

Climate-driven disparities among ecological interactions threaten kelp forest persistence

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Abstract

The combination of ocean warming and acidification brings an uncertain future to kelp forests that occupy the warmest parts of their range. These forests are not only subject to the direct negative effects of ocean climate change, but also to a combination of unknown indirect effects associated with changing ecological landscapes. Here, we used mesocosm experiments to test the direct effects of ocean warming and acidification on kelp biomass and photosynthetic health, as well as climate-driven disparities in indirect effects involving key consumers (urchins and rock lobsters) and competitors (algal turf). Elevated water temperature directly reduced kelp biomass, while their turf-forming competitors expanded in response to ocean acidification and declining kelp canopy. Elevated temperatures also increased growth of urchins and, concurrently, the rate at which they thinned kelp canopy. Rock lobsters, which are renowned for keeping urchin populations in check, indirectly intensified negative pressures on kelp by reducing their consumption of urchins in response to elevated temperature. Overall, these results suggest that kelp forests situated towards the low-latitude margins of their distribution will need to adapt to ocean warming in order to persist in the future. What is less certain is how such adaptation in kelps can occur in the face of intensifying consumptive (via ocean warming) and competitive (via ocean acidification) pressures that affect key ecological interactions associated with their persistence. If such indirect effects counter adaptation to changing climate, they may erode the stability of kelp forests and increase the probability of regime shifts from complex habitat-forming species to more simple habitats dominated by algal turfs.

Keywords: acidification, kelp, kelp forests, ocean climate change, ocean warming, temperate reefs, trophic interactions

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Introduction

Increasing emissions of carbon dioxide into the atmosphere are changing the strength of trophic and competitive interactions in the ocean via warming and acidification (Hoegh-Guldberg & Bruno, 2010; Wernberg *et al.*, 2011a; Nagelkerken & Connell, 2015). A major challenge is to assess how such change to these interactions (e.g. predation, grazing and competition) drives structural and functional changes of communities beyond species-specific responses (Bates *et al.*, 2014). Of particular concern is whether the changing strength of such interactions will resist (Connell & Ghedini, 2015; Ghedini *et al.*, 2015) or increase the risk of regime shifts from complex habitat-forming species to

less complex habitats (Johnson *et al.*, 2011; Wernberg *et al.*, 2011a,b; Connell *et al.*, 2013; Vergés *et al.*, 2014).

The influence of ocean warming and acidification on individual species and species interactions depends on the magnitude of environmental change and the characteristics of the species involved (Gooding *et al.*, 2009; Poore *et al.*, 2013) and their adaptive capacity (Hofmann *et al.*, 2014). Increasing temperatures generally enhance growth and metabolic activity and, consequently, the feeding rates of marine species, until a thermal maximum is reached, beyond which negative impacts are observed (Kordas *et al.*, 2011; Lemoine & Burkepille, 2012). Ocean acidification can also impact species differently depending on their physiological and morphological characteristics (Hendriks *et al.*, 2010; Branch *et al.*, 2013). For example, organisms that use calcium to create hard structures, such as shells, may be affected by a reduction in carbonate availability

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associated with ocean acidification (Orr *et al.*, 2005; Bijma *et al.*, 2013). In contrast, species that utilize carbon for growth (e.g. algal turfs) may benefit from the increasing carbon resources as oceans acidify (Connell & Russell, 2010; Connell *et al.*, 2013).

Kelp forests are important temperate marine habitats that have already been impacted by ocean climate change near the low-latitude margins of their distributions (Serisawa *et al.*, 2004; Wernberg *et al.*, 2010; Tuya *et al.*, 2012; Raybaud *et al.*, 2013; Voerman *et al.*, 2013). Impacts of ocean climate change on kelp forests usually result in a reduction of their complex canopies, which support high species richness, biomass and productivity (Steneck & Johnson, 2014). Prior to observations of kelp forest degradation via the direct effects of ocean climate change, it is possible that changes to supporting interactions of kelp resistance and resilience are also impacted (e.g. predation, grazing and competition) (Wernberg *et al.*, 2010). For example, where ocean climate change in trophically structured kelp forests drives a decrease in predation intensity (e.g. large fish and crustaceans), it may indirectly cause increases in grazing sea urchins (Shears & Babcock, 2002) that lead to loss of kelp canopy (see review of urchin induced regime shifts by Filbee-Dexter & Scheibling, 2014).

Once removed, kelp canopies are often replaced by urchin barrens or algal turfs, depending on a suite of ecological and environmental factors (Steneck & Johnson, 2014). While kelp forests and urchin barrens may switch between alternate states (Ling & Johnson, 2009; Steneck *et al.*, 2013), a change from kelp forests to algal turfs may be more difficult to reverse (Connell & Russell, 2010; Steneck & Johnson, 2014). Dense algal turfs compete with kelp recruits for space and the sediment trapped within turfs further inhibits kelp recruitment (Gorman & Connell, 2009). Because turfs can take advantage of increased carbon availability and grow faster in warmer water, there is growing concern that ocean warming and acidification will further enhance the competitive advantage of algal turfs over kelps (Connell *et al.*, 2013).

Here, we investigated the effects of ocean warming and acidification on key ecological interactions influencing *Ecklonia radiata* kelp forests on the east coast of Australia, focusing on the warmest part of their distribution (~30°S). At these latitudes, there are few large urchin barrens, with mosaics of kelp forests and algal turfs dominating inshore reefs. We investigated key trophic interactions involving the long-spined sea urchin (*Centrostephanus rodgersii*), a dominant kelp herbivore capable of complete canopy removal, and one of their major predators, the eastern rock lobster (*Sagmariasus verreauxi*) (Byrne & Andrew, 2013). We also examined how algal turfs might be affected by ocean climate

change as a potential inhibitor of kelp recolonization following deforestation (Gorman & Connell, 2009). Using a series of manipulative experiments, we aimed to unravel the impacts of predicted future ocean conditions on direct and indirect interactions among these key rocky reef organisms and infer potential consequences for the ongoing persistence of kelp forests towards their low-latitude margins of distribution.

Materials and methods

Experimental system

To test hypotheses about the influence of ocean temperature and acidification on kelp-related ecological interactions, four experiments were carried out with increasing trophic complexity. Specifically, we tested whether warmer sea water and increased $p\text{CO}_2$ affected the biomass and photosynthetic health of kelp (*E. radiata*), the growth of algal turfs, the change in biomass of long-spined sea urchins (*C. rodgersii*) and the predation rate of eastern rock lobsters (*S. verreauxi*) on urchins.

The experiments were undertaken in twelve, 1100 L circular, fibreglass, outdoor mesocosms (1.35 m diameter \times 0.9 m high) at the National Marine Science Centre (NMSC) in Coffs Harbour (30.3022°S, 153.1189°E), Australia. The study area was a subtropical/temperate transition zone and at the low-latitude margins of the major species under investigation (*E. radiata*, *C. rodgersii* and *S. verreauxi*). The experiments had two orthogonal factors: *warming* (two levels: current [~ 22 °C] and future [~ 25 °C]) and *acidification* (ambient [$\text{pH}_{\text{NIST}} = \sim 8.12$, $p\text{CO}_2 = \sim 450$ μtam] and future [$\text{pH}_{\text{NIST}} = \sim 7.87$, $p\text{CO}_2 = \sim 900$ μtam]) (see Table S1 for further details). The upper temperature was just within the thermal range where *E. radiata* can persist on the east coast of Australia, with 23 °C being the average summer temperature at its low-latitude limit in southern Queensland (<http://www.metoc.gov.au>). Furthermore, a decrease in pH of ~ 0.25 and an increase in ocean temperature of ~ 3 °C approximates changes predicted by the RCP 8.5 climate model for 2081–2100 (Ciais *et al.*, 2013; Collins *et al.*, 2013), as well as a change in ocean temperature that could constitute a marine heat wave (Wernberg *et al.*, 2013b; Hobday *et al.*, 2016).

Sea water was pumped from the adjacent ocean into the NMSC flow-through aquarium system and filtered at 50 μm prior to entering mesocosms at 3 L min^{-1} . Water temperature was manipulated using heater chiller units (Aquahort Ltd, Omana Beach, New Zealand). To manipulate pH, CO_2 -enriched air was created using a gas mixer (PEGAS 4000MF) and bubbled through water in the CO_2 -enriched mesocosms, while the water in the control mesocosms was bubbled with ambient air. Sea water conditions in the outdoor mesocosms, situated under shade cloth, exhibited diurnal cycles with water temperature varying by <1 °C and pH_{NIST} varying by 0.24 (~ 470 μtam) over a 24-h cycle. The large daily changes in pH were related to photosynthesis and respiration of the kelp, with minimum and maximum pHs being record in the early

morning and afternoon, respectively. These fluctuations in pH, which occur in natural kelp forests (Cornwall *et al.*, 2013), contributed to the relative high $p\text{CO}_2$ ($\sim 450 \mu\text{atm}$) recorded for ambient conditions, as daily water quality monitoring of mesocosms almost always occurred in the morning. Importantly, as a constant supply of CO_2 -enriched air was used to simulate ocean acidification, the relative difference between ambient and future pH treatment was maintained throughout the diurnal cycle.

Water temperature, salinity, conductivity and pH were measured daily (Hach HQ40d multiprobe). Total alkalinity for the system was measured weekly using a potentiometric titration (888 Titrand, Metrohm, Herisau, Switzerland) of 40 μm filtered, Hg fixed water samples. Experimental $p\text{CO}_2$ was determined using CO2SYS (Pierrot *et al.*, 2006) with constants from Mehrbach *et al.* (1973), as adjusted by Dickson & Millero (1987). The average (\pm SE) measured and calculated sea water conditions for each treatment are presented in Table S1.

Four experiments were carried out with increasing trophic complexity (see Table 1 for summary of experiments). The first experiment ran for 20 days and tested the interaction strength between kelp (*E. radiata*) and algal turf. The second experiment introduced three individual herbivorous sea urchins (*C. rodgersii*) into each mesocosm, in addition to kelp and algal turf and ran for 22 days. The third experiment introduced a single eastern rock lobster (*S. verreauxi*) into each mesocosm in addition to urchins, kelp and algal turf, and ran for 14 days. The fourth experiment lasted for 23 days and included three kelp plants, a rock lobster (*S. verreauxi*) and four sea urchins (*C. rodgersii*) to assess the consumption rate of urchins by rock lobsters and the loss of individual kelp plants over a longer time period. The duration of experiments was determined by the time required for the cover of turf on at least one algal turf growth plate to be scored at or close to 100%. For the experiments involving rock lobsters, urchin densities were maintained by daily re-stocking. Individual kelp plants were also replaced when urchins grazed through their stipe or when plants broke free due to stipe rot (often associated with an urchin grazing scar). At the end of each experiment, the mesocosms were scrubbed clean of algal turfs and biofilms.

For experiments 1–3, each mesocosm contained eight algal turf growth plates and three kelp (*E. radiata*) plants, with four growth plates positioned directly under kelp canopy and four placed away from canopy. Each algal turf growth plate was a 10 \times 10 cm PVC tile that was roughened to facilitate turf settlement and growth. Prior to being placed in the mesocosms, algal turf growth plates were seeded by placing them in a shallow raceway supplied with flowthrough sea water for 1 week with algal turf covered rocks collected from local reefs. During the seeding period, the position of each algal turf growth plate in the raceway was changed randomly on daily basis. The algal turf that grew during the experiments was predominantly filamentous (< 1 cm in height).

Subadult kelp (*E. radiata*) plants, ~ 1 m in length (mean biomass \pm SE = 308.8 \pm 11.7 g), were collected from nearby reefs and added to the mesocosms. The holdfast of each kelp plant was cleaned before being attached to a plastic grid on

Table 1 Summary of the trophic levels present (P) in each experiment and the response variable measured (M)

Experiments undertaken	Trophic levels included			Response variables measured						
	Kelp	Algal turf	Urchins	Rock lobsters	Change in kelp biomass (g day^{-1})	Loss of individual kelp plants	Effective quantum yield of kelp	Percentage cover of algal turf	Growth of urchins (g day^{-1})	Urchin feeding (Urchins day^{-1})
1. K	P	P			M	M	M			
2. K + U3	P	P	P		M	M	M		M	
3. K + U3 + L	P	P	P	P	M	M	M		M	M
4. K + U4 + L	P	P*	P	P	M	M	M		M	M

K, kelp; U, urchin; L, rock lobster. The number after U indicates the number of urchins in each mesocosm and differentiates experiments 3 and 4.

*Algal turfs grew on sides and bottom of each mesocosm.

the bottom of the mesocosms using cable ties surrounded by soft silicone tubing. Sea urchins (*C. rodgersii*) (mean biomass \pm SE = 292.6 \pm 12.8 g) were collected from nearby reefs and were acclimatized in aquarium conditions for \sim 1 month prior to being included in experiments. Large rock lobsters (*S. verreauxi*) (mean biomass \pm SE = 2.24 \pm 0.03 kg) were collected by commercial fishermen near Coffs Harbour and acclimatized in aquarium conditions for at least 1 month prior to being used in experiments. During acclimation, sea urchins and rock lobsters were fed *ad libitum* with kelp and school whiting/squid tubes, respectively. The fresh weight of kelp, urchins and lobsters was determined prior to being added to mesocosms, and again when removed at the end of the experiment, by patting dry with paper towel and weighing. The cover of algal turf was determined using per cent cover estimates following the methods of Ghedini *et al.* (2015). Given the short-term nature of our multitrophic level experiments, we did not predict substantial changes in urchin tests or fecundity. As such these parameters were not measured. Furthermore, we did not observe urchin or lobsters spawning during any of our experiments.

The photosynthetic health of kelp was measured by effective quantum yield ($\Delta F/F_m'$) on day 9 and 16, on day 9, 16 and 23 and on day 14 of experiments 1, 2 and 3, respectively. Effective quantum yield was determined using a Pulse Amplitude Modulation Fluorometer (Diving-PAM, Walz, Effeltrich, Germany), where $\Delta F = F_m' - F_t$, F_m' is the maximal fluorescence, and F_t is the steady-state fluorescence under illumination at time, t (Genty *et al.*, 1989; van Kooten & Snel, 1990). Fluorescence was measured by holding the fibreoptic of the PAM fluorometer \sim 1 mm from the kelp (*in situ* in the mesocosm) using a leaf clip. The kelp surface was then exposed to a pulsed measuring beam of weak red light (0.15 $\mu\text{mol m}^{-2} \text{s}^{-1}$, 650 nm) to measure F_t . Once the signal was stabilized (\sim 5 s), a pulse of saturating light (\sim 6000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) was applied and F_m' was recorded. Measurements commenced in the early morning, just after sunrise, and were concluded in <2 h. Ten readings per individual kelp plant were recorded on haphazardly selected areas of secondary laminae. To ensure independence in analyses, individual readings were averaged to provide a mean value of $\Delta F/F_m'$ for each mesocosm.

Statistical analyses

Univariate permutational analysis of variance (PERMANOVA) (Anderson *et al.*, 2008) was used to test hypotheses about the influence of ocean warming and acidification on each response variable separately (summarized in Table 1). These analyses mostly involved two orthogonal factors (*temperature* and *acidification*), although analyses involving the cover of algal turf also had an additional crossed factor of *canopy* and a nested random factor of *mesocosm*. All PERMANOVA analyses used Euclidean distances on untransformed data, with the exception of algal turf covers that were *arcsin* transformed to reduce variance heterogeneity (Underwood, 1997). Following this, all data used in PERMANOVA analyses did not exhibit heterogeneous dispersions (PERMDISP routine, $P > 0.05$ for all analyses, Anderson & Walsh, 2013). Full details of PERMANOVA analyses are reported in Tables S2–S5.

Results

Kelp biomass and photosynthetic yield

There was no evidence for interactions (antagonistic, synergistic or additive) between the effects of ocean warming and acidification on changes in kelp biomass (Exp. 1: kelp only (K): $F_{1,8} = 0.68$, $P = 0.47$; Exp. 2: kelp and urchins (K+U3): $F_{1,8} = 0.06$, $P = 0.82$; Exp. 3: kelp, urchins and rock lobsters (K+U3+L): $F_{1,8} = 2.01$, $P = 0.19$; Table S2). There were, however, significant effects of ocean warming with greater kelp biomass being lost at 25 °C than at 22 °C in experiments 1–3 (Fig. 1, Table S2). The loss of kelp biomass was enhanced when urchins were included in experiments (Table 2). Rather than just grazing kelp fronds, urchins detached entire kelp plants by grazing the stipe just above the holdfast or facilitating stipe rot in their grazing scars. When totalled across all experiments with urchins, there was a significantly greater loss of individual kelp plants at 25 °C than at 22 °C ($p\text{-}F_{1,8} = 1.42$, $P < 0.01$, Table S2).

Although higher water temperatures exacerbated loss of kelp biomass, there was no such influence of ocean acidification (K: $F_{1,8} = 1.15$, $P = 0.31$; K+U3: $F_{1,8} = 0.04$, $P = 0.86$; K+U3 + R: $F_{1,8} = 2.91$, $P = 0.10$, Table S2). Furthermore, neither ocean warming nor ocean acidification directly or interactively affected the effective quantum yield of kelp in any of the experiments ($P > 0.05$ for all analyses, Table S3).

Algal turf coverage

Algal turf coverage did not significantly interact among ocean warming, acidification or canopy position ($P > 0.09$ for all tests, Table S4). Algal turf coverage was, however, on average, 14.6% greater in acidified than in ambient conditions across all experiments (Fig. 1), although the difference was only significant in Experiment 2 with kelp and urchins (Fig. 1, Table S4). For all experiments that measured algal turf coverage, there was less algal turf cover under kelp canopy than away from it (Fig. 1). This was supported by significant main effects for experiments 1 and 3 (Fig. 1, Table S4). Although there was on average 38% more algal turf cover away from than under kelp canopy in Experiment 2 (Fig. 1), an anomalous result from one mesocosm caused a significant canopy \times mesocosm interaction ($F_{8,72} = 3.9$, $P < 0.05$, Table S4).

Urchin growth

There were no interactive effects of ocean warming and acidification on the growth of the sea urchin, *C. rodgersii*

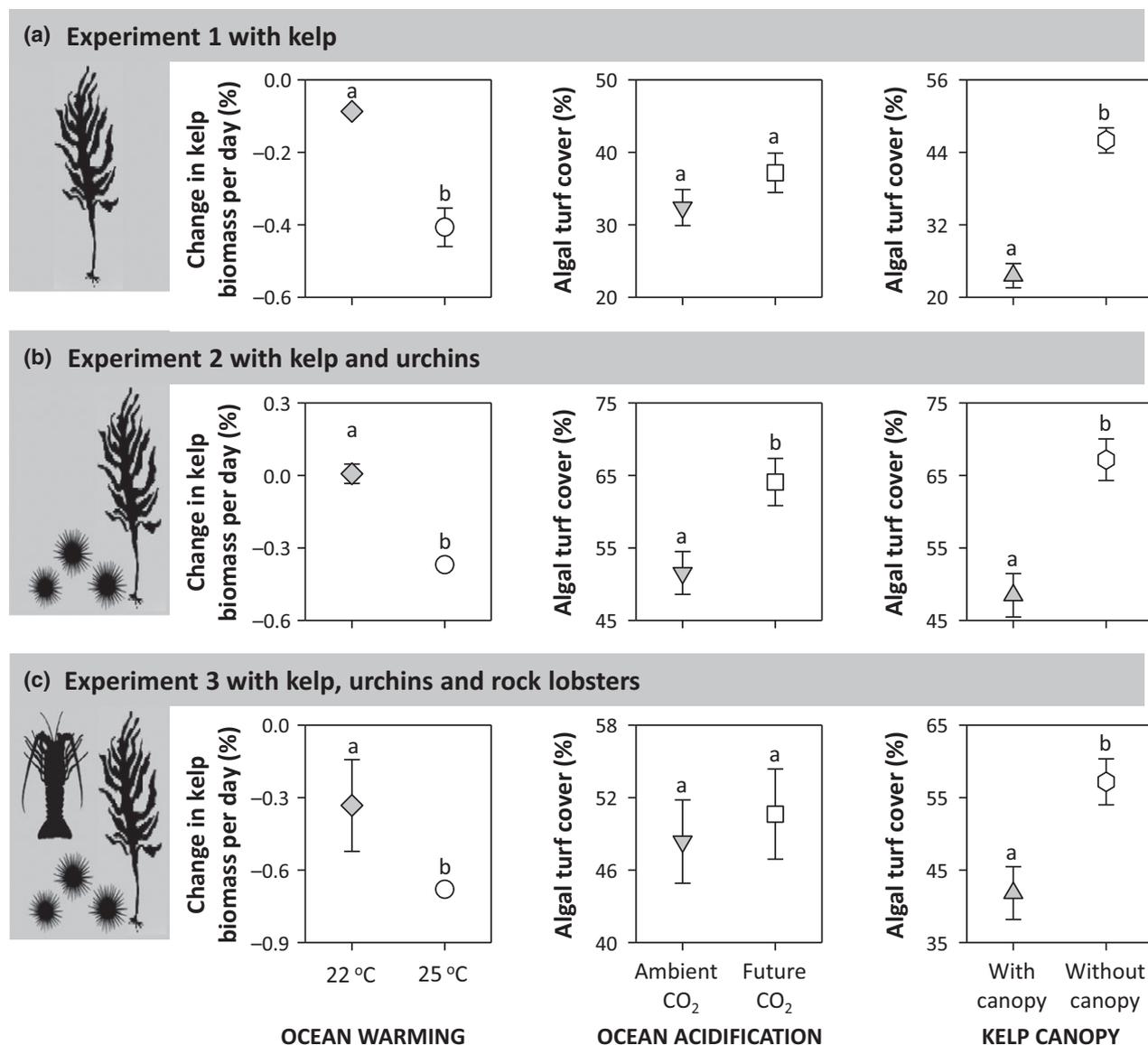


Fig. 1 Effects of ocean warming, acidification and kelp canopy on the biomass of kelp and the cover of algal turf. Results are summarized across (a) Experiment 1 with kelp and algal turf, (b) Experiment 2 with kelp, algal turf and urchins and (c) Experiment 3 with kelp, algal turf, urchins and lobsters. Points represent the means (\pm SE) of the main effects, as there were no significant ocean warming by acidification interactions. Treatments are denoted by \diamond = 22 °C, \circ = 25 °C, ∇ = ambient $p\text{CO}_2$, \square = future $p\text{CO}_2$, \triangle = with canopy and \circ = without canopy. Different letters indicate significant difference at $P < 0.05$.

(K+U3: $F_{1,8} = 1.5$, $P = 0.25$, Table S5). These urchins did, however, grow significantly faster at higher temperatures than at lower temperatures (K+U3: $F_{1,8} = 10.04$, $P < 0.05$, Table S5), although their growth rate was not influenced by ocean acidification (K+U3: $F_{1,8} = 0.75$, $P = 0.47$, Table S5).

Consumption of urchins by rock lobsters

There were no interactive effects of ocean warming and acidification on the consumption rate of urchins by

rock lobsters in Experiment 3 (K+U3+L: $F_{1,8} = 0.044$, $P = 0.87$) or Experiment 4 (K+U4+L: $F_{1,8} = 0.004$, $P = 0.93$), although there were strong effects of temperature alone (Fig. 2, Table S5). On average (\pm SE), rock lobsters ate $\sim 50\%$ fewer sea urchins per day at 25 °C (K+U3+L: 0.23 ± 0.08 ; K+U4+L: 0.18 ± 0.07) than at 22 °C (K+U3+L: 0.50 ± 0.14 ; K+U4+L: 0.44 ± 0.07) (Fig. 2, Table S5). While the effect size was similar in both experiments, this effect was only significant in Experiment 4 (Fig. 2, Table S5). A major contributing factor to this was variation caused by a single rock

Table 2 Summary of individual kelp plants detached from just above the holdfast during the experiments

Treatment	Experiment 1 (K)	Experiment 2 (K + U3)	Experiment 3 (K + U3 + L)	Experiment 4 (K + U4 + L)	Total
22 °C and ambient CO ₂	0	1	0	1	2
25 °C and ambient CO ₂	0	5	0	5	10
22 °C and future CO ₂	0	2	0	2	4
25 °C and future CO ₂	0	4	2	6	12

K, kelp; U, urchin; L, rock lobster. The number after U indicates the number of urchins in each mesocosm and differentiates experiments 3 and 4. U3: mesocosms with 3 urchins, U4: mesocosms with 4 urchins.

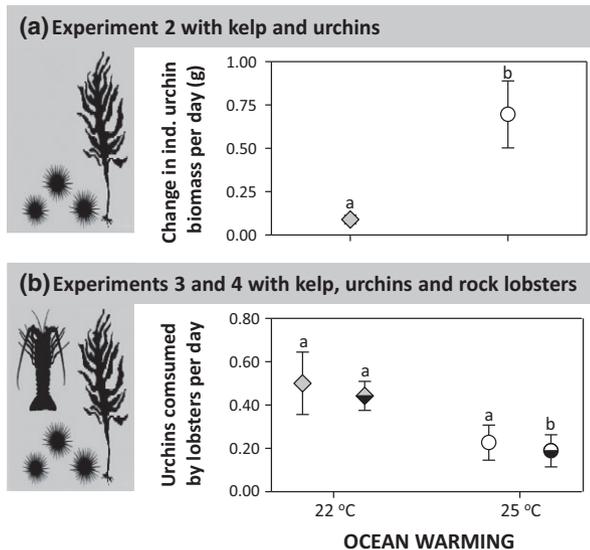


Fig. 2 Effects of ocean warming and acidification on the change in (a) urchin biomass in Experiment 2 with kelp, algal turf and urchins and (b) the consumption of urchins by lobsters in experiments 3 and 4 with kelp, algal turf, urchins and lobsters. Points represent the means (\pm SE) of the main effects, as there were no significant ocean warming by acidification interactions. Treatments are denoted by \diamond = 22 °C and \circ = 25 °C. Half black symbols indicate results of Experiment 4. Different letters indicate significant differences at $P < 0.05$.

lobster at 22 °C in Experiment 3 that only consumed two urchins throughout the 14-day experiment, whereas the other rock lobsters ate 5–16 urchins at the lower temperature. The consumption of urchins by rock lobsters was not significantly influenced by ocean acidification in either experiment (K+U3+L: $F_{1,8} = 1.416$, $P = 0.27$, K+U4+L: $F_{1,8} = 0.004$, $P = 0.95$, Table S5).

Discussion

As oceans warm and acidify in the near future, kelp forests towards their low-latitude distributional margins may face a combination of increasing direct

physiological stress and changing indirect effects via their consumers and competitors. The loss of kelp biomass associated with elevated water temperatures in our experiments was anticipated, as this direct effect has been comprehensively reviewed (Steneck & Johnson, 2014). In the case of *E. radiata*, the direct negative effects of elevated water temperature include reduced physiological performance (Staehr & Wernberg, 2009), productivity (Wernberg *et al.*, 2010) and supply/survival of recruits (Andrews *et al.*, 2014). While the mechanisms of temperature-driven loss of kelp forests are known (e.g. Wernberg *et al.*, 2013a,b), our study takes the next step by demonstrating that the negative impacts of ocean warming and acidification on kelp forests may be further exacerbated by changes to the performance of dominant grazers (urchins), their predators (rock lobsters) and a key competitor (algal turfs) within key ecological interactions that affect the stability of kelp forests.

Alterations to trophic interactions via warming (Sanford, 1999; O'Connor, 2009) may drive change to the structure and function of marine ecosystems (reviewed by Harley *et al.*, 2012; Nagelkerken & Connell, 2015). In kelp forests, such change is of particular concern when a reduction of consumption at higher trophic levels releases pressure on consumers and, in this case, indirectly increases herbivory on kelp. Here, rock lobsters reduced their consumption of urchins at elevated temperatures, while urchins increased growth rate (and presumably grazing rate) and their kelp canopy thinning capacity (by directly grazing through stipes or stimulating stipe rot) in response to ocean warming. On average, rock lobsters consumed ~50% fewer urchins at 25 °C than at 22 °C. As the low-latitude distribution of eastern rock lobsters (*S. verreauxi*) is similar to that of kelp (*E. radiata*) on the Australian east coast, it is possible that rock lobsters in the warmer treatments may have exceeded their thermal optimum resulting in a reduction in performance (Pörtner, 2010). Indeed, a closely related species (*Jasus lalandii*) exhibits reduced gut fullness at low-latitude sites compared to cooler sites situated ~2 degrees of latitude further south (Mayfield *et al.*, 2000). Beyond, or even before, their thermal

optimum, many invertebrates reduce metabolic activity and consume less food as a short-term protective mechanism (Lemoine & Burkepile, 2012; Russell *et al.*, 2013). The resulting reduced top-down pressure from rock lobsters at 25 °C potentially leads to larger populations of urchins and, therefore, has indirect trophic consequences for kelp forests (Shears & Babcock, 2002; Baum & Worm, 2009). When considering the direct impact of ocean warming on kelp and the temperature-driven disparities in the trophic performance of urchins and rock lobsters, our results suggest that kelp forests may not only have to adapt to the physiological stress of rising ocean temperatures, but they will have to do it in shifting ecological landscapes where the relative strengths of key trophic interactions are also responding to the changing environmental conditions.

The type of habitat that replaces kelp beds after deforestation has important consequences for kelp recovery. For example, the mechanisms that underpin regime shifts to urchin barrens and back to kelp forests have been well described (e.g. Johnson *et al.*, 2011; Estes *et al.*, 2013; Steneck *et al.*, 2013), while it is thought that regime shifts from kelp forests to algal turfs may be more discontinuous (Steneck & Johnson, 2014). Certainly, the multiplicative effects of climate change, eutrophication, invasive species and disease make it more difficult to predict the new alternate stable state following a major kelp decline, with the losses of *E. radiata* sometimes resulting in the formation of urchin barrens (Johnson *et al.*, 2011) and other times algal turfs (Connell *et al.*, 2008; Wernberg *et al.*, 2013a,b). Although urchin densities in our mesocosms were at the upper limit for inshore reefs off Coffs Harbour, urchin grazing did not prevent the rapid (<14–20 days) development of a lush cover of algal turf. This matches field observations that large urchin barrens are rare on inshore reefs at the low-latitude margin of *E. radiata* distribution on the east coast of Australia (i.e. north of Coffs Harbour). Furthermore, the environmental conditions that drive regime shifts from kelp forests to algal turfs will be increasingly common, with ocean warming, acidification and eutrophication all favouring algal turf formation (Russell *et al.*, 2009; Connell & Russell, 2010; Wernberg *et al.*, 2013a,b). Once established, algal turfs and associated trapped sediment strongly inhibit settlement and survival of kelp recruits (Connell & Russell, 2010), generating the hypothesis that such regime shifts can be a hysteresis where reverting to the original state requires more than removal of the altered conditions (Steneck & Johnson, 2014).

While kelp plants were not directly influenced by ocean acidification, algal turf coverage increased in response to elevated CO₂ concentrations, creating an ecological disparity favouring algal turf. Unlike algal

turfs, *E. radiata* may not be limited by carbon availability at current pCO₂ due to its ability to use bicarbonate as a carbon source (Connell *et al.*, 2013). In contrast, algal turfs may benefit from additional CO₂ in the water column (c.f. kelp vs. algal turf; Falkenberg *et al.*, 2013) because of their reliance on passive CO₂ diffusion to obtain carbon (Hepburn *et al.*, 2011). Where kelp canopies remain intact, they can suppress the expansion of turfs in acidifying oceans (Falkenberg *et al.*, 2012); a premise strongly supported by our experimental results (i.e. significantly less algal turf under canopy). However, processes that cause kelp forests to thin or fragment (e.g. storms, grazing pressure or heat waves) allow for local increases in resources (e.g. light and sediment) that combine to drive turf expansion (Russell, 2007; Wernberg *et al.*, 2013a,b; Bennett *et al.*, 2015), which will be accelerated by global increases in CO₂ and warmer oceans (Connell & Russell, 2010).

A key challenge for mesocosm experiments testing hypotheses about ocean climate change is evaluating their value for predicting changes in natural communities (Wernberg *et al.*, 2013a). Field-based evidence to corroborate our experimental results comes from comparing reefs off Coffs Harbour where the study organisms were collected. Here, reefs around offshore islands (~11 km from the coast) experience water temperatures on average 1 °C warmer than inshore reefs due to the East Australian Current (Malcolm *et al.*, 2011). As predicted from our experiments, offshore island reefs have an extremely sparse kelp cover (<0.5% offshore vs. ~65% inshore; Harriott *et al.*, 1994) and much higher densities of urchins (*C. rodgersii* mean density at 10 m is ~2.7 per m² offshore vs. <0.05 per m² inshore; Posthuma-Grbic, 2007) compared to inshore reefs. Similar patterns have been shown by Franco *et al.* (2015) using reefs in regions with ~1–2 °C difference in water temperature on the coast of Portugal. As well as less kelp, the reefs in warmer locations of Portugal had 140 times greater abundances of sea urchins than in cooler locations. As predicted from our study, their grazing assays showed ~50 times higher rates of kelp biomass consumption in the warmer locations (Franco *et al.*, 2015). In contrast to the single species of urchin used in our experiments, kelp biomass consumption will likely occur from a diverse grazer assemblage, including herbivorous fish that are key drivers of the tropicalization of temperate reefs (Vergés *et al.*, 2014; Bennett *et al.*, 2015). Importantly, our experiments demonstrate that consumer pressure was influenced by ocean warming independently of ocean acidification. There is, therefore, potential to generalize our results with field experiments at different latitudes (e.g. Franco *et al.*, 2015) or using ocean temperature

anomalies (e.g. marine heatwaves, Wernberg *et al.*, 2013a,b; Bennett *et al.*, 2015).

Overall, our experiments suggest that that future ocean conditions may affect kelp forests at the warmest part of their range both directly and indirectly (via a changing ecological landscape). The long-term stability of kelp forests varies regionally with a suite of mechanisms that underpin resistance (Ghedini *et al.*, 2015) or resilience to change (Steneck & Johnson, 2014). Kelps in low-latitude regions may be subject to change in the strength of trophic and competitive interactions that indirectly reduce the integrity of forests and their ability to recover from loss. If kelp is to persist at these low latitudes, it will also need to adapt such that its physiology and growth are not suppressed by elevated temperatures. Although there is potential for variation in the thermal tolerance of kelp (*E. radiata*) gametophytes to provide a pathway for adaptation to warmer waters (Mohring *et al.*, 2014), poleward shifts will continue in regions where warming outpaces such adaptation (Wernberg *et al.*, 2011b). In combination, therefore, kelp forests not only face the direct negative effects of warming, but also an apparent increase in consumer pressure (via ocean warming) and space competition (via ocean acidification) caused by climate-driven disparities in key ecological interactions. If these indirect effects promote increasingly challenging conditions for kelp to adapt to ocean climate change at low-latitude margins, they may accelerate regime shifts towards reefs dominated by less complex habitats (e.g. algal turfs).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. The average measured and calculated seawater conditions in the mesocosms.

Table S2. PERMANOVA analyses of changes in the biomass of kelp per day for Experiment 1 with kelp only, Experiment 2 with urchins and kelp and Experiment 3 with rock lobsters, urchins and kelp.

Table S3. PERMANOVA analyses of the effective quantum yield ($\Delta F/F'_m$) of kelp for Experiment 1 with kelp only, Experiment 2 with urchins and kelp and Experiment 3 with rock lobsters, urchins and kelp.

Table S4. PERMANOVA analyses of the percentage cover of algal turf for Experiment 1 with kelp only, Experiment 2 with urchins and kelp and Experiment 3 with rock lobsters, urchins and kelp.

Table S5. PERMANOVA analyses for changes in the biomass of urchins in Experiment 2, as well as differences in the daily consumption rate of urchins by rock lobsters in Experiment 3 and Experiment 4.