site (three sites). Both factors were treated as orthogonal, 'turf' as fixed, 'site' as random (n = 12 replicate plots). Data were Ln (X + 1) transformed before analysis to conform to assumptions of homogeneity.

Analysis of the mesocosm experiment proceeded in two steps. First, three-factor ANOVAs were used to identify if there was any difference in experimental effects between replicate mesocosms for all measures (percentage cover, dry mass and effective quantum yield). Both CO_2 and temperature were treated as fixed and orthogonal, with two levels in each factor, and two replicate mesocosms were nested within both CO_2 and temperature (n= 5 replicate samples of algae per mesocosm). No differences were detected between replicate mesocosms within treatments (i.e. no "tank" effects). Therefore, to avoid pseudoreplication within mesocosms, data for the five algal specimens within each mesocosm were averaged, and data reanalysed using two factor ANOVAs; CO_2 and temperature were again treated as fixed and orthogonal, with mesocosms as replicates. Where significant treatment effects were detected, Student-Newman-Keuls (SNK) post-hoc comparison of means was used to determine which factors differed. Percentage cover data were arcsin transformed prior to analysis to remove heterogeneity (Underwood 1981).

3. RESULTS

(a) *Ability of turfs to inhibit kelp recruitment*

The removal of turfs resulted in the greater recruitment of kelp at all three phase-shifted sites (Fig. 1a). While there was significant difference in the number of kelp recruits among the three replicate sites, the number of kelp recruits was consistently greater in removal plots than plots were turfs were left intact (turf removal × site interaction: $F_{2,66} = 6.10$, $p = 0.0037$; SNK: turf removal > turf intact at all three sites).

(b) ***Effect of future conditions on turfs***

CO_2 and temperature had an interactive effect on the percentage cover of turf-forming algae that recruited to available space (Fig. 1b; CO_2 × temperature interaction, $F_{1,4} = 7.73$, p = 0.0498). Under current CO_2 concentrations, temperature had a positive effect on the percentage cover of turfs that recruited to available space (Fig. 1b; SNK test of CO_2 × temperature interaction). In contrast, future CO_2 had no effect on the cover of turfs at ambient temperatures (17ºC). When future CO_2 and elevated temperature were present in combination, however, turfs occupied > 80 % of available space (Fig. 1b). Importantly, this represented a synergistic effect whereby turfs occupied 25 % more space than would be predicted by the independent effects of CO_2 and temperature.

Both elevated CO2 and temperature had positive effects on the dry mass of turfs (Fig. 1c; $F_{1,4}$ = 19.20, $p = 0.0119$ and $F_{1,4} = 11.39$, $p < 0.0279$, respectively). There is no graphical evidence of an interaction between these factors (Fig. 1c) as the increase in mass by CO_2 is proportionally similar between the CO_2 treatments, and vice versa. This interpretation is supported by the lack of a significant interaction term between these factors ($F_{1,4} = 0.41$, p = 0.5558; power = 0.08) as shown by the effect of temperature in each CO_2 treatment (approximately double the mass), and the effect of CO_2 in each temperature treatment (approximately double the mass) (Fig. 1c). Hence, the combined effects of CO_2 and temperature are approximately four times greater than ambient conditions.

The effects of these factors on quantum yield were relatively small; yield of turfs was 5 % greater under future CO_2 concentrations (Fig. 1d, ANOVA: $F_{1,4} = 14.11$, $p = 0.0198$) but 3 % less under elevated temperature (Fig. 1d, $F_{1,4} = 16.73$, $p = 0.0150$). Again, the proportional influence of each factor was similar within each level of the crossed factor (Fig 1d) as also indicated by the lack of a significant interaction term between these factors ($F_{1,4} = 1.24$, $p = 0.3276$; power = 0.14). Whilst we report low power for non-significant interactions, we consider the combined effects of temperature and CO_2 are indeed additive rather than multiplicative.

4. DISCUSSION

A substantial part of research into global environmental change centres on the negative effects of ocean acidification and increasing temperature on organisms that form calcareous structures (e.g. Fabry *et al.* 2008; Jokiel *et al.* 2008; Kuffner *et al.* 2008). While elevated CO_2 can be beneficial to plants in terrestrial systems (Ainsworth & Long 2005), there is little recognition of the positive effects on some non-calcareous marine species. Here, we show that predicted moderate concentrations of CO_2 and temperature had a synergistic positive effect on the abundance of non-calcareous algal turfs. Yet, it is important to recognise that such positive effects could act as perturbations in ecological systems. Turfs form a natural component of the early successional stages of kelp-dominated landscapes. Under natural conditions algal canopies inhibit these algae (Irving & Connell 2006; Eriksson *et al.* 2007; Russell 2007), but under altered environmental conditions turfs expand (Connell 2007; Russell & Connell 2007) by inhibiting kelp recruitment (i.e. eroding resilience of forests). Our results indicate that kelp loss may be exacerbated on human-dominated coasts, by the positive effects of increasing CO_2 and temperature on kelp inhibitors, motivating the need to assess such switches on coasts that are currently considered unaffected by human activity.

Recruitment that replenishes lost habitat-forming individuals is key to resilience against phase shifts in ecosystems founded on habitat-forming species (Pickett & White 1985). Disturbance is part of the dynamics of kelp forests which would otherwise fully occupy space (e.g. storms Dayton *et al.* 1984). We recognise that it is not so much the direct effects of climate stressors on kelp forests that may affect their future abundance, but rather the indirect loss of kelp via their competitors or inhibitors. Altering global (i.e. CO_2) and local (i.e. eutrophication) stressors in combination can allow turfs to expand to more rapidly occupy available space (Russell *et al.* 2009). It is noteworthy that our experimentally increased CO_2 and temperature, two inherently linked global stressors, enabled turfs to occupy nearly five times more space than under current conditions. While it may be possible to mitigate the effects of climate-driven environmental change by removing nutrient inputs (e.g. recycling wastewater and sewage, Russell & Connell 2009), such actions would not be possible in the case of synergistic effects between multiple global stressors. Indeed, understanding the degree to which these factors will combine to accelerate and expand ecosystem-shifts is of key concern (Scheffer *et al.* 2001; Suding & Hobbs 2009).

Increasing temperatures are commonly predicted to result in changes in marine communities because of a shift in the geographic ranges of species (e.g. Fields *et al.* 1993; Poloczanska *et al.* 2008). While community shifts have been observed, local conditions and competitive interactions may alter the outcomes (Helmuth *et al.* 2002; Poloczanska *et al.* 2008). In such cases, taxa that are natural components of a system may play substantially altered roles in their maintenance and disruption (Suding & Hobbs 2009). In Australia, *Ecklonia radiata* canopies have high rates of natural turnover, and their maintenance relies on rapid recruitment and replenishment into canopy-gaps in the winter months (Kennelly 1987b).

While turfs are a natural component of these kelp-dominated systems (Irving *et al.* 2004) they are ephemeral, rapidly occupying available space in summer but declining in cover and biomass over the colder months (Russell 2007; S.D. Connell, B.D. Russell, D. Gorman, A. Airoldi, unpubl. data). Importantly, *Ecklonia radiata* produce gametophytes, the smallest and therefore more susceptible stage of the life cycle, in the colder months when turfs are at their lowest abundance. Yet, we show that turfs increased in abundance under elevated temperatures, suggesting that future increases in temperature could allow turfs to be increasingly abundant throughout periods of naturally low abundance (i.e. winter). Similarly, turfs exhibit a phenological shift due to elevated nutrients (S.D. Connell, B.D. Russell, D. Gorman, A. Airoldi, unpubl. data), possibly leading to habitat shifts on urbanised coasts (Gorman *et al.* 2009). As algal turfs can inhibit kelp recruitment (Kennelly 1987a; this study), any phenological shift that allows turfs to persist though periods of kelp recruitment is likely to reduce the resilience of kelp forests to disturbance. While it is accepted that such habitat shifts are common on human-dominated coasts (Airoldi 2003; Connell 2007), temperature, unlike nutrients, will increase even on “pristine” coasts, potentially causing habitat shifts in the absence of local human populations.

Loss of canopy-forming algae can be a consequence of overgrazing by increasing urchin populations (Estes *et al.* 1998), but in many parts of the world, including most of southern Australia, such deforestation is not possible because of the types and sparse densities of herbivores (Connell & Vanderklift 2007; Connell & Irving 2008). Nevertheless, canopy-forming algae has long been disappearing from human dominated coasts lacking strong herbivory, but experiencing strong water pollution (Eriksson *et al.* 2002; Airoldi *et al.* 2008; Connell *et al.* 2008), yet the specific mechanisms underlying this loss are often a point of conjecture and contention. Previous studies have demonstrated that some more erect forms of turf-forming and foliose algae can dominate available space and inhibit canopy recruitment (Kennelly 1987a; Airoldi 2003) but, to our knowledge, ours is the first study to show that the removal of filamentous turfs can enhance the recruitment of kelp. By removing turfs from the substrate we created more available space for kelp recruits to settle and become established. As the creation of new space is a prerequisite for community change (Pickett & White 1985; Airoldi & Virgilio 1998), it is unlikely that these phase-shifted reefs (i.e. from kelp to turf dominated; Connell *et al.* 2008) will be able to return to domination by kelp canopies until the environmental conditions on these coasts revert to their more natural state (e.g. nutrients; Gorman *et al.* 2009). Nevertheless, we demonstrate that the removal of turfs can create the space necessary for the recruitment and recovery of kelp and that the observed phase-shift (Connell *et al.* 2008) may not be permanent.

While the productivity of terrestrial plants stands to increase with predicted future CO_2, especially in plants which utilise C3 photosynthesis (Ainsworth & Long 2005), there is still debate on whether this will be the case in marine algae. Most marine algae have carbon concentrating mechanisms (CCMs) which allow them to use bicarbonate for photosynthesis, meaning that photosynthesis is carbon saturated at current concentrations (Gao & McKinley 1994; Beardall *et al.* 1998). Experiments have so far been inconclusive, with some species showing carbon saturation at current CO_2 (e.g. Beer & Koch 1996; Israel & Hophy 2002), others demonstrating increased photosynthetic production with increasing CO_2 (e.g. Holbrook *et al.* 1988), and yet others switching the source of carbon with greater CO_2 availability (e.g. Johnston & Raven 1990; Schmid *et al.* 1992). Yet, general consensus within the literature seems to be that algae with CCMs will not increase productivity under future conditions (see review by Beardall *et al.* 1998). It is no surprise, then, that the positive effects of CO_2 on algae have not been a substantial part of the climate change literature; if productivity is not enhanced by elevated CO_2, then why look for ecological effects? Our experiments do not clarify this issue with respect to photosynthetic activity of algae; we found a small increase (~ 5 %) in the effective quantum yield of turfs under future concentrations of CO_2, but this seemed to be counteracted by elevated temperature. Nevertheless, it seems that elevated CO_2 conditions can cause an increase in the growth (Kubler *et al.* 1999) and abundance (Andersen & Andersen 2006; Kuffner *et al.* 2008; Russell *et al.* 2009) of non-calcareous algae and this deserves more attention. We propose that elevated inorganic carbon has positive effects on some taxa, and that the non-uniform effects among alternate taxa (review by Gao & McKinley 1994) have relatively unexplored ecological consequences, particularly if growth is limited by sources of inorganic carbon.

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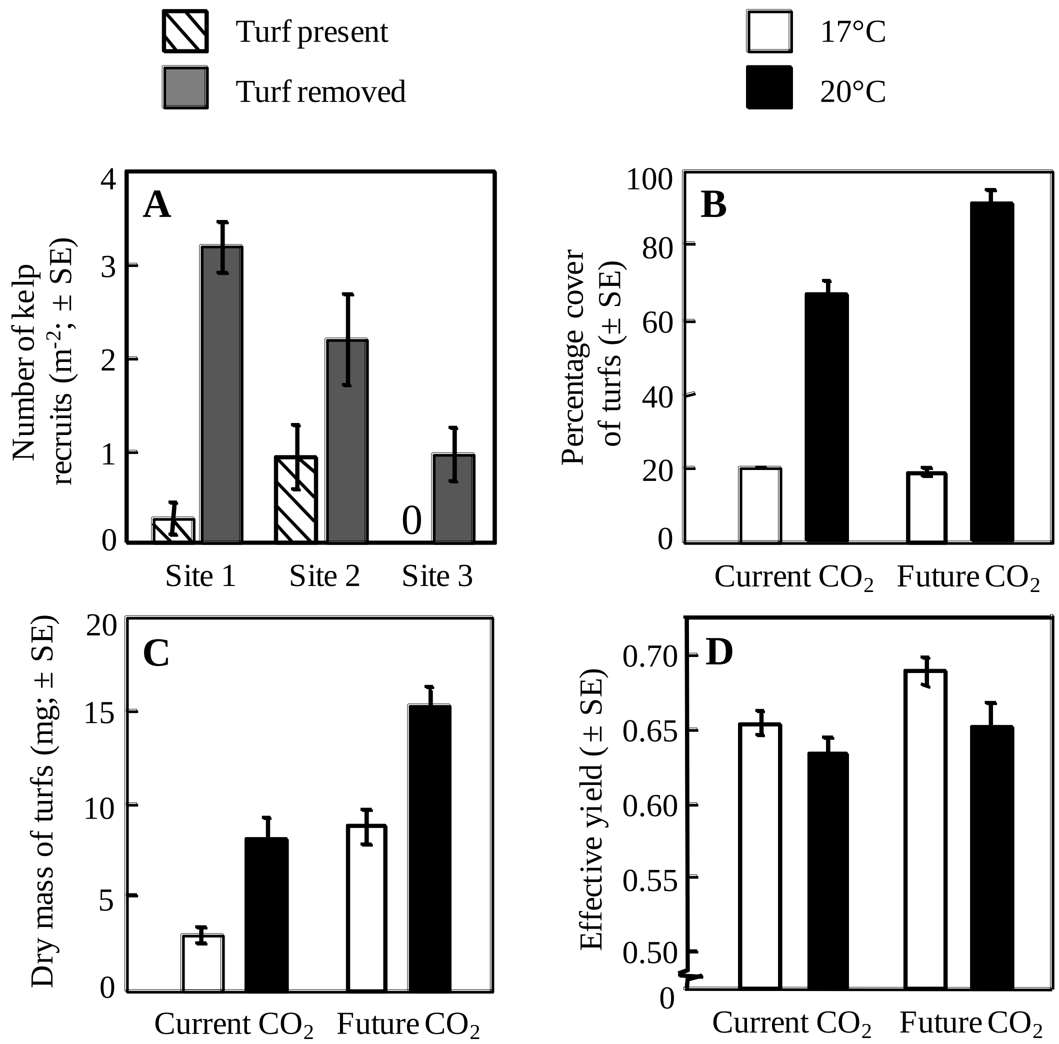
Figure Legend

Figure 1. (A) The inhibitory effect of turf on recruitment of kelp at three phase-shifted sites (i.e. kelp-domination to turf-domination) with treatments of turf presence and turf removal, and the effect of forecasted CO_2 and temperature on turfs as observed by (B) recruitment to available space (percentage cover), (C) biomass (dry mass), and (D) effective quantum yield. Note: "0" in A signifies no kelp recruits.

Fig. 1.



Turf present
Turf removed
17°C
20°C
A
Number of kelp recruits (m-2; ± SE)
4
3
2
1
0
0
Site 1
Site 2
Site 3
B
Percentage cover of turfs (± SE)
100
80
60
40
20
0
Current CO2
Future CO2
C
Dry mass of turfs (mg; ± SE)
20
15
10
5
0
Current CO2
Future CO2
D
Effective yield (± SE)
0.70
0.65
0.60
0.55
0.50
0
Current CO2
Future CO2