PUBLISHED VERSION

Laura J. Falkenberg, Sean D. Connell, Owen I. Coffee, Giulia Ghedini, Bayden D. Russell

Species interactions can maintain resistance of subtidal algal habitats to an increasingly modified world

Originally published at:
http://doi.org/10.1016/j.gecco.2015.10.003

http://hdl.handle.net/2440/106806

Original research article

Species interactions can maintain resistance of subtidal algal habitats to an increasingly modified world

Laura J. Falkenberg [a,b,*], Sean D. Connell [a], Owen I. Coffee [a], Giulia Ghedini [a], Bayden D. Russell [a,c]

[a] *Southern Seas Ecology Laboratories, School of Biological Sciences and The Environment Institute, The University of Adelaide, Adelaide, SA, Australia*
[b] *School of Energy and Resources, University College London, Adelaide, SA, Australia* [1]
[c] *Swire Institute of Marine Science and School of Biological Sciences, The University of Hong Kong, Hong Kong SAR*

A B S T R A C T

Current trends in habitat loss have been forecast to accelerate under anticipated global change, thereby focusing conservation attention on identifying the circumstances under which key species interactions retard habitat loss. Urbanised coastlines are associated with broad-scale loss of kelp canopies and their replacement by less productive mats of algal turf, a trend predicted to accelerate under ocean acidification and warming (i.e. enhanced CO_2 and temperature). Here we use kelp forests as a model system to test whether efforts to maintain key species interactions can maintain habitat integrity under forecasted conditions. First, we assessed whether increasing intensity of local human activity is associated with more extensive turf mats and sparser canopies via structured field observations. Second, we experimentally tested the hypothesis that intact canopies can resist turf expansion under enhanced CO_2 and temperature in large mesocosms. In the field, there was a greater proportion of turf patches on urbanised coasts of South Australia than in agricultural and urban catchments in which there was a greater proportion of canopy-forming algae. Mesocosm experiments revealed this expansion of turfs is likely to accelerate under increases in CO_2 and temperature, but may be limited by the presence of intact canopies. We note that even in the presence of canopy, increases in CO_2 and temperature facilitate greater turf covers than occurs under contemporary conditions. The influence of canopy would likely be due to shading of the understorey turfs which, in turn, can modify their photosynthetic activity. These results suggest that resistance of habitat to change under human-dominated conditions may be managed via the retention of key species and their interactions. Management that directly reduces the disturbance of habitat-forming organisms (e.g. harvesting) or reverses loss through restoration may, therefore, reinforce habitat resistance in an increasingly stressful world.

* Corresponding author at: School of Energy and Resources, University College London, Adelaide, SA, Australia. Tel.: +61 8 8110 9974.
E-mail address: l.falkenberg@ucl.ac.uk (L.J. Falkenberg).
[1] Present address.

1. Introduction

The resistance of ecological systems to modified environmental conditions is strongly influenced by interactions among species which underlie the mechanisms for ecosystem persistence or loss (Connell and Ghedini, 2015). Foundation species, which strongly influence community structure by modifying physical conditions and ecosystem processes (*sensu* Dayton, 1972), are of particular importance in such dynamics (Bruno and Bertness, 2001; Jones et al., 1996; Lawton, 1994). Variation in the occurrence of foundation species may be of increasing importance where human activities drive greater environmental change (Bruno et al., 2003; Halpern et al., 2007). Where present, foundation species may limit the influence of environmental conditions. In the absence of foundation species, however, environmental conditions could otherwise facilitate expansion of alternate species that promote shifts away from the historically dominant states (Jones et al., 1997; Sasaki and Lauenroth, 2011). Despite their potential influence in ameliorating the effects of abiotic change, populations of foundation species are fragmented as a consequence of human activities (Airoldi and Beck, 2007; Ellis, 2011; Ellison et al., 2005). This loss has the potential to increase the susceptibility of the associated systems to global climate change. Ameliorating the effects of global climate change through management of key species will, therefore, depend on understanding both the conditions that determine the distribution and abundance of key species, and also how the associated resistance will be influenced by global change.

Canopy-forming algae are a dominant feature of temperate marine waters in both hemispheres where they provide key ecosystem services (Airoldi and Beck, 2007; Connell et al., 2008; Steneck et al., 2002). On coastlines adjacent to growing populations, however, these ecosystems have often been modified to an extent that following natural disturbance events, such as storms, otherwise ephemeral mat-forming turf algae can persist (Airoldi et al., 2008; Gorgula and Connell, 2004; Reed and Foster, 1984). Where mats persist they can then cause intergenerational decline and loss of canopy-dominated habitats (Connell et al., 2008; Eriksson et al., 2002). Importantly, therefore, the degradation of these habitats not only encompasses the loss of canopies, but also the expansion of morphologically-simple and opportunistic species. Where such shifts occur, the newly-established configuration is typically comprised of species perceived to be of less value to human societies than those of the system they replaced, making prevention of such change advantageous (Dudgeon et al., 2010; Hobbs et al., 2006). Understanding the nature of any link between the intensity of human activity and structure of marine habitats will be relevant to managing ecological sustainability of increasingly human-dominated coasts (Gorman et al., 2009).

While relatively localised human activities have driven such changes historically, in the future ecosystem structure will be influenced by the pervasive impacts of globally-growing human populations. In contrast to the historical impacts, all coastal systems are anticipated to be impacted by the global enrichment of CO_2 and increased temperatures, regardless of human use in the associated terrestrial catchment. Such changes to CO_2 and temperature could affect algae and the habitats they form (Hepburn et al., 2011; Raven and Hurd, 2012). In the ecosystem considered here, a key role of global change is anticipated to be its positive effect on turfs. Enriched CO_2 and increased temperature can facilitate greater covers of turfs by increasing the rate and efficiency of their physiological processes (Connell and Russell, 2010; Falkenberg et al., 2013b; Russell et al., 2009). Where CO_2 has this effect on turfs it could potentially enhance their capacity to exist as a persistent rather than ephemeral habitat and modify their ecological role (reviewed in Connell et al., 2013). Where canopies are able to persist, however, the expansion of turfs may be restricted. The strength of this biotic interaction can be sufficient to restrict the growth of turfs even where the opportunistic functional group is favoured by other abiotic conditions that modify resource availabilities (e.g. elevated nutrients and future CO_2; Falkenberg et al., 2012). It will be important, therefore, to consider the response of the turfs in the presence of algal canopies. If the strength of these ecological interactions are maintained under future conditions, turfs may continue to be restricted under conditions of warming and elevated CO_2 that are otherwise anticipated to facilitate their expansion.

In this study, we combine field surveys and large mesocosm experiments to test two hypotheses; (1) that there will be more extensive algal canopies (forests) where human use of adjacent terrestrial catchments is less intensive (i.e. 'natural' and 'agricultural' catchments) and turfs will be more extensive adjacent to urbanised coast of intensive use (i.e. 'urbanised' catchments), and, (2) the positive response of turfs to forecasted levels of future, globally-modified conditions (i.e. predicted CO_2 and temperature) will be reduced in the presence of algal canopies. Understanding the influence of key species has implications for management of coastal habitats, as actions to maintain or re-establish canopies could potentially constrain the expansion of turf algae on urban coasts and the further degradation of these ecosystems under forecasted global conditions.

2. Materials and Methods

2.1. Quantifying the localised impact of current human populations

We tested for an association between terrestrial catchments of different intensity of human use and habitat structure by quantifying composition of algal cover and patch size. The survey was conducted in the early Austral summer (January–March, 2005). Sites for field observations were classified as areas adjacent to natural, agricultural and urban catchments interspersed along the south Australian coastline, with sites ($n = 4$ per catchment type) selected based on human use (DEWNR, 2014). 'Natural' catchments were those used for nature conservation (i.e. nature parks or managed

resource protection areas) with little or no development and were similar to 'agricultural' catchments that supported livestock grazing or light cropping. 'Urban' catchments were intensely populated and used primarily for residential purposes.

2.1.1. Sampling methods

Habitat composition was quantified in terms of percentage cover of all canopy-forming algae (i.e. *Ecklonia radiata*, *Cystophora* spp., *Sargassum* spp.) and mat-forming turf algae on rocky substratum. Here, 'turf' is used as a functional group term to denote mats of low-growing algae < 5 cm canopy height in mixed assemblages that were mainly composed of the algal genus *Feldmannia* (Connell et al., 2014). Sampling was conducted on rocky reef adjacent to each catchment type with the relative sizes of patches of canopy and turfs quantified using replicate 1×100 m transects ($n = 4$ per site) separated by 50–100 m. Transects were orientated perpendicular to the shoreline and started as close to mean low water as prevailing conditions would allow. Sampling stopped at either the seaward edge of the rock or, if the rock extended past this point, at 100 m. The type of algal habitat was identified along each transect at a scale of 1×1 m by identifying the dominant habitat in each 1 m^2 area, with particular care taken when sampling units with coverage of both algal types. The diameter of individual patches of habitat was determined by measuring the beginning and end of each point where the patch intersected the transect line.

2.2. Forecasting the effects of global change

The effects of canopy presence or absence on turfs under modified CO_2 and temperature conditions were considered in a mesocosm experiment (see 'Experimental site and set-up' below for detail) that ran for 21 days in the Austral winter (July–August, 2013). Experimental mesocosms had combinations of canopy (kelp, *Ecklonia radiata*; present vs. absent), CO_2 (current vs. future) and temperature (ambient vs. elevated) in a crossed design. Canopy was either present (kelp at densities similar to those observed at the collection site, c. 10 m^{-2}) or absent (as occurs in many human-impacted catchments). The target CO_2 and temperature levels were based on the current ambient levels found in waters where experimental organisms were collected (current CO_2, pH: 8.12, 356 ppm; ambient temperature, 14.5 °C) and future projection scenario IS92a for the year 2100 (future CO_2, 0.15 pH units lower than ambient at $\sim$7.98, 600 ppm; elevated temperature, 2.5 °C higher than ambient at 17 °C) (Meehl et al., 2007).

2.2.1. Experimental site and set-up

Experimental mesocosms were located outdoors in natural sunlight at SARDI (South Australian Research and Development Institute) Aquatic Sciences, West Beach, South Australia (34.94°S, 138.50°E). The 2300 L flow-through experimental mesocosms (cylindrical, polyethylene, 1720 mm diameter $\times$ 1365 mm high, TeamPoly, Australia) were covered with material (high density polyethylene with woven scrim, SolarPro, PolyFab, Australia) that transmits incoming radiation ($\sim$45% and 30% of ambient PAR and UVB respectively) creating a light environment representative of shallow subtidal habitats in the region ($\sim$5–8 m depth; Russell, 2007; Russell et al., 2011). The mesocosms were filled with natural seawater pumped from the adjacent ocean which would be classified as 'urban' above, therefore, initial seawater chemistry (i.e. before experimental manipulation) was characteristic of these waters. A flow rate of 4 L min^{-1}, or 2.5 total volume turnovers per day, was used to maintain water quality. A total of 12 mesocosms were used with three replicates for each $CO_2 \times$ temperature combination. Within these, each tank was divided with canopy present in one half and absent in the other half.

2.2.2. Experimental treatments

The presence or absence of canopy was manipulated by either having a canopy of algae (*Ecklonia radiata*) present or absent (for further detail see 'Experimental algae' below). The effect of canopy cover on water column light was quantified both under and outside of the canopy using a light metre at the conclusion of the experimental period (LI-COR, Lincoln, Nebraska, USA). In the presence of canopy, light availability was significantly lower than that which occurred in the absence of canopy (mean $\pm$ SE; present: 30.45 ± 2.50 μmol m^{-2} s^{-1} vs. absent 126.49 ± 9.10 μmol m^{-2} s^{-1}, $F_{(1, 22)} = 121.44, p = 0.001$). CO_2 concentrations were maintained by aerating the tanks at a rate of 15 L min^{-1} with either ambient atmospheric air (current), or air enriched with CO_2 to a set concentration (future) with a gas mixer (Pegas 4000 MF, Columbus Instruments, Columbus Ohio, USA). Total alkalinity (A_T) and pH of seawater were measured eight times over the three week experimental period with samples taken between 10:00 and 13:00 and analysed using a potentiometric titrator (888 Titrando, Metrohm, USA). Concentrations of pCO_2, carbonate (CO_3^{2-}) and bicarbonate (HCO_3^-) were then calculated from measured A_T, pH, salinity and temperature using the CO2SYS program for Excel (Pierrot et al., 2006) with constants from Mehrbach et al. (1973) as adjusted by Dickson and Millero (1987). The pH and concentration of CO_3^{2-} were significantly reduced under future CO_2 compared with current CO_2 treatments (pH current: 8.12 ± 0.03 vs. future: 7.95 ± 0.03, $F_{(1, 10)} = 244.27, p = 0.001$; CO_3^{2-} current: 233 ± 14 μmol kg^{-1} vs. future: 171 ± 11 μmol kg^{-1}, $F_{(1, 10)} = 196.81, p = 0.004$), while pCO_2 and HCO_3^- were significantly increased under future CO_2 conditions (pCO_2 current: 356 ± 32 ppm vs. future: 559 ± 47 ppm, $F_{(1, 10)} = 237.61, p = 0.007$; HCO_3^- current: 1990 ± 37 μmol kg^{-1} vs. future: 2136 ± 26 μmol kg^{-1}, $F_{(1, 10)} = 123.4, p = 0.006$) and there was

no significant difference in A_T (current: 2564±3 µmol kg^{-1} vs. future: 2556±4 µmol kg^{-1}, $F_{(1, 10)} = 0.753$, $p = 0.437$). The temperature within each mesocosm was controlled using an individual heater/chiller unit (TC-60 Aquarium Chillers, TECO Refrigeration Technologies, Ravenna, Italy) such that there was diurnal variation whereby temperature increased during the day and decreased at night by ∼2 °C in all mesocosms (i.e. both ambient and elevated temperature mesocosms). Temperature was measured concurrently with sample collection for analysis of A_T and pH (i.e. eight times over the experimental period, between 1000 and 1300). Temperature was significantly higher in elevated than ambient treatments (ambient: 14.5 ±0.1 ° C vs. elevated: 17.1 ±0.2 ° C; $F_{(1, 10)} = 174.16$, $p = 0.002$).

2.2.3. Experimental algae

The canopy-forming kelp and mat-forming turf algae used in experiments were collected from adjacent areas of rocky reef at Granite Island, Victor Harbor, South Australia (33.55° S, 138.61° E), one of the 'urban' sites in the habitat survey. The canopy algae were the kelp *Ecklonia radiata*, while 'turf' is again used as a functional group term to denote mats of low-growing algae (<5 cm canopy height) in mixed assemblages that were mainly composed of the algal genus *Feldmannia* (Connell et al., 2014). The algae were collected still attached to their natural substrate and acclimated in holding mesocosms at ambient conditions for thirty days before the experiment commenced. When allocated to experimental mesocosms, canopy algae were uniformly distributed across mesocosms ($n = 10$ individuals per each half of the tank), with their arrangement following a standardised pattern.

The response of turfs to the experimental treatments was quantified in terms of cover of algae that recruited and photosynthetic characteristics which indicate how much solar energy can be converted to fixed carbon and can be used to assess the influence of factors which may influence algal health (specifically EQY, MQY, rETR and ETR$_{max}$, discussed below). The recruitment of turfs was quantified by adding bare recruitment substrate (5 × 10 cm fibreboard panels) to the mesocosms at the commencement of the experimental period ($n = 5$ per mesocosm). The space available for recruitment was, therefore, consistent both where kelp were absent and present. Following 21 days of treatment, the percentage cover of turfs on each recruitment panel was quantified by visually estimating cover with the point-intercept method using a 5 × 10 cm array with 20 points (as described in Falkenberg et al., 2014). Photosynthetic parameters were measured using a submersible diving Pulse Amplitude Modulated (PAM) fluorometer (Walz, Germany). Algae were measured *in situ* in treatment mesocosms following 25 days of treatments. Fluorescence of the algae was measured predawn (between 0400 and 0700) and midday (between 1130 and 1530) to attain the MQY and EQY, respectively. Measures of quantum yield indicate the probability that the energy of a photon absorbed will be used for photosynthesis and can range from 0 (if the process does not respond to light) to 1 (if every photon absorbed contributes to the process); if the algae is stressed both the Effective and Maximum Quantum Yield values can be reduced. Measures were taken by using a spacer to hold the fibre optic probe of the PAM fluorometer ∼3 mm from the algal specimen and exposing it with an initial pulsed measuring beam of red light (0.15 µmol m^{-2} s^{-1}, 650 nm) immediately followed by a pulse of saturating actinic light (0.8 s, 6000 µmol m^{-2} s^{-1}). For both MQY and EQY a measure was taken from each replicate recruitment substrate ($n = 5$ per mesocosm, $n = 3$ mesocosms per treatment). In addition, Rapid Light Curves (RLCs) were measured using the photon flux densities of 0, 39, 72, 106, 152, 231, 320, 495 and 729 µmol m^{-2} s^{-1}, each of 10 s duration, followed by a saturating pulse of light. These measures were taken during daylight hours (between 1030 and 1500), from a subset of the replicate recruitment panels ($n = 3$ per mesocosm, $n = 3$ mesocosms per treatment). The RLCs were later used to calculate the ETR and ETR$_{max}$ as follows: ETR = PSII × PFD × leaf absorbance ×0.5 where PSII is the EQY, PFD is the provided photon flux density at the time and point of measurement, leaf absorbance factor is a constant of 0.84 (see Irving et al., 2004; Russell et al., 2011) and 0.5 is a constant assuming equal distribution of photons absorbed by the two photosystems (Beer et al., 2002). ETR, an approximation of the rate of electrons pumped through the photosynthetic chain, is closely related to photosynthetic activity. ETR$_{max}$ is the maximum value obtained at any of the nine irradiances measured and indicates the maximum photosynthetic capacity.

2.2.4. Statistical analysis

Four-factor PERMANOVA was used to test the response of mat-forming algae to experimental conditions in terms of percentage cover and photosynthetic characteristics (MQY, EQY and rETR$_{max}$). The factors of canopy cover, CO_2 and temperature were treated as fixed and orthogonal, with two levels in each factor (canopy, present vs. absent; CO_2, current vs. future; temperature, ambient vs. elevated) while the factor of tanks was treated as random and nested within canopy, CO_2 and temperature, and had three levels. Data for the replicate recruitment panels from each mesocosm were used as replicates ($n = 5$). The magnitude of effects (ω^2) was calculated (following Vaughn and Corballis, 1969; Graham and Edwards, 2001) to assess which factor, or combination of factors, primarily contributed to the responses under experimental treatments. Physico-chemical conditions within mesocosms were analysed using one-way ANOVAs in which the factor being analysed had two levels; the factor of canopy cover (present vs. absent) was used to test the light conditions, the factor of CO_2 (current vs. future) was used to test the carbonate conditions and the factor of temperature (ambient vs. elevated) was used to test the temperature conditions. Measurements were averaged across sampling occasions ($n = 1$ for light, $n = 8$ for carbonate conditions and temperature), with mesocosms used as replicates ($n = 3$). Where significant treatment effects were detected, we then ran Student–Newman–Keuls (SNK) post hoc comparison of means.
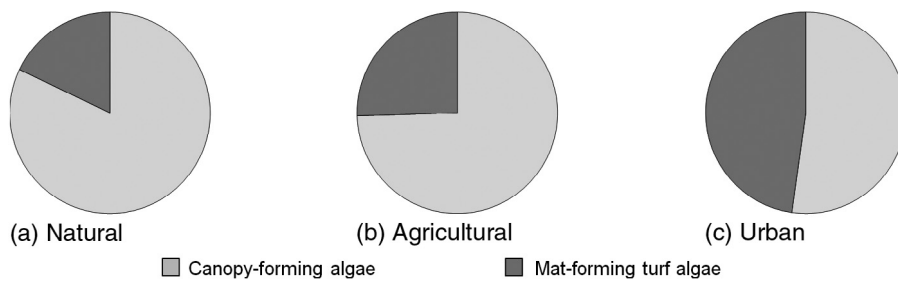
Fig. 1. Proportion of patches with canopy forming algae (light grey) or mat-forming turf algae (dark grey) in catchments classified as (a) natural, (b) agricultural or (c) urban.
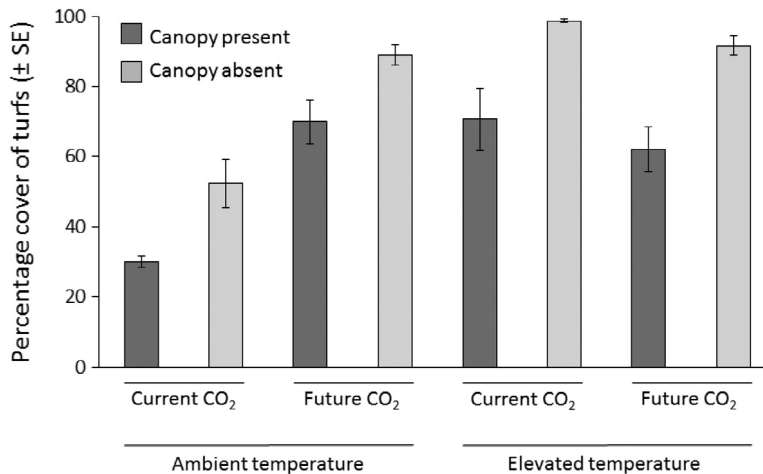

Fig. 2. The percentage cover (%± SE) of mat-forming turf algae that recruited to initially unoccupied substratum under manipulated canopy (present vs. absent), CO_2 (current vs. future) and temperature (ambient vs. elevated).

3. Results

3.1. Quantifying the localised impact of current human populations

Catchment type had a significant influence on the distribution of both canopy- and mat-forming algae (Fig. 1). There was a trend for more patches of canopy, and fewer patches of turfs, in natural catchments. The proportion of canopy algae was slightly less in agricultural catchments, with more turfs. Finally, in urban catchments there was again less canopy algae and more turfs, with the proportion of these two algal types almost the same.

3.2. Forecasting the effects of global change

The presence of an algal canopy restricted the recruitment of turfs under all CO_2 and temperature combinations, with canopy presence or absence the treatment of largest influence ($\omega^2 = 0.41$; Fig. 2; Table S1). The difference in turf cover between where canopy algae was present and absent was similar for each set of treatment conditions, with a reduction of approximately 25% (Fig. 2). In both the presence and absence of algal canopy CO_2 and temperature caused an increase in the cover of turfs. This manifested as an interaction whereby the effect of combined CO_2 and temperature did not increase the cover above that observed where either condition was enriched in isolation, probably as covers approached 100% (Fig. 2; Table S1).

The Maximum Quantum Yield (MQY) and Effective Quantum Yield (EQY) of recruited turfs were both greater where canopy was present than where it was absent for all combinations of CO_2 and temperature treatments (Fig. 3; Table S2). The difference between the EQY (measured at midday sunlight) of turfs in the presence and absence of canopy was much greater than the difference observed in MQY (measured at night) (Fig. 3). The ETR_{max} of turfs was lower in the presence of canopy compared to where it was absent (Fig. 4; Table S3), with a trend for the ETR_{max} to occur at a lower photon flux density for turfs in the presence of canopy algae ($152 \, \mu mol \, m^{-2} \, s^{-1}$) than in the absence of canopy algae ($231 \, \mu mol \, m^{-2} \, s^{-1}$) (Fig. 4).
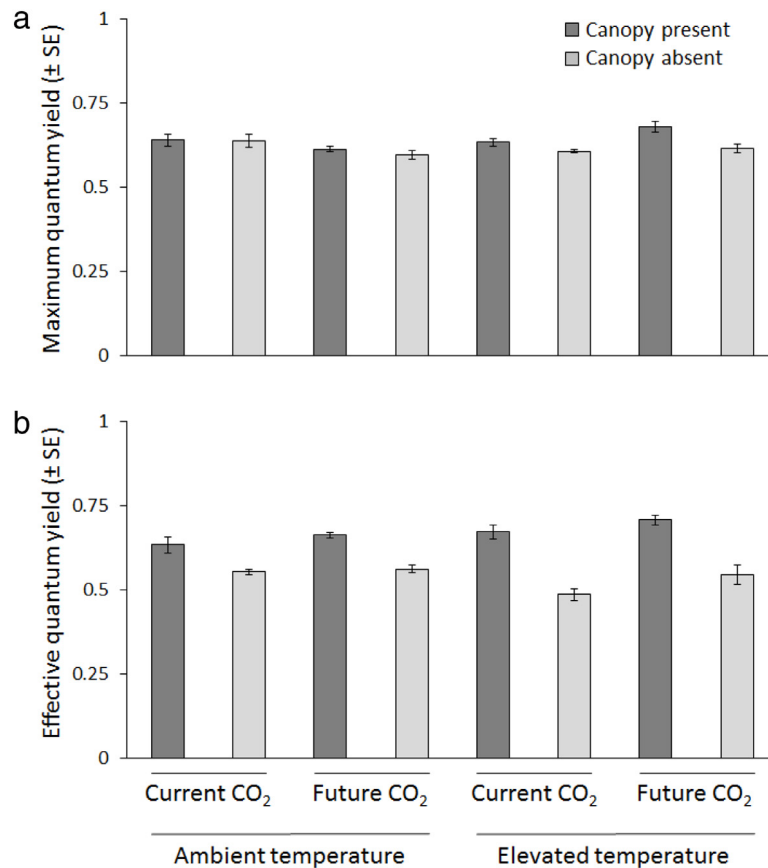
Fig. 3. The (a) maximum quantum yield ($\pm$SE) and (b) effective quantum yield ($\pm$SE) of mat-forming turf algae that recruited to initially unoccupied substratum under manipulated canopy (present vs. absent), CO_2 (current vs. future) and temperature (ambient vs. elevated).

Fig. 4. Rapid light curves (RLCs) of electron transport rate (μmol electrons m^{-2} s^{-1}) ($\pm$SE) for mat-forming turf algae that recruited to initially unoccupied substratum under manipulated canopy (present vs. absent), $CO_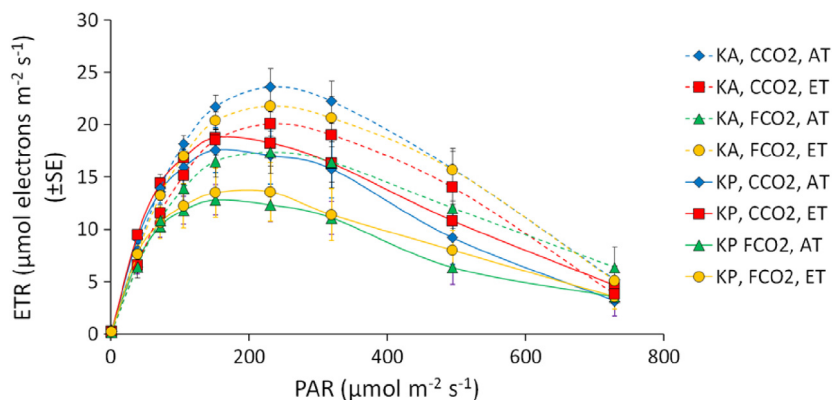2$ (current vs. future) and temperature (ambient vs. elevated). KP, kelp present; KA, kelp absent; CCO_2, current CO_2; FCO_2, future CO_2; AT, ambient temperature; ET, elevated temperature.

4. Discussion

The balance among key interacting species, such as foundation species and their competitors, contributes to determining resistance to change and maintenance of ecosystem structure. As functional groups are differentially affected by human-driven change in environmental conditions, this balance is likely to become increasingly disrupted, potentially prompting ecosystem shifts (reviewed in Folke et al., 2004, Harley et al., 2006, Scheffer et al., 2001). Previous studies have suggested in the system considered here, shifts may occur from algal canopies to mats of turf under altered environmental conditions

(reviewed in Falkenberg et al., 2010, Russell and Connell, 2012). Here, we show that there are currently sparser canopies and more expansive turf mats on coasts of intense human use. This pattern of occurrence in 'urban' areas may set the conditions for the greater influence of climate change through the expansion of turfs under elevated CO_2 and warming (e.g. Connell and Russell, 2010). In contrast, canopies are still present along coastlines of less intense human use and they may suppress turfs and mitigate some of the effects of modified conditions. Targeted management to retain or reintroduce algal canopies before global change manifests could, therefore, be an important approach to enhance resistance and facilitate the persistence of these otherwise vulnerable habitats.

That habitats occur as mosaics is frequently emphasised as a characteristic of coastal ecology (e.g. Connell and Irving, 2008, Paine and Levin, 1981, Sousa, 1984). It has been proposed, however, that human activities can modify the relative occurrence and patchiness of the alternative habitats. Such change has been observed for a variety of habitats, including the shift from corals to macroalgae (McCook et al., 2007), 'constitutional' seagrass species to 'non-constitutional' species (Montefalcone et al., 2007) and saltmarshes to mangroves (Saintilan and Williams, 1999). Similar patterns can be found in systems historically dominated by algal canopies. On the Mediterranean coastline, for example, low-shore rocky habitats are often dominated by the canopy algae *Cystoseria*. The canopies of these algae are, however, frequently replaced by assemblages of turfs and mussels; a change attributed to their proximity to urban areas (Benedetti-Cecchi et al., 2001). Similarly, in the South Australian system considered here, evidence is accumulating to suggest that areas of algal forests near human populations are being replaced by algal mats (Connell et al., 2008; Gorgula and Connell, 2004; Gorman et al., 2009). Our results provide additional insight into the relative proportions of these habitats associated with catchments characterised by different patterns of human use. Specifically, our results indicate that in habitats near natural catchments there was a trend for a greater proportion of canopy and a lesser proportion of turfs than were observed in coastal habitats adjacent to urban catchments. While there was more canopy than turf algae in both natural and agricultural catchments, in urban catchments the relative proportions of these algae (and their size distributions) were about the same. While we did not explicitly assess the mechanism underlying the observed change in this study, it has previously been shown that elevated nutrient inputs to marine systems associated with human land-use can be associated with the phase-shift from canopy to turf (examples can be drawn from South Australia, Gorman et al., 2009, Connell et al., 2008; Baltic Sea, Worm et al., 1999; North Sea, Eriksson et al., 2002; Mediterranean Sea, Rodriguez-Prieto and Polo, 1996).

Ecosystem structure may be further modified in the future, as global conditions could release certain functional groups, but not others, from the limitations that they currently experience. Specifically, enriched CO_2 and increased temperature can lead to the expansion of algal mats, with greater covers observed where either condition is manipulated in isolation from the other, potentially enabling turf expansion and replacement of canopies (this study, Connell and Russell, 2010, Russell et al., 2009). Enriched CO_2 has been proposed to influence primary productivity via increased carbon availability and enhanced photosynthetic rates (reviewed in Connell et al., 2013, Hepburn et al., 2011, Low-Décarie et al., 2014). Increased productivity and growth in algal turfs under enriched CO_2 conditions may reflect increased photosynthetic rates either because: (1) more CO_2 is available for passive diffusion (release from limitation), or, (2) these algae can switch from the use of carbon concentrating mechanisms to passive diffusion, thus reducing the metabolic costs of photosynthesis (Falkenberg et al., 2013b; Raven et al., 2011). Similarly, increased temperature also drove greater covers of turfs. Such patterns align with the natural history of this system; that is, the taxa that form these algal mats are typically ephemeral, rapidly expanding to occupy available space in the warm summer months (Connell and Russell, 2010; Russell and Connell, 2005). It is increasingly being recognised, however, that the combination of enriched CO_2 and increased temperatures can facilitate the expansion of turf at greater rates (e.g. Connell and Russell, 2010). Both enriched CO_2 and increased temperature could, therefore, drive the expansion of turf algae in the future by enhancing their productivity and growth.

Although forecasted environmental conditions are anticipated to facilitate turfs and increase the probability of loss of foundation species, biotic interactions may modify these direct effects and enhance system resistance. The current study suggests that where canopies are retained, their presence may constrain the expansion of turfs despite the otherwise strong effects of enriched CO_2 and increased temperature. While there are a number of mechanisms by which canopies can influence turf cover, we suggest a disproportionately strong mechanism centres on reduction of photosynthetic rates in turfs. That canopies influence understory algae via shading is an explanation derived from classical experiments showing the effects of canopy-shade on understorey communities (Reed and Foster, 1984) and covers of turfs (Connell, 2005; Russell, 2007). Here, we identified that the presence of a kelp canopy reduced light available to turfs by ∼70% (∼125 μmol m^{-2} s^{-1} outside canopy vs. ∼40 μmol m^{-2} s^{-1} under canopy), driving greater maximum Electron Transport Rate (ETR$_{max}$) of turfs outside canopy compared to the turfs which occurred under the canopy. Further, the ETR$_{max}$ of turfs in the absence of a canopy was observed at higher light intensities than for those turfs where canopy was present. These differences in ETR are expected to be related to photosynthetic activity if it had been measured by oxygen evolution or CO_2 uptake (Beer, 1989; Ralph and Gademann, 2005), and are consistent with adaptation to shaded conditions by understorey species (Lüder et al., 2002; Watanabe et al., 1992). In contrast, the Effective Quantum Yield (EQY) of turfs was higher where canopy was present than where it was absent. We suggest that this reduction of EQY in the absence of canopy is a manifestation of greater photoinhibition due to greater light intensities. Importantly, the similarity of Maximum Quantum Yield (MQY) of turfs inside and outside canopies indicates that while there may be a short-term effect of altered light condition (as reflected in the EQY), there was no long-term change or damage to the photosynthetic apparatus of the algae. That is, recovery of MQY under all experimental conditions indicates there was no damage of PSII, but rather transient, reversible down-regulation of photosynthetic efficiencies, which can be considered a mechanism of photoprotection (Bischof et al., 2000). Therefore,

while there appeared to be photoinhibition of turfs outside kelp canopies under the higher light intensities they maintained greater productivity, allowing them to expand more rapidly than turfs under canopies.

Ecosystems may resist future environmental change via the strengthening of key species interactions (Connell and Ghedini, 2015; Ghedini et al., 2015). Indeed, there is increasing evidence that canopies can limit the expansion of turf algae under a range of modified conditions (i.e. increased nutrients, Gorman et al., 2009; nutrients × CO_2, Falkenberg et al., 2012; temperature × CO_2, this study). This effect reflects the strength of canopy–understory interactions (Connell, 2005; Russell, 2007) that influence competitors, even under modified local and global conditions. Therefore, where key species are able to persist, their strong competitive interactions may enhance community stability and resistance to disturbance (Falkenberg et al., 2012). Habitat-forming species often structure communities by suppressing their competitors (Grime, 1998; Stachowicz, 2001), but in circumstances of their decline a dramatic shift in community structure can occur as competitive interactions are disrupted and previously restricted species expand (Connell et al., 2013; Pickett and White, 1985). Similar results have been shown where key consumers are either retained within, or removed from, ecosystems. In this system, the presence of gastropod grazers has been shown to continue to restrict the occurrence of turf algae under forecasted conditions (Falkenberg et al., 2014; Ghedini et al., 2015) where physiological limits are not exceeded (Mertens et al., in press). The persistence of key species will, therefore, be crucial for determining the effect of change at both local and global scales. In this system, maintaining the mechanism that enables the continued dominance of canopies over turfs will be dependent on the presence of the foundation species that mediate this mechanism. It appears that in this system, it will be important to manage the effects associated with local human populations (such as nutrient-rich discharges) so that canopies are present within a system when global change manifests. Where key species are less able to persist due to locally modified conditions, however, their occurrence may be positively managed. Examples from other systems reveal such strategies could include the implementation of MPAs that manage the direct and indirect effects of kelp loss (Gianni et al., 2013; Shears and Babcock, 2002) or reintroduced through active intervention (Campbell et al., 2014). Indeed, the power of local management may have been under-estimated in its ability to reduce the effects of global change (but see Falkenberg et al., 2013a, Ghedini et al., 2013).

In conclusion, we emphasise the potential for species interactions to modify the impacts of accelerating environmental changes that accumulate across scales from local urbanisation to global CO_2 enrichment and warming. Current patterns of urbanisation are associated with the loss of algal forests and the expansion of structurally simple algal mats. Where strong interactions are retained, however, they may modify the effect of global change. In particular, our experiments reveal that where foundation species, such as kelp, are retained, they continue to modify environmental conditions such that their persistence is favoured even under conditions that would otherwise be expected to facilitate their loss (e.g. enriched CO_2, increased temperature) (Wernberg et al., 2010; Johnson et al., 2011; Falkenberg et al., 2012). These results indicate that management towards maintaining or re-establishing populations of foundation species may limit ecosystem decline under large-scale global change. Local management therefore has the potential to enhance resistance to a largely unmanageable global-scale problem.

Acknowledgements

Appendix A. Supplementary data

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.gecco.2015.10.003.

References

Airoldi, L., Balata, D., Beck, M.W., 2008. The gray zone: relationships between habitat loss and marine diversity and their applications in conservation. J. Exp. Mar. Biol. Ecol. 366, 8–15.

Airoldi, L., Beck, M.W., 2007. Loss, status and trends for coastal marine habitats of Europe. Oceanogr. Mar. Biol. Annu. Rev. 45, 345–405.

Beer, S., 1989. Photosynthesis and photorespiration of marine angiosperms. Aquat. Bot. 34, 153–166.

Beer, S., Bjork, M., Hellblom, F., Axelsson, L., 2002. Inorganic carbon utilization in marine angiosperms (seagrasses). Funct. Plant Biol. 29, 349–354.

Benedetti-Cecchi, L., Pannacciulli, F., Bulleri, F., Moschella, P.S., Airoldi, L., Relini, G., Cinelli, F., 2001. Predicting the consequences of anthropogenic disturbance: large-scale effects of loss of canopy algae on rocky shores. Mar. Ecol. Prog. Ser. 214, 137–150.

Bischof, K., Hanelt, D., Wiencke, C., 2000. Effects of ultraviolet radiation on photosynthesis and related enzyme reactions of marine macroalgae. Planta 211, 555–562.

Bruno, J.F., Bertness, M.D., 2001. Habitat modification and facilitation in benthic marine communities. In: Bertness, M.D., Gaines, S.D., Hay, M.E. (Eds.), Marine Community Ecology. Sinauer, Sunderland, pp. 201–218.

Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Inclusion of facilitation into ecological theory. Trends Ecol. Evolut. 18, 119–125.

Campbell, A.H., Marzinelli, E.M., Vergés, A., Coleman, M.A., Steinberg, P.D., 2014. Towards restoration of missing underwater forests. PLoS One 9, e84106.

Connell, S.D., 2005. Assembly and maintenance of subtidal habitat heterogeneity: synergistic effects of light penetration and sedimentation. Mar. Ecol. Prog. Ser. 289, 53–61.

Connell, S.D., Foster, M.S., Airoldi, L., 2014. What are algal turfs? Towards a better description of turfs. Mar. Ecol. Prog. Ser. 495, 299–307.

Connell, S.D., Ghedini, G., 2015. Resisting regime-shifts: the stabilising effect of compensatory processes. Trends Ecol. Evol. 30, 513–515.

Connell, S.D., Irving, A.D., 2008. Integrating ecology with biogeography using landscape characteristics: a case study of subtidal habitat across continental Australia. J. Biogeography 35, 1608–1621.

Connell, S.D., Kroeker, K.J., Fabricius, K.E., Kline, D.I., Russell, B.D., 2013. The other ocean acidification problem: CO_2 as a resource among competitors for ecosystem dominance. Philos. Trans. R. Soc. B 368.

Connell, S.D., Russell, B.D., 2010. The direct effects of increasing CO_2 and temperature on non-calcifying organisms: increasing the potential for phase shifts in kelp forests. Proc. R. Soc. B 277, 1409–1415.

Connell, S.D., Russell, B.D., Turner, D.J., et al., 2008. Recovering a lost baseline: missing kelp forests from a metropolitan coast. Mar. Ecol. Prog. Ser. 360, 63–72.

Dayton, P.K., 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. In: Parker, B.C. (Ed.), Proceedings of the Colloquium on Conservation Problems in Antarctica. Allen Press, Lawrence, KS.

DEWNR (Department of Environment, Water and Natural Resources) 2014. Nature Maps. South Australia, Government of South Australia.

Dickson, A.G., Millero, F.J., 1987. A comparison of the equilibrium constants for the dissociation of carbonic acid in seawater media. Deep Sea Res. Part A 34, 1733–1743.

Dudgeon, S.R., Aronson, R.B., Bruno, J.F., Precht, W.F., 2010. Phase shifts and stable states on coral reefs. Mar. Ecol. Prog. Ser. 413, 201–216.

Ellis, E.C., 2011. Anthropogenic transformation of the terrestrial biosphere. Phil. Trans. R. Soc. A 369, 1010–1035.

Ellison, A.M., Bank, M.S., Clinton, B.D., et al., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Front. Ecol. Environ. 3, 479–486.

Eriksson, B.K., Johansson, G., Snoeijs, P., 2002. Long-term changes in the macroalgal vegetation of the inner Gullmar Fjord, Swedish Skagerrak coast. J. Phycol. 38, 284–296.

Falkenberg, L.J., Burnell, O.W., Connell, S.D., Russell, B.D., 2010. Sustainability in near-shore marine systems: promoting natural resilience. Sustainability 2, 2593–2600.

Falkenberg, L.J., Connell, S.D., Russell, B.D., 2013a. Disrupting the effects of synergies between stressors: improved water quality dampens the effects of future CO_2 on a marine habitat. J. Appl. Ecol. 50, 51–58.

Falkenberg, L.J., Connell, S.D., Russell, B.D., 2014. Herbivory mediates the expansion of an algal habitat under nutrient and CO_2 enrichment. Mar. Ecol. Prog. Ser. 497, 87–92.

Falkenberg, L.J., Russell, B.D., Connell, S.D., 2012. Stability of strong species interactions resist the synergistic effects of local and global pollution in kelp forests. PLoS One 7, e33841.

Falkenberg, L.J., Russell, B.D., Connell, S.D., 2013b. Contrasting resource limitations of marine primary producers: implications for competitive interactions under enriched CO_2 and nutrient regimes. Oecologia 172, 575–583.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L, Holling, C.S., 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annu. Rev. Ecol. Evol. Syst. 35, 557–581.

Ghedini, G., Russell, B.D., Connell, S.D., 2013. Managing local coastal stressors to reduce the ecological effects of Ocean acidification and warming. Water 5, 1653–1661.

Ghedini, G., Russell, B.D., Connell, S.D., 2015. Trophic compensation reinforces resistance: herbivory absorbs the increasing effects of multiple disturbances. Ecol. Lett. 18, 182–187.

Gianni, F., Bartolini, F., Airoldi, L., et al., 2013. Conservation and restoration of marine forests in the Mediterranean Sea and the potential role of Marine Protected Areas. Adv. Oceanogr. Limnol. 4, 83–101.

Gorgula, S.K., Connell, S.D., 2004. Expansive covers of turf-forming algae on human-dominated coast: the relative effects of increasing nutrient and sediment loads. Mar. Biol. 145, 613–619.

Gorman, D., Russell, B.D., Connell, S.D., 2009. Land-to-sea connectivity: linking human-derived terrestrial subsidies to subtidal habitat change on open rocky coasts. Ecol. Appl. 19, 1114–1126.

Graham, M.H., Edwards, M.S., 2001. Statistical significance versus fit: estimating the importance of individual factors in ecological analysis of variance. Oikos 93, 505–513.

Grime, J., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J. Ecol. 86, 902–910.

Halpern, B.S., Silliman, B.R., Olden, J.D., Bruno, J.P., Bertness, M.D., 2007. Incorporating positive interactions in aquatic restoration and conservation. Front. Ecol. Environ. 5, 153–160.

Harley, C.D.G., Hughes, A.R., Hultgren, K.M., et al., 2006. The impacts of climate change in coastal marine systems. Ecol. Lett. 9, 228–241.

Hepburn, C.D., Pritchard, D.W., Cornwall, C.E., Mcleod, R.J., Beardall, J., Raven, J.A., Hurd, C.L., 2011. Diversity of carbon use strategies in a kelp forest community: implications for a high CO_2 ocean. Global Change Biol. 17, 2488–2497.

Hobbs, R.J., Arico, S., Aronson, J., et al., 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. Glob. Ecol. Biogeogr. 15, 1–7.

Irving, A.D., Connell, S.D., Elsdon, T.S., 2004. Effects of kelp canopies on bleaching and photosynthetic activity of encrusting coralline algae. J. Exp. Mar. Biol. Ecol. 310, 1–12.

Johnson, C.R., Banks, S.C., Barrett, N.S., Cazassus, F., Dunstan, P.K., Edgar, G.J., Frusher, S.D., Gardner, C., Haddon, M., Helidoniotis, F., Hill, K.L., Holbrook, N.J., Hosie, G.W., Last, P.R., Ling, S.D., Melbourne-Thomas, J., Miller, K., Pecl, G.T., Richardon, A.J., Ridgway, K.R., Rintoul, S.R., Ritz, D.A., Ross, D.J., Sanderson, J.C., Shepard, S.A., Slotwinski, A., Swadling, K.M., Taw, N., 2011. Climate change cascades: shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. J. Exp. Mar. Biol. Ecol. 400, 17–32.

Jones, C.G., Lawton, J.H., Shachak, M., 1996. Organisms as ecosystem engineers. In: Ecosystem Management. Springer, pp. 130–147.

Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78, 1946–1957.

Lawton, J.H., 1994. What do species do in ecosystems? Oikos 367–374.

Low-Décarie, E., Fussmann, G.F., Bell, G., 2014. Aquatic primary production in a high-CO_2 world. Trends Ecol. Evolut. 29, 223–232.

Lüder, U.H., Wiencke, C., Knoetzel, J., 2002. Acclimation of photosynthesis and pigments during and after six months of darkness in *Palmaria decipens* (Rhodophyta): A study to simulate Antarctic winter sea ice cover. J. Phycol. 38, 904–913.

McCook, L.J., Folke, C., Hughes, T.P., Nystrom, M., Obura, D., Salm, R., 2007. Ecological resilience, climate change and the Great Barrier Reef. In: Johnson, J.E., Marshall, P.A. (Eds.), Climate Change and the Great Barrier Reef. Great Barrier Reef Marine Park Authority and Australian Greenhouse Office, Townsville, pp. 75–96.

Meehl, G.A., Stocker, T.F., Collins, W.D., Friedlingstein, P., Gaye, A.T., Gregory, J.M., Kitoh, A., Knutti, R., Murphy, J.M., Noda, A., Raper, S.C.B., Watterson, I.G., Weaver, A.J., Zhao, Z.-C., 2007. Global climate projections. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom, New York, USA.

Mehrbach, C., Culberson, C.H., Hawley, J.E., Pytkowicz, R.M., 1973. Measurement of the apparent dissociation constants of carbonic acid in seawater at atmospheric pressure. Limnol. Oceanogr. 18, 897–907.

Mertens, N.L., Russell, B.D., Connell, S.D., Escaping herbivory: ocean warming as a refuge for primary producers where consumer metabolism and consumption cannot pursue. Oecologia, http://dx.doi.org/10.1007/s00442-015-3438-8.

Montefalcone, M., Morri, C., Peirano, A., Albertelli, G., Bianchi, C., 2007. Substitution and phase shift within the *Posidonia oceanica* seagrass meadows of NW Mediterranean Sea. Estuar. Coast. Shelf Sci. 75, 63–71.

Paine, R.T., Levin, S.A., 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecol. Monograph 51, 145–178.

Pickett, S.T.A., White, P.S., 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, San Diego.

Pierrot, D., Lewis, E., Wallace, D.W.R., 2006. MS Excel program developed for CO_2 system calculations. ORNL/CDIAC-105a, Oak Ridge, Tennessee, Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US Department of Energy.

Ralph, P.J., Gademann, R., 2005. Rapid light curves: a powerful tool to assess photosynthetic activity. Aquat. Bot. 82, 222–237.

L.J. Falkenberg et al. / Global Ecology and Conservation 4 (2015) 549–558

Raven, J., Giordano, M., Beardall, J., Maberly, S., 2011. Algal and aquatic plant carbon concentrating mechanisms in relation to environmental change. Photosynth. Res. 109, 281–296.

Raven, J.A., Hurd, C.L., 2012. Ecophysiology of photosynthesis in macroalgae. Photosynth. Res. 113, 105–125.

Reed, D.C., Foster, M.S., 1984. The effects of canopy shading on algal recruitment and growth in a giant kelp forest. Ecology 65, 937–948.

Rodriguez-Prieto, C., Polo, L., 1996. Effects of sewage pollution in the structure and dynamics of the community of *Cystoseria mediterranea* (Fucales, Phaeophyceae). Sci. Mar. 60, 253–263.

Russell, B.D., 2007. Effects of canopy-mediated abrasion and water flow on the early colonisation of turf-forming algae. Mar. Freshw. Res. 58, 657–665.

Russell, B.D., Connell, S.D., 2005. A novel interaction between nutrients and grazers alters relative dominance of marine habitats. Mar. Ecol. Prog. Ser. 289, 5–11.

Russell, B.D., Connell, S.D., 2012. Origins and consequences of global and local stressors: incorporating climatic and non-climatic phenomena that buffer or accelerate ecological change. Mar. Biol. 159, 2633–2639.

Russell, B.D., Passarelli, C.A., Connell, S.D., 2011. Forecasted CO_2 modifies the influence of light in shaping subtidal habitat. J. Phycol. 47, 744–752.

Russell, B.D., Thompson, J.I., Falkenberg, L.J., Connell, S.D., 2009. Synergistic effects of climate change and local stressors: CO_2 and nutrient-driven change in subtidal rocky habitats. Global Change Biol. 15, 2153–2162.

Saintilan, N., Williams, R.J., 1999. Mangrove transgression into saltmarsh environments in south-east Australia. Glob. Ecol. Biogeogr. 8, 117–124.

Sasaki, T., Lauenroth, W.K., 2011. Dominant species, rather than diversity, regulates temporal stability of plant communities. Oecologia 166, 761–768.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. Nature 413, 591–596.

Shears, N.T., Babcock, R.C., 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. Oecologia 132, 131–142.

Sousa, W.P., 1984. Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of succession. Ecology 1918–1935.

Stachowicz, J.J., 2001. Mutualism, facilitation, and the structure of ecological communities. Bioscience 51, 235–246.

Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.A., Tegner, M.J., 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. Environ. Conserv. 29, 436–459.

Vaughn, G.M., Corballis, M.C., 1969. Beyond tests of significance: estimating strength of effects in selected ANOVA designs. Psychol. Bull. 72, 204–213.

Watanabe, J.M., Phillips, R.E., Allen, N.H., Anderson, W.A., 1992. Physiological response of the stipitate understory kelp, *Pterygophora californica* Ruprecht, to shading by the giant kelp, *Macrocystis pyrifera* C. Agardh. J. Exp. Mar. Biol. Ecol. 159, 237–252.

Wernberg, T., Thomsen, M.S., Tuya, F., Kendrick, G.A., Staehr, P.A., Toohey, B.D., 2010. Decreasing resilience of kelp beds along a latitudinal temperature gradient: potential implications for a warmer future. Ecol. Lett. 13, 685–694.

Worm, B., Lotze, H.K., Bostroem, C., Engkvist, R., Labanauskas, V., Sommer, U., 1999. Marine diversity shift linked to interactions among grazers, nutrients and propagule banks. Mar. Ecol. Prog. Ser. 185, 309–314.