

## LETTER

# Decreasing resilience of kelp beds along a latitudinal temperature gradient: potential implications for a warmer future

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### Abstract

Successful mitigation of negative effects of global warming will depend on understanding the link between physiological and ecological responses of key species. We show that while metabolic adjustment may assist Australasian kelp beds to persist and maintain abundance in warmer waters, it also reduces the physiological responsiveness of kelps to perturbation, and suppresses canopy recovery from disturbances by reducing the ecological performance of kelp recruits. This provides a warning not to rely solely on inventories of distribution and abundance to evaluate ecosystem function. The erosion of resilience is mediated by a shift in adult-juvenile interactions from competitive under cool to facilitative under warm conditions, supporting the prediction that positive interactions may become increasingly important in a warmer future. Kelp beds may remain intact but with a lower threshold for where additional impacts (e.g., extreme storms or reduced water quality) will lead to persistent loss of habitat and ecological function.

### Keywords

Climate change, comparative experimental approach, disturbance and recovery, ecological function, human impacts, linking physiology and ecology, ocean temperature, stress, threshold.

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## INTRODUCTION

Marine habitats such as coral reefs, seagrass meadows and kelp beds, are socially and economically important, and their ecosystem services are estimated to be worth trillions of dollars to the global economy each year (Costanza *et al.* 1997). Human impacts in marine habitats have resulted in widespread environmental degradation (Jackson *et al.* 2001; Pandolfi *et al.* 2003; Lotze *et al.* 2006). Historically, habitat loss, as a consequence of destructive fishing, disease, land reclamation and reduced water quality, has been a leading cause of loss of biodiversity and ecosystem services (Lotze *et al.* 2006; Airoidi & Beck 2007). Global warming is an additional, more recent threat to marine habitats (Hughes *et al.* 2003; Harley *et al.* 2006; Lotze *et al.* 2006; Orth *et al.* 2006; Poloczanska *et al.* 2007; Hawkins *et al.* 2008).

Foundation species control communities and ecological processes by modifying the environment and resources of other organisms. Ecological theory predicts that global warming will increase the importance of foundation species in maintaining ecosystem function because they can ameliorate environmental stress (Bruno *et al.* 2003; Halpern *et al.* 2007). Successful mitigation of negative effects of global warming, for example, through targeted conservation or rehabilitation efforts, will therefore depend critically on understanding how foundation species (i.e., corals and other suspension feeding invertebrates, seagrasses and kelps) respond to elevated temperatures in combination with other concurrent perturbations (Harley *et al.* 2006; Poloczanska *et al.* 2007). A rapidly growing body of observational evidence clearly documents the broad effects of climate change on global biota, but it provides little or no information on the synergistic effects of multiple concurrent

changes that are likely to produce complex interactive responses (Harley *et al.* 2006; Hawkins *et al.* 2008). Evidence for how global warming might affect ecological processes is particularly scant in marine habitats (Richardson & Poloczanska 2008) and, because of the challenges of controlling temperature in subtidal environments, experiments are mostly confined to laboratory studies and small-scale intertidal manipulations (e.g., Moore *et al.* 2007; Russell *et al.* 2009). The comparative experimental approach, where identical experiments are conducted simultaneously in regions with different temperature regimes, has been advocated as an alternative for field-based studies (Menge *et al.* 2002; Osovitz & Hofmann 2007).

Kelp beds are a dominant feature of temperate waters in both hemispheres (Steneck *et al.* 2002). Kelps are cool-water species and elevated temperatures are stressful for them (e.g., Kirkman 1984). The abundance of kelp is therefore expected to decrease as ocean temperature increase towards their tolerance limit (Brown 1984). Like other organisms, kelps have a capacity to undergo metabolic or structural changes (acclimatize) to adjust their physiological performance in response to seasonal variation in temperature (Davison 1991) and similar metabolic adjustments may, at least partially, offset physiological constraints of chronically warm environments (Stähr & Wernberg 2009). Identifying the nature and magnitude of potential ecological costs of metabolic and structural change is key to understanding the impacts of climate change on the distribution of organisms and ecological function (Clarke 2003; Osovitz & Hofmann 2007; Edmunds & Gates 2008).

Storms are a major cause of physical disturbance and localized canopy loss in most kelp beds (e.g., Dayton & Tegner 1984). When the canopy is lost, there are profound changes to local environmental conditions (Wernberg *et al.* 2005; Irving & Connell 2006). In order for the canopy to regenerate, either existing recruits must acclimatize to the new canopy-free conditions and grow, or new recruits must establish (Graham 1997; Toohey & Kendrick 2007). These recovery processes will become increasingly important to the maintenance of kelp beds, and preserving their ecological function, if climate change causes storm intensity to increase as predicted (Harley *et al.* 2006; IPCC 2007).

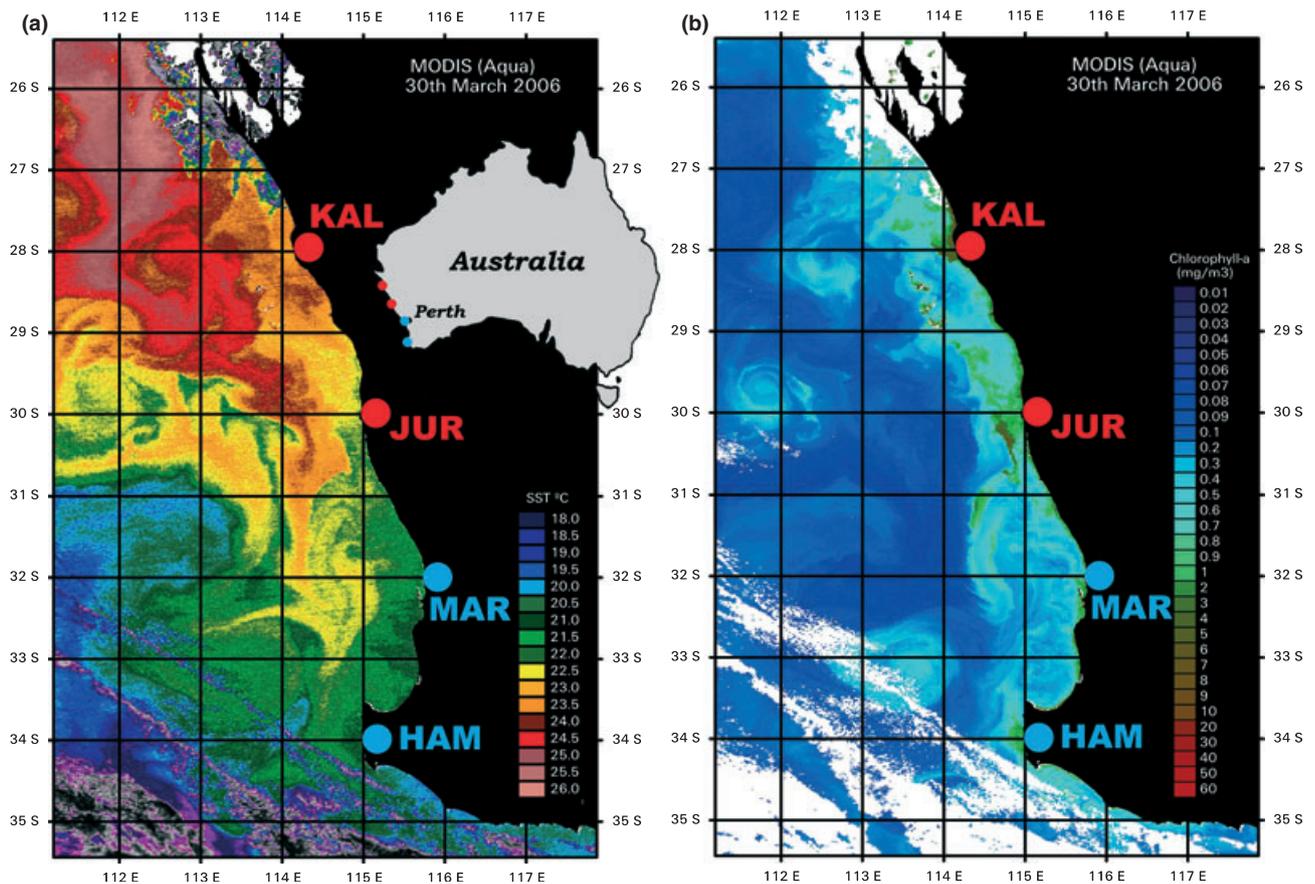
In temperate marine ecosystems, gradients in ocean temperature often co-vary with upwelling of nutrient-rich water or consumer pressure, making it difficult to draw unambiguous conclusions about the influence of temperature (e.g., Dayton & Tegner 1984). However, the coastal waters of the southwest coast of Australia are lacking major upwelling zones (Pearce 1991) and strong grazing pressure (molluscs: Wernberg *et al.* 2008; fish and urchins: Vanderklift *et al.* 2009), and the region is characterized by an increase in ocean temperature from south to north (Smale & Wernberg 2009), and consistently low nutrient levels

( $[\text{NO}_x + \text{NH}_x] < 2.2 \mu\text{M}$ ; Keesing *et al.* 2006; Lourey *et al.* 2006) (Fig. 1). We took advantage of these unique oceanographic conditions to experimentally assess the links between physiological and ecological performance of a southern hemisphere kelp and the cost of living in a warming ocean climate. We tested the hypotheses that: (1) the abundance of kelp decreases towards its northern (warm) distribution limit, (2) a reduction in the temperature sensitivity of metabolic processes assists kelps in maintaining physiological performance in warmer temperature regimes, (3) this metabolic adjustment to temperature regimes reduces the capacity to respond physiologically to perturbations such as disturbances of different intensity and (4) temperature regime and intensity of disturbance interact to negatively affect the recruitment and growth of kelps, and the subsequent post-disturbance recovery of the kelp bed. We show that while metabolic adjustment underpins maintained kelp abundance across climate regimes, it reduces physiological responsiveness to perturbation and erodes the capacity for canopy regeneration (resilience) by reducing the ecological performance of kelp recruits.

## MATERIALS AND METHODS

### Environment

We studied subtidal rocky reefs within four regions of Western Australia (Fig. 1). These regions span a temperature gradient of 2–4 °C (Smale & Wernberg 2009; Table 1), which correspond to the range of predicted increases in ocean temperature for the region over the coming 25–50 years (Poloczanska *et al.* 2007). All reefs in this study were exposed to south-westerly swell, separated by > 1 km, and located at similar depths of 8–12 m with no differences in mean depth among regions (ANOVA, reef depth:  $F_{3,20} = 1.0$ ;  $P = 0.428$ ;  $n = 24$  reefs, six in each of four regions). Water temperature was measured *c.* 5 cm above the bottom at three reefs in each region (see below, Table 1, see also Figure S1 in Appendix S1). Water samples were collected immediately above the kelp canopy on three occasions (November 2006, March, June 2006) and the concentration of inorganic nitrogen ( $\text{NO}_2 + \text{NO}_3$ ) measured (samples were stored on ice immediately upon returning to the surface, and sent frozen for analysis by a commercial analytical laboratory). In concordance with the findings of the previous studies (Keesing *et al.* 2006; Lourey *et al.* 2006), nitrogen concentrations were low at all times (range *c.* 0.25–2  $\mu\text{M}$ , Figure S2), and there were no differences among regions at any of the sampling times (ANOVA,  $[\text{NO}_x]$ :  $F_{3,6} = 1.60$ ;  $P = 0.284$ ,  $n = 12$  reefs, three in each of four regions, see Table S2 in Appendix S2). Differences in light among regions due to latitude (5–10%) were small and masked by differences caused by variation in



**Figure 1** Satellite images of sea surface temperature (a, SST) and chlorophyll *a* (b, Chl *a*) in the waters off the coast of south-western Australia. The warm, southward flow of the Leeuwin Current is clearly visible from the SST (a). As indicated by the SST and Chl *a* (a commonly used proxy for nutrient conditions), there are no areas of upwelling or abrupt changes in temperature or nutrient concentrations (see Pearce 1991 for a general account of this pattern). Our surveys and experiments focused on four regions separated by  $\approx 2^\circ$  latitude ( $\approx 250$  km coastline): Kalbarri (KAL), Jurien Bay (JUR), Marmion (MAR) and Hamelin Bay (HAM). These four regions span a gradient in ocean temperature of  $2\text{--}4^\circ\text{C}$  (Smale & Wernberg 2009) where grazing pressure (Wernberg *et al.* 2008; Vanderklift *et al.* 2009) and nutrient concentrations (Keesing *et al.* 2006; Lourey *et al.* 2006) are consistently low (see also Figures S1 and S2). For the disturbance experiment (cf. Figure S3), the four regions were grouped into cool (blue) and warm (red) regions. (Satellite images courtesy of SeASAP Canarias).

the depth of individual reefs within each region ( $\approx 25\%$ ) (see calculations in Stæhr & Wernberg 2009). All reefs were dominated by a low canopy of the perennial kelp *Ecklonia radiata* (C. Ag.) J. Agardh, a ubiquitous foundation species that affects biodiversity and ecological functioning on most shallow reefs in temperate Australasia (e.g., Wernberg *et al.* 2005; Irving & Connell 2006). *Ecklonia radiata*, the only kelp in Western Australia, and probably the most ecologically important macroalga in temperate Australasia, is a predominantly southern hemisphere species that resembles common northern hemisphere kelps such as *Eisenia arborea* and *Laminaria digitata*.

### Kelp distribution

To test if the abundance of kelp decreases with increasing ocean temperature, we surveyed kelp canopy cover, kelp

biomass, and the density of juvenile kelp (=recruits) at 24 reefs extending towards the northern (warm) range limit for *E. radiata* in Western Australia [Kalbarri (KAL), Fig. 1]. As a result of the perennial life history of *E. radiata*, spatial patterns of abundance are likely to be consistent across seasons. Kelp canopy cover (relative distance of along 25 m transects,  $n = 10$  per reef) and canopy biomass (all plants harvested from  $0.25\text{ m}^2$  quadrats,  $n = 6$  per reef) were measured at six reefs within each region in November 2005. Canopy cover included monospecific *E. radiata* canopies and mixed fucalcan/kelp canopies of  $> 50\%$  *E. radiata*. Canopy biomass included *E. radiata* only. The density of kelp recruits (counts within  $3.14\text{ m}^2$  plots,  $n = 16$  per reef) was determined at three reefs within each region. Kelp recruits were defined as life stages 1 and 2 (simple lamina with no or only a few side laterals), and adults as stage 3 (complex thallus with multiple second and third order side

**Table 1** Ocean temperature and kelp canopy characteristics

Region	Temperature			Kelp canopy cover (% of reef)	Kelp biomass (kg fresh weight 0.25 m <sup>-2</sup> )	Kelp recruit density (sporophytes m <sup>-2</sup> )
	Annual mean, °C	Annual max, °C	Days > 19 °C			
Cool climate						
Hamelin Bay (34 S)	19.48 ± 0.03	21.93 ± 0.02	234 ± 3	70 ± 3.3	0.64 ± 0.10	12.2 ± 3.5
Marmion (32 S)	20.28 ± 0.02	23.69 ± 0.08	253 ± 2	67 ± 3.3	0.76 ± 0.07	7.7 ± 1.4
Warm climate						
Jurien Bay (30 S)	20.74 ± 0.03	24.23 ± 0.10	340 ± 4	67 ± 2.6	0.78 ± 0.12	6.0 ± 1.2
Kalbarri (28 S)	21.88 ± 0.03	24.29 ± 0.02	365 ± 0	77 ± 4.1	0.56 ± 0.10	5.2 ± 1.5

Water temperature, measured at the reef surface, and kelp canopy characteristics, within each of the four regions (mean ± SEM,  $n = 3$  reefs for temperature and kelp recruits, and  $n = 6$  reefs for kelp cover and biomass). The two southern and the two northern regions were grouped as cool and warm climate respectively, for the disturbance experiment (cf. Fig. 1, Figure S3). 19 °C is a threshold previously demonstrated to negatively affect the growth and productivity of *Ecklonia radiata* (Kirkman 1984). See Smale & Wernberg (2009) for a detailed description of the oceanographic climatology of the study regions.

laterals) (Kirkman 1981, 1984). Cover, biomass and density values were averaged for each reef.

### Metabolic adjustment

The presence and extent of metabolic adjustments to prevailing temperature regimes along the latitudinal gradient was tested by measuring oxygen metabolism (photosynthesis and respiration) at different experimental temperatures (10–30 °C) and irradiances (0–530  $\mu\text{E m}^{-2} \text{s}^{-1}$ ) of kelp tissues from 16 reefs (four per region). Further details on methods and additional results from these tests can be found in Stæhr & Wernberg (2009).

### Disturbance experiment

A field experiment with identical manipulations in each of the four regions, tested physiological responses to perturbation, and whether ocean climate would interact with increasing severity of perturbation to negatively affect the ecological performance of kelp recruits (recruitment, growth) and recovery of the adult canopy. The experiment mimicked the effects of increasing perturbation (e.g., canopy loss from storms) by manipulating the intensity of disturbance to the existing canopy (partial and complete canopy removal; Figure S3). Plots of partial [57.3% ± 1.6 SEM ( $n = 4$  regions) reduction in stipe density = moderate disturbance] and complete (100% reduction = severe disturbance) canopy removal were established on three reefs in each region (Figure S3). The difference in canopy density between these manipulations was large enough to cause a fourfold increase in sub-canopy light availability (Wernberg *et al.* 2005). Because of the depth of all reefs, it is unlikely that treatments also caused a marked increase in UV

exposure (Wood 1987). There were six plots of each disturbance intensity at all reefs; plot sizes were 2, 4 and 8 m diameter ( $n = 2$  of each). Initial analyses did not find any effects of extent of disturbance (plot size) on kelp recruitment and growth ( $P > 0.05$ ). Here, we were interested in the broad patterns between temperature regimes (represented by regions) and with the response to increased intensity of disturbance and, consequently, we averaged across clearing sizes (extent of disturbance) and replicates within a reef. Kelp recruits were collected from the 12 reefs (three in each region) where experimental disturbances were established and transplanted into the centre of each experimental plot: four recruits were attached to a 0.5 m piece of sisal rope by braiding their holdfasts into the twine of the rope, and secured to the bottom with cable ties around old kelp holdfasts. Across the four regions, a total of 576 kelp recruits were transplanted into the experimental disturbances. Transplants were collected again after 80 days and brought back for measurements of physiological performance and growth (described below).

The disturbance experiment was initiated in February 2006 and staggered in time across regions [first to last  $\approx$  1.5 month; order: Jurien Bay (JUR)-Hamelin Bay (HAM)-Marmion (MAR)-KAL]. Over the initial 80 days of the experiment, where recruitment and recruit growth were tested, differences in sea temperature were negligible between the two southern regions (HAM vs. MAR) and the two northern regions (JUR vs. KAL) respectively, whereas the difference between these two groups (HAM, MAR vs. JUR, KAL) was highly significant (ANOVA, temperature: ocean climate:  $F_{1,2} = 144.5$ ;  $P = 0.007$ ; Table S1). Consequently, HAM and MAR were grouped as 'cool' ocean climate (mean temperature over the initial 80 days: 20.2 °C ± 0.03 SEM,  $n = 2$  regions) and JUR and

KAL as 'warm' ocean climate ( $22.0\text{ }^{\circ}\text{C} \pm 0.10\text{ SEM}$ ,  $n = 2$  regions). Moreover, the prevalence of temperatures  $> 19\text{ }^{\circ}\text{C}$  (a threshold previously shown to negatively affect *E. radiata* growth and productivity, Kirkman 1984) suggest that substantial differences in chronic temperature exposure are captured in this cool/warm division (Table 1, Smale & Wernberg 2009), and it was therefore maintained for the analysis of long-term recovery. For growth, only reefs from the two 'extreme' regions (HAM and KAL) were included because climate-related growth responses could not be reliably assessed on recruits at MAR, where the apical ends of many transplants in complete clearings were damaged, presumably by sporadic grazing, which in our experience can happen occasionally at all locations. The omission of MAR and JUR did not affect the overall interpretation of growth responses (Figure S4).

### Physiological and ecological responses to disturbance

Physiological responses to perturbation (canopy loss) were inferred from photosynthetic performance of the kelp recruits transplanted into each plot (cf. 'Disturbance experiment'). Pulse-amplified modulated (PAM) fluorometry measured photosynthesis by proxy of chlorophyll *a* fluorescence from photosystem II (diving PAM-2000; Waltz GmbH, Effeltrich, Germany). PAM fluorometry is a widely used tool to assess the physiological status of plants (including macroalgae), particularly where field conditions or large volumes of samples make direct assessments of oxygen metabolism impossible. The quantum efficiency [ $\Phi$ ; slope of the light-dependent part of the electron transfer rate (ETR)-E curve] and maximum ETR ( $\text{ETR}_{\text{max}}$ ) were calculated from rapid light curves (RLCs; eight light intensities with an illumination interval of 30 s). Under steady-state photosynthesis,  $\Phi$  and  $\text{ETR}_{\text{max}}$  may be analogous to the photosynthetic efficiency ( $\alpha$ ) and maximum rate of photosynthesis respectively. Although steady-state photosynthesis may require slightly longer illuminations than used here, these parameters still provide a very useful tool to compare relative physiological performance across standardized treatments (reviewed by Enriquez & Borowitzka in press). Measurements were taken in the late afternoon on epiphyte free sections of two randomly selected thalli from each plot. Absorption was measured for each individual thallus, and a dark adaptation period of 15 min was used before measurements. All photobiological measurements followed the same procedures and machine settings as previously used successfully to assess photobiological responses of kelp recruits to canopy loss in this system (see Toohey *et al.* 2004; Toohey & Kendrick 2007 for technical details). Growth was determined as the percentage increase in length of transplanted kelp recruits based on before/after measurements. Concurrently, net

recruitment was determined within the centre  $3.14\text{ m}^2$  of each plot (before/after counts of all stage 1 and 2 kelp recruits within a circle of 2 m diameter). Recovery of adult canopy was measured as the change in stage 3 adult density within the centre  $3.14\text{ m}^2$  of each plot after 20 months, which should be sufficient time for canopy recovery (Kennelly & Underwood 1993; Toohey & Kendrick 2007). Recruits and adult kelps were counted in a total of  $452\text{ m}^2$  of reef twice (before/after implementation of disturbances).

## RESULTS

### Kelp distribution

The hypothesis that kelp abundance would decrease with increasing ocean temperature towards the northern (warm) limit of its distribution was rejected for adult kelp because there were no significant relationships between mean ocean temperature and the cover or biomass of kelp canopies (least squares linear regression, canopy cover:  $r^2 = 0.09$ ,  $P = 0.15$ ; biomass  $r^2 = 0.02$ ,  $P = 0.50$ ,  $n = 24$  reefs, six in each region) nor were there any differences in means among regions (ANOVA, kelp abundance: cover:  $F_{3,20} = 1.93$ ;  $P = 0.16$ ; biomass:  $F_{3,20} = 0.54$ ;  $P = 0.66$ ; Table 1, Table S3). By contrast, the density of kelp recruits was inversely related with increasing mean ocean temperature (slope =  $-36.1\%$ ,  $r^2 = 0.37$ ,  $P = 0.04$ ,  $n = 12$  reefs, three in each region; Table 1), suggesting a gradual reduction in the competency of either reproduction, recruitment, or recruit survival with increasing ocean temperature.

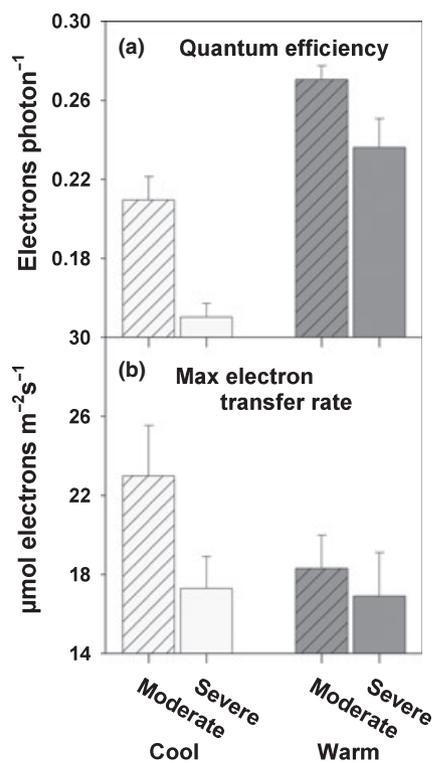
### Metabolic adjustment

The hypothesis that kelps adjust key metabolic processes to prevailing ocean temperatures was supported as we found a strong negative relationship between annual mean ocean temperature (Table 1) and the temperature sensitivity ( $Q_{10}$ , cf. Table 2 in Stæhr & Wernberg 2009) of both maximum net photosynthesis and dark respiration (least squares linear regression, photosynthesis: slope =  $-31.7\%$ ,  $r^2 = 0.69$ ,  $P < 0.001$ ; respiration: slope =  $-35.7\%$ ,  $r^2 = 0.75$ ,  $P < 0.001$ ,  $n = 16$  reefs, four in each region). The underlying mechanisms likely included reduced pigment, nutrient and enzyme concentrations (Davison 1991; Stæhr & Wernberg 2009). These cellular components also determine physiological responses to environmental conditions other than temperature (e.g., light), and the reduction in  $Q_{10}$  at higher ocean temperatures therefore implies a concurrent reduction in the overall capacity to respond to environmental change and stress in general. Our physiological experiments did not separate contributions from acclimatization (a phenotypic response) and adaptation (a genotypic response),

but they clearly demonstrated that metabolic adjustment assists kelps in maintaining a positive carbon balance across chronically different temperature regimes.

### Physiological performance

The hypothesis that metabolic adjustments in response to warm climates have implications for the capacity to respond to perturbations was supported. Increasing intensity of disturbance affected both quantum efficiency ( $\Phi$ ) and maximum ETR ( $ETR_{max}$ ), but the magnitude of the effect differed between cool and warm ocean climate (ANOVA, photo-physiology: quantum efficiency:  $F_{1,2} = 19.70$ ,  $P = 0.047$ ; maximum ETR:  $F_{1,2} = 22.65$ ,  $P = 0.041$ ; Fig. 2, Table S4): the effect was smaller under warm compared with cool conditions ( $\Phi$ : 13% vs. 28%,  $ETR_{max}$ : 9% vs. 24%). In other words, the photosynthesis of kelp recruits growing in the warm ocean climate did not respond as strongly to an increase in the intensity of physical



**Figure 2** Photo-physiological status ( $\Phi$  = quantum efficiency,  $ETR_{max}$  = maximum electron transport rate) of kelp recruits 80 days after being transplanted into experimental plots of moderate (partial canopy clearing, hashed bars) and severe (complete canopy removal, open bars) physical disturbance (cf. Figure S3) in cool (light shade) and warm (dark shade) ocean climate (mean + SEM,  $n = 2$  regions).  $P_{climate \times intensity} < 0.05$  for both  $\Phi$  and  $ETR_{max}$ . Full data analyses are presented in Table S4.

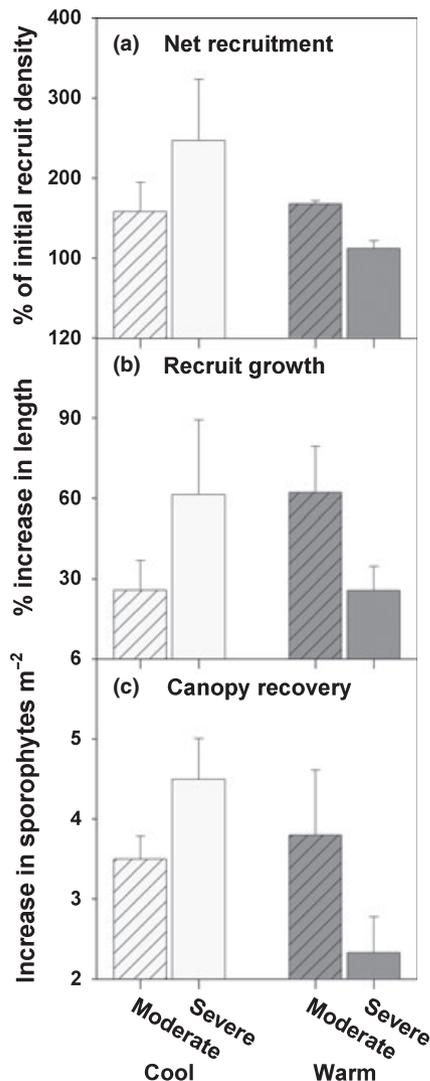
disturbance and the associated change in light conditions, as did recruits in the cool ocean climate.

### Ecological performance

The hypothesis that ocean climate and increasing severity of perturbation would interact to negatively affect the ecological performance (recruitment, growth) of kelp recruits and recovery of the adult canopy was also supported. Moreover, there was an interaction between ocean climate and intensity of disturbance, with higher recruitment following severe compared with moderate disturbance in the cool climate, but the reverse in the warm ocean climate (ANOVA, recruitment: climate  $\times$  intensity:  $F_{1,2} = 24.61$ ;  $P = 0.038$ ; Fig. 3a, Table S5). An identical pattern was observed for recruit growth (ANOVA, growth: climate  $\times$  intensity:  $F_{1,8} = 5.44$ ;  $P = 0.048$ ; Fig. 3b, Table S6). Importantly, in contrast to rapid recovery in the cool climate, these short-term effects on recruit performance translated into suppressed canopy recovery almost 2 years later in the warm climate (ANOVA, canopy recovery: climate  $\times$  intensity:  $F_{1,18} = 4.55$ ;  $P = 0.047$ ; Fig. 3c, Table S7). These results demonstrate that kelp beds in low-latitude chronically warm climates have a reduced capacity for recovery following intense physical disturbance (i.e., they have a lower resilience), and they indicate that the vulnerability of early life-stage processes drive this impact.

### DISCUSSION

Kelps influence community structure on and far from reefs (Steneck *et al.* 2002), so any impacts of global warming on kelps would have broad cascading effects across temperate marine ecosystems. Through identical experiments at different latitudes, we have shown that metabolic adjustment assists the kelp *E. radiata* in maintaining high abundances across a range of different environments extending towards the species' northern range limit in Western Australia. We have also shown that kelp beds at northern latitudes have a lower resilience to external perturbations (e.g., physical and biological disturbance, deteriorating water quality, disease or competition from invasive species) than kelp beds at southern latitudes, and we have shown that this is a consequence of low abundances of recruits, reduced physiological responsiveness and increased reliance on surviving adults to maintain high net recruitment, recruit growth and canopy recovery. Attributing this effect to one or more environmental drivers is difficult because of the correlative nature of comparative experiments. However, even if we cannot unequivocally rule out potential influences from factors such as light, nutrients, wave exposure or herbivory, we believe temperature is likely to be the main driver because this is the most prominent



**Figure 3** Ecological performance of kelp recruits (a, b), and recovery of adult canopy (c), in response to different intensities of experimental disturbance (hashed bars: partial canopy removal; open bars: complete canopy removal); in cool (light shade) and warm (dark shade) ocean climate (Figure S3). Net recruitment (a, mean + SEM,  $n = 2$  regions) and growth (b, mean + SEM,  $n = 3$  reefs) was assessed after 80 days. Recovery of adult canopy (c, mean + SEM,  $n = 2$  regions) was measured after 20 months.  $P_{\text{climate} \times \text{intensity}} < 0.05$  for recruitment, growth and canopy recovery. Full data analyses are presented in Tables S5, S6 and S7.

environmental factor to vary consistently along the coastline (Smale & Wernberg 2009). Thus, while metabolic adjustment underpins the broad ecological tolerance of kelp beds, the physiological costs of thermal stress bring them closer to a threshold where sudden or persistent changes (loss of habitat and ecological function) may occur as the accumulated effect of continuous failure to recover (Gorman & Connell 2009; Harley & Paine 2009).

The erosion of resilience was mediated by a shift in the direction of ecological interactions between adult kelps and their recruits from negative (competitive) under cool (benign) to positive (facilitative) under warm (adverse) conditions. This switch in direction of intraspecific interactions is interesting because it took place across a gentle gradient in temperature across  $c. 7^\circ$  latitude. By contrast, to our knowledge, similar reversals of ecological interactions have previously only been documented in environments characterized by steep environmental gradients across relatively short distances (e.g., alpine and intertidal habitats, Bertness & Ewanchuk 2002; Callaway *et al.* 2002). We did not observe any obvious mechanisms that could explain this switch. We suggest that there is not necessarily a single causal factor but that the general stress level increases the sensitivity and susceptibility to cumulative and synergistic effects of multiple sub-lethal pressures (e.g., light stress, disease, sediment smothering or meso-grazers) that could be ameliorated by the presence of surviving adults.

The consistent canopy abundance (pattern) across latitudes despite reduced resilience (process) demonstrates how patterns can be maintained even if the strength and direction of processes underpinning ecological function change. The implication in the face of global warming is that current kelp habitats may remain intact but in a state where they are more susceptible to additional stressors such as reduced water quality, disturbance or disease. This provides a clear warning to conservation biologists not to rely solely on inventories of distribution and abundance to evaluate ecosystem health and functioning. Whether *E. radiata* and other kelps will be able to maintain ecological function under projected global warming will also depend on how rates of physiological adjustment scale with rates of environmental change. Many temperate algae acclimatize physiologically to an annual cycle of temperature change that is at least 2–5 times greater than the temperature changes predicted for global warming (Davison 1991; IPCC 2007). Responding to slightly higher ocean temperatures on scales of years to decades is therefore unlikely to pose a direct physiological problem for most kelp populations. However, reduced resilience, as a consequence of physiological adjustment to elevated temperatures, will exacerbate effects of concurrent increases in other stressors and perturbations caused by human activities, including reduced water quality (Airoldi & Beck 2007), shifts in herbivore abundance (Ling 2008), and physical disturbance from more intense storms (Harley *et al.* 2006; IPCC 2007). The consequences will potentially include complete loss of kelp habitat or increased fragmentation of existing kelp beds, leading to a loss of biodiversity and ecological function (Steneck *et al.* 2002; Graham 2004; Ling 2008), particularly at the range-edges where physiological stress is greatest or around urban centres (e.g., Connell *et al.* 2008) where other

concurrent pressures are greatest. Southern Australia has the longest (> 3000 km) east-west facing temperate coastline in the world, and a southward shift in isotherms equivalent to the gradient encompassed by this study, implies that increased temperatures and any associated effects on kelps, would affect a very large area. Moreover, because kelps and other organisms cannot shift their range further south, any southward shift of the northern range-edge will imply a net loss of area for the affected species.

It has been proposed that the broad physiological tolerances of kelps, and their great potential for canopy regeneration, make kelp beds relatively robust to global warming (Steneck *et al.* 2002). Concerns for the future resilience of kelp beds, and other coastal habitats, have therefore focused extensively on top-down effects from removal of predators and herbivores (Jackson *et al.* 2001; Steneck *et al.* 2002; Pandolfi *et al.* 2003). We do not discount the serious threat from altered consumer pressure, but by linking abundance patterns, metabolic adjustment, and ecological performance of kelps in different temperature regimes, we have demonstrated that global warming in all likelihood is eroding the resilience of Australasian kelp beds through impacts on bottom-up processes. Pressing questions in restoration and conservation ecology centre around the extent to which physiological adjustment is important in negotiating chronically stressful environments (Edmunds & Gates 2008), what the ecological costs of these physiological changes are (Clarke 2003), and how stressful the environment needs to be before positive interactions become important in driving community organization (Halpern *et al.* 2007). Our findings suggest that physiological adjustment enable the existence of Australasian kelp beds in chronically warm environments, but that the ecological cost is a reduced resilience such that, in these kelp beds, the *c.* 2 °C increase in ocean temperature that is likely to occur (IPCC 2007), will be sufficiently stressful to make canopy recovery and persistence more dependent on positive interactions between adult kelp and kelp recruits. The implications for conservation and management of kelp beds, and other marine habitats, are potentially huge: synergistic effects of increasing ocean temperature and intensity of disturbance on resilience, demonstrate that our current understanding of community dynamics and vulnerability, may not apply in a future warmer climate.

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## SUPPORTING INFORMATION

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

**Appendix S1** Supplementary figures.

**Figure S1** Water temperature measured every 15 min between 23 April 2006 and 22 April 2007 at all four locations.

**Figure S2** Concentration of inorganic nitrogen immediately above the kelp canopy in each region.

**Figure S3** Photographs of intact kelp canopy, partial canopy removal and complete canopy removal.

**Figure S4** Growth of kelp recruits in response to experimental treatments when including damaged recruits from Marmion.

**Appendix S2** Tables of statistical analyses.

**Table S1** ANOVA testing for differences in ocean temperature.

**Table S2** ANOVA testing for differences in nitrogen concentration.

**Table S3** ANOVA testing for differences in kelp canopy cover and canopy biomass.

**Table S4** ANOVA testing for differences in quantum efficiency and maximum electron transfer rate.

**Table S5** ANOVA testing for differences in net recruitment of kelp.

**Table S6** ANOVA testing for differences in growth of transplanted kelp recruits.

**Table S7** ANOVA testing for differences in adult canopy recovery.

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