

LETTER

Tropical herbivores provide resilience to a climate-mediated phase shift on temperate reefs

Scott Bennett,^{1*} Thomas Wernberg,¹ Euan S. Harvey,² Julia Santana-Garcon¹ and Benjamin J. Saunders²

Abstract

Climate-mediated changes to biotic interactions have the potential to fundamentally alter global ecosystems. However, the capacity for novel interactions to drive or maintain transitions in ecosystem states remains unresolved. We examined temperate reefs that recently underwent complete seaweed canopy loss and tested whether a concurrent increase in tropical herbivores could be maintaining the current canopy-free state. Turf-grazing herbivorous fishes increased in biomass and diversity, and displayed feeding rates comparable to global coral reefs. Canopy-browsing herbivores displayed high ($\sim 10\,000\text{ g }100\text{ m}^{-2}$) and stable biomass between 2006 and 2013. Tropical browsers had the highest abundance in 2013 and displayed feeding rates approximately three times higher than previously observed on coral reefs. These observations suggest that tropical herbivores are maintaining previously kelp-dominated temperate reefs in an alternate canopy-free state by grazing turfs and preventing kelp reestablishment. This remarkable ecosystem highlights the sensitivity of biotic interactions and ecosystem stability to warming and extreme disturbance events.

Keywords

Climate change, coral reef, fishes, kelp, regime shift, tropicalisation.

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INTRODUCTION

Understanding how climate-driven changes in biotic interactions will alter the ability of ecosystems to absorb disturbance while retaining their fundamental structure, function and feedbacks (i.e. ecological resilience) is a current challenge for ecologists (Zarnetske *et al.* 2012). The erosion of ecological resilience is often associated with a reduction in functional capabilities within the ecosystem. For example, over-harvesting higher trophic levels can lead to a release of constraints on lower trophic levels and subsequent over or under-grazing of vegetation (Pace *et al.* 1999; Schmitz *et al.* 2000; Bertness *et al.* 2014). Resilience can also be modified by the addition of novel species and functional groups into ecosystems (Wardle *et al.* 2011; Vergés *et al.* 2014a). Functional alteration of this kind is increasingly common under climate change as tropical species begin to inhabit temperate habitats (Last *et al.* 2011; Poloczanska *et al.* 2013; Wernberg *et al.* 2013), and temperate species establish in polar regions (Kortsch *et al.* 2012; Krause-Jensen *et al.* 2012). These changes, in turn create the potential for exacerbated or dampened impacts of climate change on ecosystems.

In marine systems, herbivores have a profound effect on benthic primary producers (Poore *et al.* 2012) and can be pivotal to the resilience of benthic ecosystems (Bellwood *et al.* 2004; Ling *et al.* 2009a; Bertness *et al.* 2014). Herbivore range expansions into new ecosystems, facilitated by climate warming, can severely alter trophic interactions that have stabilised over long time scales, undermining the stability of that system

(Ling *et al.* 2009b; Vergés *et al.* 2014a). Temperate ecosystems are particularly vulnerable to range expansions of tropical herbivores with the potential to exploit vegetation (Vergés *et al.* 2014b). This is due to the high diversity of species and functional groups in tropical regions (Burkepile & Hay 2008; Rasher *et al.* 2013), many of which are not normally found in temperate areas.

Fishes are dominant herbivores on coral reefs and can be divided into several functional groups, depending on their feeding mode and ecosystem role (Bellwood *et al.* 2004). Broadly, ‘browsers’ feed primarily on foliose and canopy-forming seaweeds, while ‘grazers’ feed primarily on epilithic algal turfs. Grazers, including ‘scrapers’ and ‘excavators’ (*sensu* Bellwood & Choat 1990), are fundamental to the maintenance and resilience of coral-dominated reefs (Bellwood *et al.* 2004; Mumby *et al.* 2006). Their high feeding rates on algal turfs maintains low algal and sediment biomass, thereby facilitating the settlement, growth and persistence of corals. Browsing herbivores are thought to provide critical resilience to coral reefs by consuming canopy forming seaweeds and facilitating phase shift reversals of degraded reefs back to coral dominant states (Bellwood *et al.* 2006). In contrast, molluscs and urchins are the primary herbivores in most temperate ecosystems, with fish generally playing a less important role (Poore *et al.* 2012; but see Taylor & Schiel 2010 and; Pages *et al.* 2012). Temperate herbivores generally do not have a critical influence on the resilience of healthy temperate reefs, which are production-dominated systems as opposed to the consumer-dominant dependence of healthy coral reefs

¹School of Plant Biology & UWA Oceans Institute, University of Western Australia, 39 Fairway, Crawley, 6009 WA, Australia

²Department of Environment and Agriculture, Curtin University, Bentley, WA 6102, Australia

*Correspondence and present address: Scott Bennett, Department of Environment and Agriculture, Curtin University, Bentley, WA 6102, Australia.
E-mail: scott.bennett1@curtin.edu.au

(Fig. 1, Connell *et al.* 2011). However, an increase in tropical herbivore functional groups in temperate marine ecosystems has the potential to introduce unprecedented top down control and, theoretically at least, undermine the stability of vegetated habitats (Vergés *et al.* 2014a). This could occur through over-consumption by browsers, driving a shift from canopy to turf dominance and/or benthic grazers maintaining canopy-free states, particularly where physical disturbance temporarily suppresses production by removing the canopy (Fig. 1).

In order for herbivores to maintain and/or drive a transition from seaweed canopies to a canopy-free state, seaweed consumption rates will need to exceed reef-wide production rates. At the reef scale, the flux of both of these processes will depend on the total biomass of herbivores and seaweed canopy (i.e. higher canopy cover or total biomass results in higher total biomass production on the reef, Fig. 1). Low fish biomass will result in diffuse consumption rates per unit area, which in a canopy-dominated state will result in net production across the reef and high canopy resilience (i.e. healthy temperate reef, Fig. 1). In a canopy-free state, low herbivore biomass reduces the resilience of that state by enabling canopy seaweeds to recruit and grow. This relationship is particularly relevant for roving herbivorous fishes, which can have large home ranges spanning several kilometres (Welsh & Bellwood 2014) meaning that feeding effort is widely dispersed across the reef (c.f. sea urchins where low consumer biomass at the reef scale can still lead to patches of barren formation at the meter scale; Flukes *et al.* 2012).

High herbivore biomass on the other hand will reduce the resilience of the canopy and increase the resilience of canopy-free states. Under consumption-dominated conditions,

resource demand (and therefore feeding rates per unit of seaweed) increase with decreasing canopy availability, thereby exacerbating canopy loss, prevent the establishment of canopy species and further increase the resilience of canopy-free conditions (i.e. healthy coral reef). Furthermore, as canopy-free area increases, grazers will become increasingly important to maintain low biomass turf-dominated conditions. While roving grazers, capable of maintaining canopy-free conditions are generally uncommon on temperate reefs, the poleward movement of tropical herbivores into temperate reef systems due to warming could potentially increase grazing rates to a level where this is possible (Vergés *et al.* 2014a).

In 2011, a marine heatwave off the coast of south-west Australia caused unprecedented impacts on temperate reef ecosystems and resulted in major modification of benthic habitats and tropicalisation of fish communities (Fig. S1, Wernberg *et al.* 2013; Smale & Wernberg 2013). Canopy cover declined by 40% in some regions with some reefs even more severely affected (Wernberg *et al.* 2013). Here, we examined reefs that were dominated by extensive canopy cover prior to the 2011 heatwave (Wernberg *et al.* 2010), but have since become dominated by algal turfs. We ask whether an increase in tropical herbivores could be maintaining the current canopy-free reef state on these temperate reefs. We compared the trophic structure and biomass of the fish community before and after the 2011 marine heatwave and quantified consumption rates by herbivores feeding on the substratum, translocated kelp recruits, solitary kelp adults and adult kelp patches. Finally, we compared the observed browsing and grazing rates from these tropicalised temperate reefs to rates reported from coral reef ecosystems globally, where herbivores are known to play

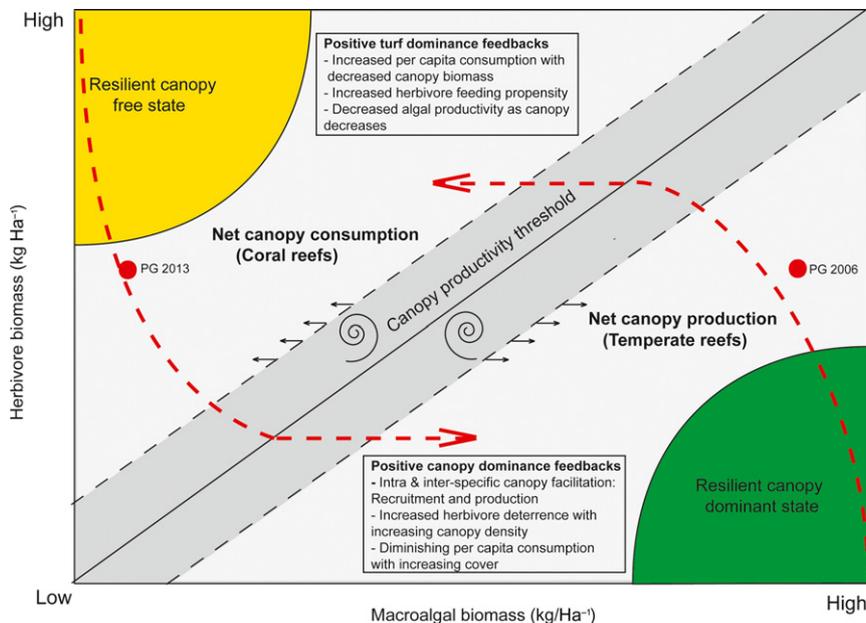


Figure 1 Heuristic model depicting the resilience of canopy and canopy-free states on reefs. Resilience is determined by the relative rates of canopy production vs. consumption, which scale as a function of seaweed and browsing herbivore biomass, respectively. Ecosystems in the bottom right half of the figure have net production (i.e. algal production outweighs herbivore consumption) and will remain/return in a canopy-dominated state (i.e. healthy temperate reefs). Ecosystems in the top left half of the figure have net consumption, and will move towards a canopy-free state (i.e. healthy coral reefs). The diagonal solid line represents the threshold where production and consumption are equal, and the grey area represents uncertainty around the shape of the relationship. The red dashed line illustrates the possible forward and reverse shift trajectories by modifying herbivore numbers. Small black arrows illustrate the influence of positive feedbacks described in the boxes.

a fundamental role in maintaining canopy-free states (Bellwood *et al.* 2004). Our findings provide insight into the capacity for tropical herbivores to maintain an alternate canopy-free state on temperate reefs and highlight the sensitivity of biotic interactions and ecosystem stability to warming.

METHODS

Fish and benthic surveys

The study was conducted on the coastal sandstone reefs off Port Gregory, Western Australia (28.2° S, 114.2° E). Changes in fish and benthic community structure since the 2011 marine heatwave were examined using diver operated stereo video (stereo-DOV) surveys conducted at six wave-exposed reefs in June 2006 and repeated in May–June 2013 using standardised methodology (Watson *et al.* 2005). The stereo-DOV system comprised of two Sony digital cameras mounted 700 mm apart on a base bar, inwardly converged at 8°. An image synchronising diode was mounted in front of the cameras field of view and a chain-man cotton counter was mounted on the side to measure the length of each transect. Twelve 25 × 5 m transects were swum along each reef at a pace of approximately 2 min per transect, with the cameras approximately 50 cm above the reef angled slightly downward enabling the reef surface to be observed throughout the video. At least a 10 m gap was left between replicate transects.

DOV video analyses

To enable accurate fish length measurements, the stereo-camera pair was calibrated before and after each field expedition using the software CAL (SeaGIS Pty Ltd, Victoria, Australia) following Harvey & Shortis (1998). The video footage obtained by the stereo-DOV was analysed using the software 'EventMeasure (Stereo)' (SeaGIS Pty Ltd) and 'Vision Measurement System' (Robson *et al.* 2006). All fish observed were identified to the lowest taxonomic level possible, counted and measured to the nearest millimetre (fork length). Due to morphological similarity, limited visibility and distance to the camera, *Kyphosus bigibbus*, *K. sydneyanus* and *K. gladius* were not distinguishable on all transects, and therefore the three species were pooled for the analysis (but see 'herbivory video analysis' below). Initial phase (IP) *Scarus ghobban* and *S. schlegeli* were also not distinguishable on all transects and were therefore pooled, as IP individuals constituted the majority of the parrotfish abundance. Fish species were assigned to one of six general trophic groups based on observed feeding patterns (herbivores only) and FishBase (Froese & Pauly 2014). Species abundances were converted to biomass using length–weight relationships from Western Australian Fisheries research reports, primary literature (Taylor & Willis 1998; Kulbicki *et al.* 2005) or FishBase (Froese & Pauly 2014). Biogenic habitat cover was analysed from the videos by estimating per cent cover along the 12 replicate transects at each site. Video footage was paused every 10 s (~ 2 m) and benthic cover was quantified within a 1 m² area of the image where the benthos was clearly visible. Care was taken to ensure no overlap in benthos occurred among the analysed frames. This was repeated 10 times on each transect, generating 120

measurements of benthic cover per site. The biogenic habitat was classified as either 'Canopy' (*Ecklonia radiata* and *Sargassum* spp), 'Small foliose algae', algae less than 15 cm in length (primarily *Lobophora variegata*, *Padina* sp, *Asparagopsis taxiformis*), 'Hard coral' (primarily *Plesiastrea versipora*, *Montipora mollis*, *Goniastrea aspera* and *Pocillopora damicornis*), or 'Turf'. Turfs were classified as all reef surfaces covered by multispecific epilithic algal turfs, analogous to those observed on coral reefs (*c.f.* Connell *et al.* 2014) and generally less than 1 cm in height.

Herbivory measurements

Herbivore feeding rates were measured in November 2013 in Port Gregory at two of the surveyed reefs which experienced complete seaweed canopy loss between 2006 and 2013. The two reefs were separated by approximately 2 km and feeding trials were conducted at 7–10 and 5–6 m depth respectively. To test whether the resident herbivore population could prevent canopy recovery on the reef, *Ecklonia radiata* (a small kelp) adults and recruits were translocated from Marmion (31.82° S, 115.70° E) to Port Gregory. *Ecklonia radiata* was used as it is the dominant canopy seaweed throughout temperate Australia, and it was the most abundant canopy species in Port Gregory prior to its disappearance in 2011 (Fig. 2a). Translocated kelps were collected whole, with the holdfast intact and transported to the laboratory in cool, damp and dark calico bags, where they were individually weighed, measured and tagged. The kelps were then stored in cool damp and dark conditions throughout their transportation and deployed back into the sea within 24 h of collection.

Kelps were randomly allocated between the two sites and deployed as solitary recruits ($n = 20$ per site, fresh weight = 4.5 ± 0.4 g, mean \pm SE), solitary adults ($n = 10$ per site, fresh weight = 441.3 ± 23.2 g) or patches of adult kelps ($n = 3$ patches of eight kelps per site; $c. 3399 \pm 227$ g fresh weight m⁻²). Two exclusion cages were set up at each site to control for non-herbivore-related kelp loss. Cages contained either adult kelps ($n = 2$) or recruits ($n = 4$) and were constructed with 600 × 600 × 500 mm stainless steel frames covered in 10 × 10 mm mesh. For kelp patches, eight individuals were attached to a 1 m² section of steel mesh, reflecting mean natural densities along the coast of Western Australia (de Bettignies *et al.* 2013). Replicate patches were separated by at least 20 m on the reef. Solitary kelp adults and recruits were haphazardly arranged on the reef, separated by at least 5 m from one another. Kelps and controls were deployed for a 24 h period before being recollected, weighed and measured. Three kelp patches retained significant biomass after the initial 24 h and were redeployed along with the controls for an additional 24 h. Some recruits were bleached after 24 h (a sign of transplant stress) and were therefore removed from analyses. All kelps were entirely consumed within 48 h.

Herbivory video analyses

Underwater video cameras (GoPro Hero3, GoPro Inc, San Mateo, California USA) were used to assess the relative feeding rates on the transplanted kelp (browsing) and background feeding rates (grazing) on the algal turfs. At each site, three

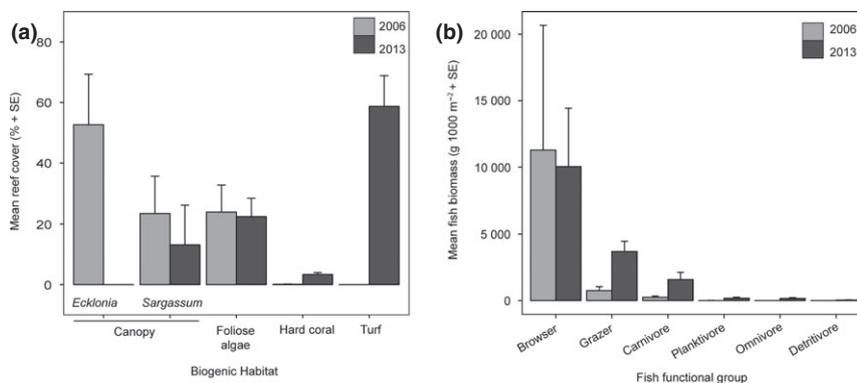


Figure 2 Mean habitat cover (a) and fish trophic composition (b) across six reefs in 2006 (light grey) and 2013 (dark grey). Foliose algae represents small (< 15 cm) non-canopy-forming seaweeds such as *Lobophora variegata*, *Padina* spp., and *Asparagopsis* spp.

replicate 3 h video recordings were taken during daylight hours between 08:00 and 16:00, within each 24 h period of kelp deployment, or until the kelp was completely consumed. Unlike the DOV footage, good visibility and the close proximity (1–2 m) of kelp transplants to the camera enabled the kypheids and scarids to be distinguished to species level. Background grazing rates on algal turfs were quantified by haphazardly selecting and filming 2 m² turf-dominated patches of reef. Three replicate patches of reef were filmed for 3 h at a time in each site, with each patch separated by at least 10 m. This was repeated daily for 5 days resulting in 15 replicate filming periods at each site.

Feeding rates on kelps and algal turfs were analysed using EventMeasure software (SeaGIS Pty Ltd) by quantifying the bite rates by each fish species over the course of the filming period in each of the respective habitats. Feeding rates on turf were not quantified in videos containing adult kelps, to avoid any potential impact on the feeding behaviour of turf-algal grazers (Hoey & Bellwood 2011). The maximum number of individuals of each species within the field view at the same time (MaxN) was also recorded as a conservative measure of relative abundance (Cappo *et al.* 2003).

Literature comparison

Feeding rates measured in the current study were compared to published rates observed throughout global coral reef systems. Feeding rates were extracted from published papers, tables and figures using the Data Thief software (Tummers 2006). Browsing rates were standardised by the biomass of the herbivores, the biomass of the seaweed assay available for consumption and the period of exposure. Studies or treatments were only used where the seaweed assay was placed into coral dominated, or canopy-free areas (primarily reef crest or outer reef flat), where consumption rates are highest (Hoey & Bellwood 2010). Feeding rates on the benthos by herbivorous fishes were standardised by the grazing area and time (1 m² h⁻¹). For studies where bite rates per unit area were not reported, values were estimated based on the reported percentage of reef area grazed per unit time using a conservative mean bite size reported in the literature (16 mm², equivalent to a 10–15 cm, TL, *Scarus rivulatus*; after Bonaldo & Bellwood 2008). Note that feeding rates by scrapers

reported in the literature were not standardised by fish biomass. Where the feeding rates of multiple species were individually reported, the feeding rates of all reported species were summed to determine the total mean browsing or grazing pressure.

Data analyses

To assess whether the per cent cover of benthic functional groups and fish trophic group biomass differed between years, one-way ANOVA were performed for each group. Benthic cover data were square-root arcsine transformed to improve the normality and homoscedasticity of the proportional data. To determine whether rates of kelp biomass removal varied between sites (between subject effect) and days (within subject), repeated measures ANOVA were used (following Hoey & Bellwood 2011). Because different number of patches ($n = 3$ per site) and solitary kelps ($n = 10$ per site) were deployed, consumption rates for these treatments were analysed separately. The biomass lost by each kelp was standardised by subtracting the mean biomass loss of controls from treatment loss values. Data were checked for normality and homogeneity of variance through visual inspection of scatter plots and the distribution of residuals and no transformation took place.

RESULTS

Changes to fish and benthic functional groups

Port Gregory experienced complete kelp loss between 2006 and 2013 (ANOVA, $F_{1,10} = 9.929$, $P = 0.013$, Fig. 2a), and a dramatic increase in turf-algal cover from 0% to $58.7 \pm 10.1\%$ (mean \pm SE, Fig. 2a, $F_{1,10} = 33.57$, $P < 0.001$). The other dominant canopy species *Sargassum* spp., showed variable changes in abundance, whereby it completely disappeared from five reefs but remained abundant in one reef resulting in a non-significant overall change from $23.5 \pm 12.2\%$ (mean \pm SE) to $13.1 \pm 13.1\%$ ($F_{1,10} = 0.334$, $P = 0.576$). The cover of small foliose algae remained unchanged ($F_{1,10} = 0.019$, $P = 0.892$).

Fish trophic structure was dominated by herbivores, with the combined biomass of browsers and grazers constituting

87.5% of total fish biomass. Large macroalgal browsers contributed the most biomass, approximately $10\,040 \pm 4560$ g 100 m^{-2} (mean \pm SE) and did not differ significantly between years ($F_{1,10} = 0.014$, $P = 0.907$, Fig. 2b). Browser biomass was overwhelmingly dominated by three species, *Kyphosus bigibbus*, *K. sydneyanus* and *K. gladius*. Together these species constituted 98.8 and 92.5% of total browser biomass in 2006 and 2013 respectively and did not differ in biomass between years ($F_{1,10} = 0.014$, $P = 0.907$). It was not possible to distinguish between these three species in the DOV surveys, however, based on feeding videos *K. bigibbus* had the highest relative abundance in 2013 (mean MaxN = 27 ± 8.88 SE), followed by *K. sydneyanus* (mean MaxN = 1.63 ± 0.63) and *K. gladius* (mean MaxN = 0.43 ± 0.22). Turf-algal grazers had the second highest biomass, and were higher in 2013 compared to 2006 (Fig. 2b, ANOVA, $F_{1,10} = 12.95$, $P = 0.004$) driven primarily by an increased biomass of *Scarus ghobban* and *S. schlegeli* (Table S1). Carnivores also had higher biomass in 2013 compared to 2006 (ANOVA, $F_{1,10} = 5.92$, $P = 0.035$), primarily because of the appearance of 13 tropical species, not observed previously, and an increase in benthic invertebrate feeders, like *Choerodon rubescens* (Table S1). The remaining three trophic groups (planktivores, detritivores and omnivores) constituted less than 3% of the observed fish biomass. Within these trophic groups, the pomacentrids *Abedefduf*

bengalensis (ANOVA, $F_{1,10} = 5.276$, $P = 0.044$) and *Pomacentrus milleri* (ANOVA, $F_{1,10} = 6.365$, $P = 0.03$) both displayed significant increases in abundance and biomass (Table S1).

Herbivory rates on kelp

The total biomass of *Ecklonia* (15.1 ± 0.5 kg per site, mean \pm SE) was consumed within 48 h of deployment (Fig. 3a). Patches of adult kelps were heavily grazed at both sites, with 'Site 1' and 'Site 2' completely consumed after 24 and 48 h, respectively (Fig. 3a, Table S2). Similarly solitary kelps at both sites were heavily grazed with only 6.7 ± 0.8 and $20.3 \pm 5\%$ of initial biomass remaining after 24 h (Fig. 3a, Table S3). Kelp recruits were heavily grazed, but not to the same extent as adult kelps. The proportion of biomass remaining of recruits transplanted within adult patches was $41.0 \pm 17.7\%$ and for solitary recruits $27.4 \pm 4.5\%$ after 24 h of exposure (Fig. 3b).

Feeding rates on the kelp were driven primarily by large schools of the tropical herbivore *Kyphosus bigibbus*, and to a lesser extent by the two large species of temperate herbivores *K. sydneyanus* and *K. gladius* (Fig. 4). In total 38 078 bites were recorded on kelp, from five species. *K. bigibbus* averaged 3103 ± 1925 bites h^{-1} and 77.9% of all bites taken, compared to 484 ± 268 bites h^{-1} (15.1% of total bites) by *K. sydney-*

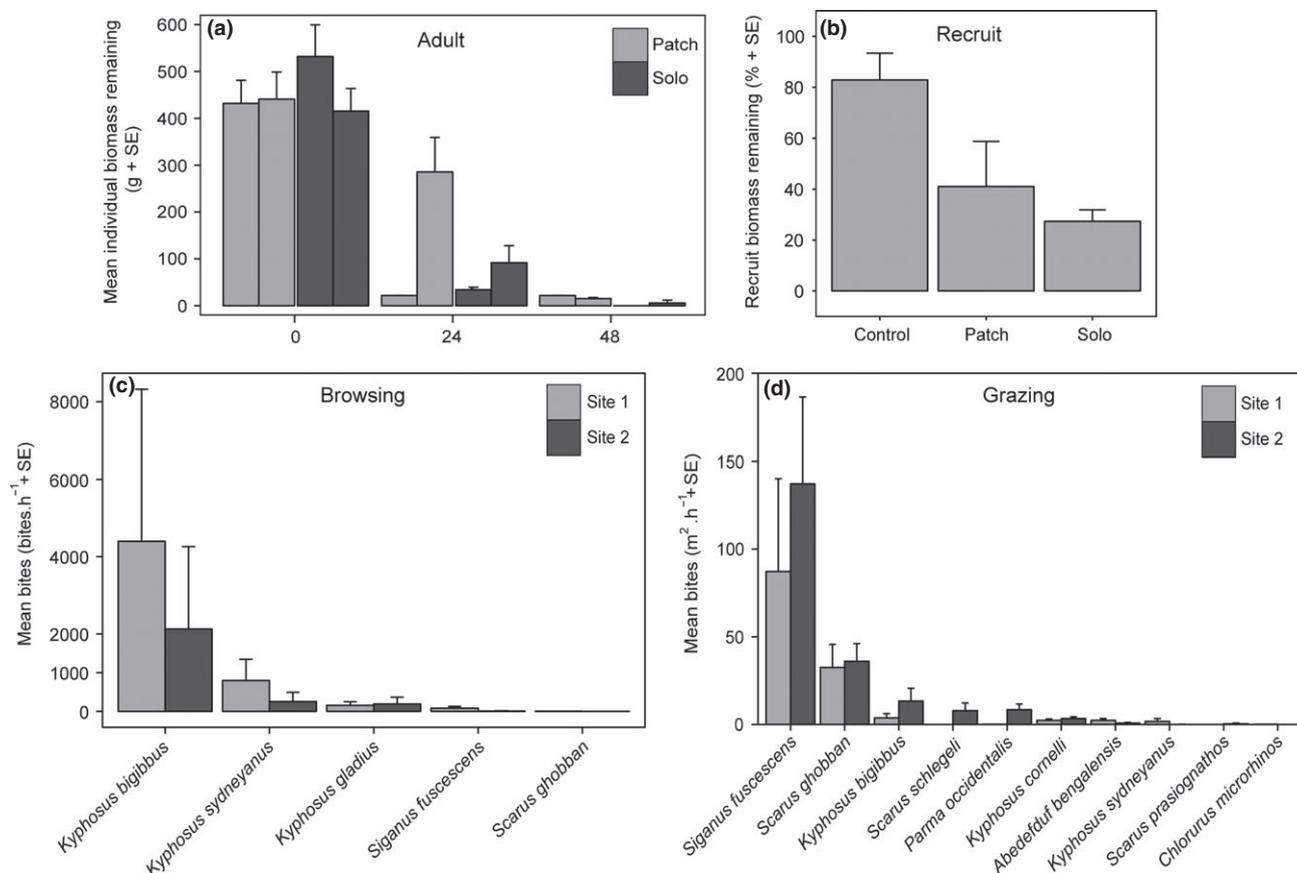


Figure 3 Consumption and bite rates on transplanted kelps and bite rates on epilithic algal turfs. (a) Mean biomass of individual kelps remaining in patches and solitary on the reef over the course of 48 h. The two bars for each treatment represent the different sites. (b) Mean proportion of kelp recruit thallus weight consumed by herbivores over 24 h, averaged between sites. (c) Mean species bite rates on kelp transplants per hour of filming at two sites. (d) Mean species bite rates on the substratum per $1\text{ m}^2\text{ h}^{-1}$, between at two sites.

anus and 173 ± 101 bites h^{-1} (5.7% of total bites) by *K. gladius* (Fig. 3c). The remaining two species, *Siganus fuscescens* and *Scarus ghobban* accounted for less than 1.5% of total bites. When standardised by relative abundance (mean MaxN), *K. sydneyanus* (296 ± 164.4 bites $\text{individual}^{-1} \text{h}^{-1}$) and *K. gladius* (173 ± 101 bites $\text{individual}^{-1} \text{h}^{-1}$) displayed higher per-capita feeding rates than *K. bigibbus* (115 ± 71 bites $\text{individual}^{-1} \text{h}^{-1}$). The high total feeding rates by *K. bigibbus* were therefore driven by intense, sporadic feeding frenzies by large schools (MaxN = 156, Table S4), which consumed approximately 14.3 kg of *Ecklonia* within 10 min throughout one site, accounting for the site variation in consumption rates after 24 h.

Grazing rates on substratum

A total of 26 161 bites were recorded on the substratum, among 10 fish species. *Siganus fuscescens* recorded the highest grazing rates, accounting for 66.8% of total bites, followed by *Scarus ghobban* and *Kyphosus bigibbus* which accounted for 20.3 and 5.2% of the total bites, respectively (Fig. 3d). Grazing by both *S. fuscescens* and *K. bigibbus* was driven by the sporadic appearance of large schools (MaxN = 112 and 156 respectively, Fig. 4). In contrast, feeding rates by *S. ghobban* were driven by a more constant presence of solitary individuals or small schools (MaxN = 5).

Comparison with global coral reef systems

Macroalgal browsing and substratum grazing rates recorded on the temperate reefs of Port Gregory were comparable to

rates reported throughout the world's coral reefs (Table 1, Table 2). Browsing rates in Port Gregory were higher than any previously reported browsing rates on coral reefs using comparable methodology when standardised by filming time, assay biomass and herbivore biomass. Mean grazing rates on the substratum in Port Gregory (172 bites $\text{m}^2 \text{h}^{-1} \pm 50$ SE) were ranked fourth out of seven comparable studies from coral reefs globally (Table 2). The highest reported grazing rates (1684 bites $\text{m}^2 \text{h}^{-1}$) were from Lizard Island on the Great Barrier Reef (Bellwood & Fulton 2008), followed by the Abrolhos Archipelago in Brazil (315 bites $\text{m}^2 \text{h}^{-1}$; Longo & Floeter 2012) and Fiji (258 bites $\text{m}^2 \text{h}^{-1}$; Rasher *et al.* 2013).

DISCUSSION

Herbivore resilience of canopy-free state

Herbivores appear to be providing high resilience to the new canopy-free state on temperate reefs in Port Gregory through high turf-algal grazing rates and very high kelp consumption rates, thereby preventing the reestablishment of seaweed canopies. The biomass and diversity of grazers, particularly parrotfish, increased significantly between 2006 and 2013, resulting in benthic grazing rates comparable to coral reef ecosystems globally. Grazing herbivores play a critical role on coral reefs, by cropping turfs and consuming canopy recruits, preventing the establishment of canopy-forming species like *Sargassum* while in turn facilitating coral recruitment and growth (Bellwood *et al.* 2004; Mumby *et al.* 2006). Unlike coral reefs, high turf-algal grazing rates on temperate reefs are quite remarkable given that, with the exception of territorial scalyfins

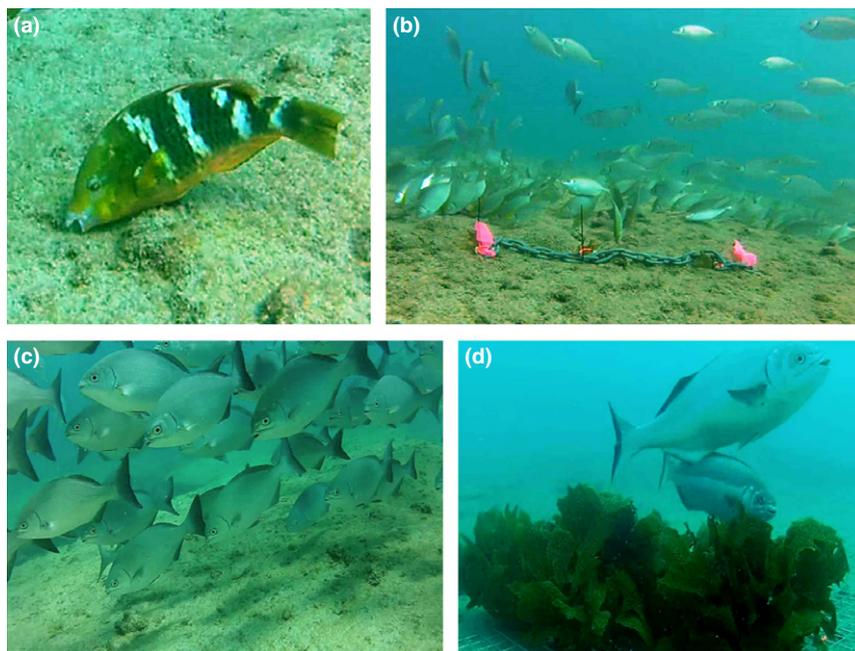


Figure 4 Identity of dominant tropical (a–c) and temperate (d) herbivore species in Port Gregory above reef which was previously covered by kelp canopies. (a) *Scarus ghobban* primarily caused the increase in grazer biomass from 2006 to 2013 and was the second most prolific grazer. (b) *Siganus fuscescens* recorded the highest number of bites on the substratum, driven by large roving schools. (c) *Kyphosus bigibbus* was the most prolific kelp browser and formed large roving schools. (d) *Kyphosus gladius* (above) and *Kyphosus sydneyanus* (below) feeding on transplanted *Ecklonia radiata* patches.

Table 1 Comparison of mean feeding rates by herbivorous fishes in the current study, with rates reported on global coral reefs

Feeding type	Algal species	Mean bite rate (bites kg _H ⁻¹ kg _A ⁻¹ h ⁻¹)	Dominant herbivores	Reef	Region	References
Macroalgal browsing	<i>Ecklonia radiata</i>	3836.06	<i>Kyphosus biggibus</i> , <i>Kyphosus sydneyanus</i> , <i>Kyphosus gladius</i>	Port Gregory	Temperate, Western Australia	This study
	<i>Sargassum</i> spp	1250.68	<i>Naso unicornis</i>	Lizard Island	Great Barrier Reef, Australia	Hoey & Bellwood (2009)
	<i>Sargassum</i> spp	210.37	<i>Siganus canaliculatus</i> , <i>Siganus doliatus</i>	Orpheus Island		Fox & Bellwood (2008a)
	<i>Sargassum</i> spp	322.45	<i>Kyphosus vagiensis</i>	Orpheus Island		Hoey & Bellwood (2011)
	<i>Sargassum</i> spp	880.30	<i>Naso unicornis</i> , <i>Siganus canaliculatus</i> , <i>Siganus doliatus</i>	Low Isles		Bennett & Bellwood (2011)
	<i>Sargassum</i> spp	595.13	<i>Kyphosus vagiensis</i> , <i>Naso unicornis</i> , <i>Siganus canaliculatus</i> , <i>Siganus doliatus</i>	Whitsunday Islands		Bennett & Bellwood (2011)
	<i>Sargassum</i> spp	29.56	<i>Kyphosus vagiensis</i> , <i>Naso unicornis</i> , <i>Siganus canaliculatus</i> , <i>Siganus doliatus</i>	Keppel Islands		Bennett & Bellwood (2011)
	<i>Sargassum</i> spp	135.54	<i>Kyphosus vagiensis</i>	Bundegi	Ningaloo Reef, Australia	Michael <i>et al.</i> (2013)
	<i>Sargassum</i> spp	54.21	<i>Scarus</i> spp	Mandu		Michael <i>et al.</i> (2013)
	<i>Sargassum</i> spp	198.79	<i>Naso unicornis</i>	Point Cloates		Michael <i>et al.</i> (2013)
	<i>Sargassum</i> spp	162.65	<i>Kyphosus biggibus</i>	Maud		Michael <i>et al.</i> (2013)
	<i>Sargassum</i> spp	162.65	<i>Kyphosus vagiensis</i>	Gnarloo		Michael <i>et al.</i> (2013)
	<i>Sargassum</i> spp	688.08*	<i>Siganus puelloides</i>		Seychelles	Chong-Seng <i>et al.</i> (2014)

Macroalgal browsing rates were standardised by the biomass of the herbivores, the biomass of the seaweed assay available for consumption and by the period of exposure. Coral reef feeding rates were only used where the seaweed assay was placed onto coral-dominated areas (primarily reef crest or outer reef flat), where grazing rates are highest. All reported grazing rates employ standardised video methods. * denotes that bites are not standardised by herbivore biomass.

(*Parma* spp, Saunders *et al.* 2014), fish grazers are normally an uncommon functional group in these systems. Moreover, unlike healthy coral reef systems where high coral cover concentrates turf-algal grazing onto a relatively small proportion of reef area, Port Gregory reefs displayed between 60 and 80% turf-algal cover, meaning that grazing effort was dispersed over a large area.

Browsers are also likely to increase the resilience of the canopy-free state in Port Gregory by readily consuming kelp recruits and preventing the establishment of canopy species. Kelp transplants were consumed within 24–48 h and observed browsing rates were at least three times higher than has previously been observed on coral reef systems, illustrating the heavily consumption-dominated state of the system. Furthermore, maintenance of the canopy-free state by herbivores is likely to be self-reinforcing as both browsing and grazing herbivores preferentially occupy and feed in reef areas with low algal biomass (Hoey & Bellwood 2011). The vast increase in turf-dominated habitat therefore provides a feedback mechanism that is likely to promote further herbivore recruitment and population growth in this system.

Contributing factors influencing reef resilience

Herbivores may have the capacity to maintain a turf-dominated state in Port Gregory, but they are not the only obsta-

cle to kelp recovery in the region. Temperate reefs along the mid-west coast of Australia represent the warm rear-edge of kelp distribution (Wernberg *et al.* 2010). The oceanography of the region is characterised by the pole-ward flowing Leeuwin Current, which brings warm tropical water along the south western coastline of the continent thereby maintaining oligotrophic conditions and relatively stable warm water temperatures year round (Waite *et al.* 2007). The directional flow of the Leeuwin current supplies tropical larvae and propagules to temperate regions, and warming background conditions means that conditions are becoming increasingly favourable for tropical species and unfavourable for temperate species (Wernberg *et al.* 2013). At the same time, kelp connectivity is linked to the flow of the Leeuwin current (Coleman *et al.* 2011), making kelp recovery a slow prospect and dependent on supply of propagules from cooler higher latitudes, which may be poorly adapted to warmer conditions.

Influence of browsers on seaweed canopy resilience

While the drivers of canopy loss cannot be unequivocally determined from this experiment, the timing of canopy loss was consistent with observed impacts of the 2011 marine heat-wave on seaweed canopies elsewhere in the region (Smale & Wernberg 2013; Wernberg *et al.* 2013). Kelp canopies displayed high cover (60–80% of reef surfaces) and interannual

Table 2 Comparison of mean grazing rates on epilithic algal turf between the current study and global coral reefs

Feeding type	Algal species	Mean bite rate (bites m ² h ⁻¹)	Reef area grazed (% m ² month ⁻¹)	Dominant herbivores	Reef	Region	References
Grazing	Turf/EAM	172 ± 50		<i>Scarus ghobban</i> , <i>Siganus fuscus</i>	Port Gregory	Temperate Western Australia	This Study
		60.6*	70		Northern GBR	Great Barrier Reef, Australia	Hoey & Bellwood (2008)
		45.1*	52	<i>Scarus rivulatus</i>	Orpheus Island GBR		Fox & Bellwood (2008b)
		1684.6		<i>Scarus</i> IP, <i>Scarus psittacus</i> , <i>Siganus</i> spp <i>Acanthurus bahianus</i>	Lizard Island GBR		Bellwood & Fulton (2008)
		315			Abrolhos Archipelago,	NE Brazil	Longo & Floeter (2012)
		59.2			Conch Reef,	Florida Keys, USA	Burkpile & Hay (2011)
		258		<i>Acanthurus nigricauda</i> , <i>Ctenchaetus striatus</i> , <i>Scarus</i> spp		Fiji	Rasher <i>et al.</i> (2013)

Feeding rates on the substratum by herbivorous fishes were standardised by the grazing area and time (1 m² h⁻¹). * denotes studies where bite rates per unit area were not reported and values were estimated based on the reported percentage of reef area grazed per unit time using a conservative mean bite size (16 mm², equivalent to a 10–15 cm, TL, parrot fish) (Bonaldo & Bellwood 2008). Note that feeding rates by scrapers reported in the literature were not standardised by fish biomass.

stability throughout the region in the 10 years prior to the 2011 heatwave, before completely disappearing by 2013 (observations in 2001, Wernberg *et al.* 2003; 2006–2008, Wernberg *et al.* 2010; and December 2010, < 1 month prior to the heatwave, TW personal observation). At the same time, browser biomass did not change between 2006 and 2013. These observations suggest that high browser biomass alone was unlikely to have caused the observed canopy loss, as canopies appear to have been supporting these large browser communities in a stable production-dominated state for at least the 5 years before and after the 2006 observations. Rather, the timing of canopy loss suggests that high thermal anomalies during the marine heatwave may have resulted in temperature stress that directly and indirectly impacted kelps (Fig. S1, Pearce & Feng 2013; Wernberg *et al.* 2013), driving the transition to a consumption-dominated state. High browser biomass would have nevertheless lowered the resilience of the canopy-dominated state and may have exacerbated the rate of kelp loss during the heat wave through (1) indirect effects, such as physiological stress within kelps leading to an increase in palatability and higher feeding rates by browsing herbivores, (2) increased metabolic rates among herbivores, leading to a spike in herbivore bite rates or (3) a combination these and other factors.

This disturbance-driven model of transition is consistent with Graham *et al.* (2013), who proposed that extreme disturbance events in conjunction with the necessary protection and management of herbivore populations could lead to phase shift reversals on degraded coral reefs. Currently, the ability of fishes to drive transitions from canopy to turf dominance at a landscape scale remains an open question (Hoey & Bellwood 2011; Chong-Seng *et al.* 2014; Vergés *et al.* 2014a). Our observations suggest that large-scale disturbance events may be critical for transitions towards canopy-free states, particularly in the context of other temperate or coral reef systems where browser communities are often much smaller than

those observed here, even in unfished, functionally healthy systems (e.g. outer Great Barrier Reef, Hoey & Bellwood 2010). While further research is necessary to identify the ratio between herbivore and canopy biomass around the critical threshold where reefs transition between production and consumption dominance, our observations raise important questions about the capacity of browsers to drive canopy-turf transitions in the absence of additional forces suppressing net canopy production.

SUMMARY

Our findings demonstrate that high browsing and grazing rates by primarily tropical herbivores are providing resilience to novel turf-dominated conditions on temperate reefs formerly dominated by seaweed canopies. These findings highlight a potential vulnerability of many temperate reef systems worldwide, particularly in the face of increasing frequency and intensity of extreme events (Cai *et al.* 2015) and predicted climate-driven range expansions of tropical species onto temperate reefs globally (Vergés *et al.* 2014a). More broadly, the fundamental transformation of the structure and processes driving temperate reef function observed here highlights the potential sensitivity of biotic interactions and ecosystem stability to climate warming and extreme disturbance events.

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AUTHORSHIP

S.B and T.W conceived the idea and decided upon the sampling design. S.B collected herbivory data and S.B and J.S.G analysed video feeding footage. B.S, E.H, J.S.G and S.B collected and analysed the DOV fish community data. S.B, J.S.G and T.W analysed the data. S.B wrote the manuscript with contributions from all authors.

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