

# Long-term empirical evidence of ocean warming leading to tropicalization of fish communities, increased herbivory, and loss of kelp

Adriana Vergés<sup>a,b,c,1</sup>, Christopher Doropoulos<sup>a,d,e</sup>, Hamish A. Malcolm<sup>f</sup>, Mathew Skye<sup>a,b</sup>, Marina Garcia-Pizá<sup>a,b</sup>, Ezequiel M. Marzinelli<sup>a,b,c,g</sup>, Alexandra H. Campbell<sup>a,b,c</sup>, Enric Ballesteros<sup>h</sup>, Andrew S. Hoey<sup>i</sup>, Ana Vila-Concejo<sup>j</sup>, Yves-Marie Bozec<sup>e,i</sup>, and Peter D. Steinberg<sup>a,c,g</sup>

<sup>a</sup>Centre for Marine Bio-Innovation, School of Biological, Earth, and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia; <sup>b</sup>Evolution and Ecology Research Centre, School of Biological, Earth, and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia; <sup>c</sup>Sydney Institute of Marine Science, Mosman, NSW 2088, Australia; <sup>d</sup>Commonwealth Scientific and Industrial Research Organization Oceans and Atmosphere, Dutton Park, QLD 4102, Australia; <sup>e</sup>Marine Spatial Ecology Lab, Australian Research Council Centre of Excellence for Coral Reef Studies, School of Biological Sciences, The University of Queensland, St. Lucia, QLD 4072, Australia; <sup>f</sup>Marine Ecosystem Research, Fisheries NSW, Department of Primary Industries, Coffs Harbour, NSW 2450, Australia; <sup>g</sup>Singapore Centre for Environmental Life Sciences Engineering, Nanyang Technical University, Singapore 637551, Singapore; <sup>h</sup>Centre d'Estudis Avançats de Blanes (Consejo Superior de Investigaciones Científicas), 17300 Blanes, Girona, Spain; <sup>i</sup>Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia; and <sup>j</sup>Geocoastal Research Group, School of Geosciences, The University of Sydney, Sydney, NSW 2006, Australia

Edited by Juan Carlos Castilla, Universidad Catolica de Chile, Santiago, Chile, and approved October 19, 2016 (received for review July 1, 2016)

Some of the most profound effects of climate change on ecological communities are due to alterations in species interactions rather than direct physiological effects of changing environmental conditions. Empirical evidence of historical changes in species interactions within climate-impacted communities is, however, rare and difficult to obtain. Here, we demonstrate the recent disappearance of key habitat-forming kelp forests from a warming tropical-temperate transition zone in eastern Australia. Using a 10-y video dataset encompassing a 0.6 °C warming period, we show how herbivory increased as kelp gradually declined and then disappeared. Concurrently, fish communities from sites where kelp was originally abundant but subsequently disappeared became increasingly dominated by tropical herbivores. Feeding assays identified two key tropical/subtropical herbivores that consumed transplanted kelp within hours at these sites. There was also a distinct increase in the abundance of fishes that consume epilithic algae, and much higher bite rates by this group at sites without kelp, suggesting a key role for these fishes in maintaining reefs in kelp-free states by removing kelp recruits. Changes in kelp abundance showed no direct relationship to seawater temperatures over the decade and were also unrelated to other measured abiotic factors (nutrients and storms). Our results show that warming-mediated increases in fish herbivory pose a significant threat to kelp-dominated ecosystems in Australia and, potentially, globally.

climate change | macroalgae | plant-herbivore interactions | range shifts | tropicalization

**S**tudies on the ecological impacts of climate change generally focus on the direct effects of increasing temperature on individual species (1). A recent metaanalysis of long-term datasets (>20 y) from terrestrial and freshwater environments, however, shows that climate-mediated alterations to species interactions can be more important than the direct effects of temperature (2). Indeed, novel species interactions following species distribution shifts have already underpinned some of the most profound community-level impacts of climate change in the past (3) and are likely to underpin them in the future (4, 5). There is therefore an urgent need to better understand shifting species interactions to adequately predict the impacts of climate change.

In many coastal marine systems, macrophytes such as kelp and seagrasses are the dominant biogenic habitat formers, supporting hundreds of species—including economically important fishes, abalone, and lobster (6, 7)—such that changes in their abundance cascade throughout the entire ecosystem (8, 9). Plant-herbivore interactions play an important role in structuring these

marine systems (10), as illustrated by the dramatic community shifts that occur when natural levels of herbivory are altered (11). Thus, macrophyte-dominated marine systems are likely to be highly vulnerable to climate-mediated changes in herbivory, but our understanding of this is still very limited and largely based on laboratory experiments (12, 13).

Herbivory is widely recognized as a leading cause of kelp deforestation on mid- to high-latitude reefs (6, 8). In contrast, at lower latitudes near the warm edge of distribution of many kelp species, deforestation has been generally linked to oceanographic anomalies in temperature, nutrients, or salinity (14, 15). Recently, however, the range expansion of tropical herbivorous fishes has been proposed as a new and potentially important driver of kelp deforestation (16). A recent review identified 80 species of tropical and subtropical herbivorous fishes expanding their ranges into temperate reefs in association with poleward-flowing boundary currents around the globe (16). The impacts of these warmwater herbivores can be much greater than those of native species, as documented in the eastern Mediterranean (17, 18).

## Significance

Most studies of the impact of global warming focus on the direct physiological impacts of climate change. However, global warming is shifting the distribution of many species and leading to novel interactions between previously separated species that have the potential to transform entire ecological communities. This study shows that an increase in the proportion of warm-water species ("tropicalization") as oceans warm is increasing fish herbivory in kelp forests, contributing to their decline and subsequent persistence in alternate "kelp-free" states. These tropical and subtropical herbivores are increasingly impacting temperate algal communities worldwide, posing a significant threat to the long-term stability of these iconic ecosystems and the valuable services they provide.

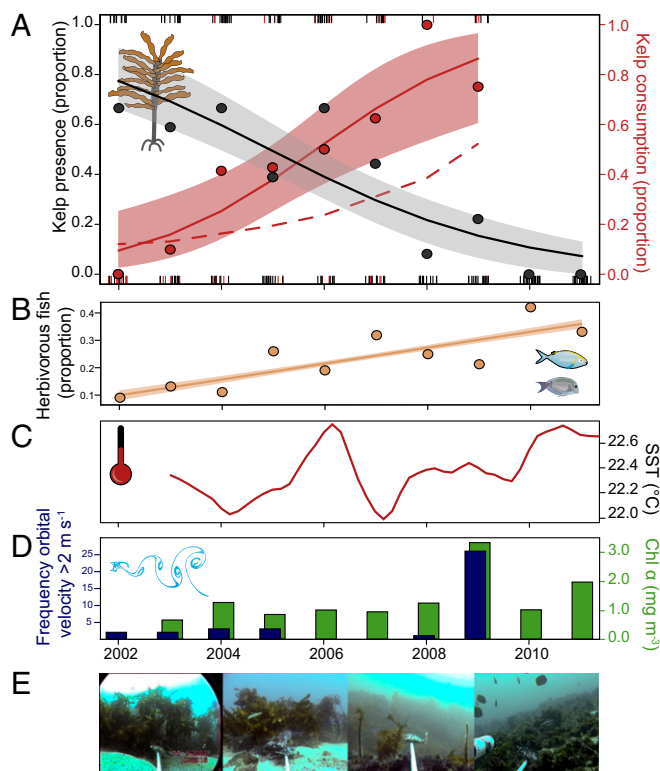
Author contributions: A.V., H.A.M., E.M.M., A.H.C., and P.D.S. designed research; A.V., C.D., H.A.M., M.S., M.G.-P., E.M.M., A.H.C., E.B., A.S.H., A.V.-C., and Y.-M.B. performed research; A.V., C.D., M.S., E.M.M., A.H.C., A.V.-C., and Y.-M.B. analyzed data; and A.V., H.A.M., M.S., E.M.M., A.H.C., E.B., A.S.H., A.V.-C., Y.-M.B., and P.D.S. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

<sup>1</sup>To whom correspondence should be addressed. Email: a.verges@unsw.edu.au.

This article contains supporting information online at [www.pnas.org/lookup/suppl/doi:10.1073/pnas.1610725113/-DCSupplemental](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1610725113/-DCSupplemental).



There were clear differences through time in fish community structure between reefs where kelp was never present and reefs where kelp declined. Total fish and herbivorous fish communities at reefs with and without kelp were initially different (~2002–2007), but were similar by ~2008–2011. These temporal changes differed among habitats for the total fish community [Fig. S3A; PERMANOVA, Time by Habitat: pseudo- $F_{(1,336)} = 3.9$ ,  $P < 0.001$ ] but were additive for the herbivorous fish community [Time: pseudo- $F_{(1,336)} = 19.4$ ,  $P < 0.001$ ; Habitat: pseudo- $F_{(1,336)} = 7.2$ ,  $P < 0.01$ ; Fig. S3B].

As kelp abundance declined, an increase in the proportion of kelp with bite marks may be expected even if overall consumption rates remained stable, due to the concentration of feeding on fewer kelp. We ran a simulation model to estimate whether the observed levels of herbivory among the BRUV replicates from 2002 to 2009 were different than what would be expected due to the decline in kelp resources. The model results show that from 2005 onward the observed levels of herbivory were ~25–50% higher than expected from feeding being concentrated on fewer kelp (Fig. 1A), suggesting a temporal increase in overall consumption rates.

To further examine the potential role of herbivores in kelp deforestation, we used a space for time approach and compared the macroherbivore community (fish and urchins) and algal consumption rates between sites within the study region where kelp is absent (offshore reefs) and the closest sites where kelp is still abundant (inshore reefs, Fig. S4). Herbivory was quantified on both transplanted kelps and on the surrounding epilithic algal matrix (EAM) (sensu ref. 22).

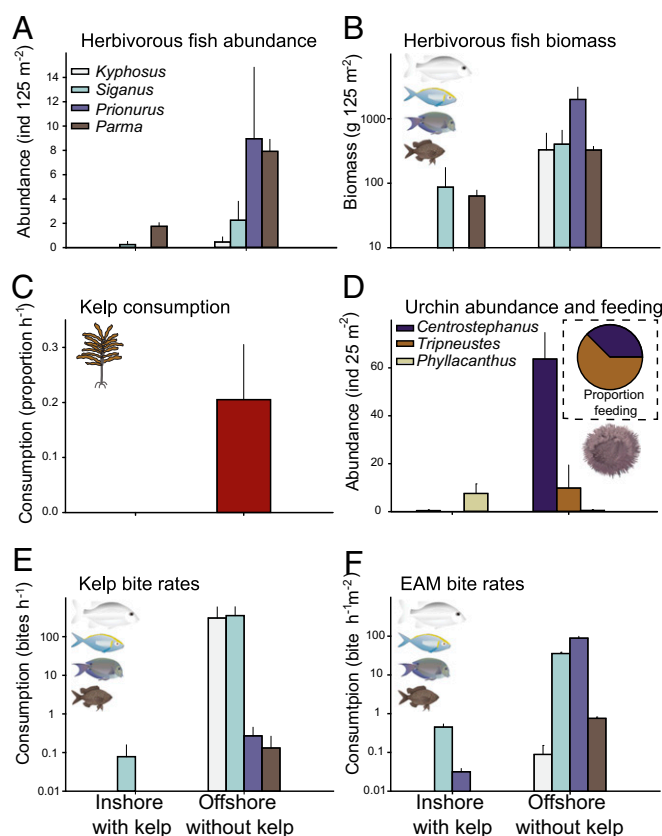
The abundance and biomass of herbivorous fishes were over 10 times greater at offshore sites without kelp than at inshore kelp-dominated sites [Fig. 3A and B; abundance: pseudo- $F_{(1,35)} = 11.7$ ,  $P < 0.001$ ; biomass: pseudo- $F_{(1,35)} = 8.7$ ,  $P < 0.01$ ]. This difference was largely driven by the higher abundance (Fig. 3A) and biomass (Fig. 3B) of *Siganus fuscus* and *Parma unifasciata*, and the presence of *Kyphosus bigibbus* and *Prionurus microlepidotus* at the offshore sites. Sea urchin abundance was ninefold higher at offshore than inshore sites (Fig. 3D).

Filmed kelp bioassays were used to quantify herbivory rates in inshore/offshore sites with and without kelp, respectively. Kelp bioassays were only consumed at offshore sites, where kelp is no longer present, with herbivores consuming on average 21% ( $\pm 10$  SEM) of the initial kelp frond area offered per hour (Fig. 3C). Analysis of video footage showed that, out of 15 herbivorous fish species identified in underwater visual censuses, 2 tropical/subtropical species were responsible for >90% consumption of kelp: the rabbitfish *S. fuscus* and the drummer *K. bigibbus*, both averaging >300 bites per hour (Fig. 3E; Movie S1 and Movie S2, respectively). At the inshore sites, we only recorded consumption of kelp in one instance, where *S. fuscus* took seven bites, but no measurable impact on the kelp fronds was recorded.

Herbivorous sea urchins also consumed tethered kelp in 13% of the offshore tethered assays. Although the temperate sea urchin *Centrostephanus rodgersii* was six times more abundant than the tropical *Tripterygion*, the latter consumed the tethered kelp at 1.6 times the rate of *C. rodgersii* when present (Fig. 3D, Inset, and Movie S3).

Feeding on the EAM (from hereon referred to as “grazing”) at the offshore sites was dominated by the most abundant fish species, the subtropical surgeonfish *P. microlepidotus*. Its grazing rates averaged ( $\pm$ SE) 86.58  $\pm$  9.96 bites·h<sup>-1</sup>·m<sup>-2</sup>, eightfold higher than *S. fuscus*, and more than eightfold higher than any other taxa (Fig. 3F). At the inshore habitat, we recorded a total of only 57 EAM bites by *S. fuscus* from two occurrences, and 3 bites for *P. microlepidotus* from one individual (average  $\pm$  SE: 0.45  $\pm$  0.09 and 0.03  $\pm$  0.01 bites·h<sup>-1</sup>·m<sup>-2</sup>, respectively).

The two main consumers of kelp fronds in the filmed assays, *S. fuscus* and *K. bigibbus*, were rarely recorded from the BRUV samples (4% and 2% of all replicates, respectively), and no changes in the abundance of either species were observed through time (Fig. S5A and B). In contrast, the grazer *P. microlepidotus*



**Fig. 3.** Differences in herbivore communities and kelp consumption between inshore sites where kelp still naturally occurs and offshore sites where kelp is no longer found. (A) Abundances and (B) biomass of dominant herbivorous fish; (C) proportion of kelp consumed per hour; (D) urchin abundance and (Inset) proportion of urchins observed feeding on kelp bioassays when present; (E) fish bite rates on kelp; (F) fish bite rates on the epilithic algal matrix (EAM). Note the log y axes on B, E, and F. Error bars represent SEM.

showed a significant linear increase in abundance with time, but only at sites that originally hosted kelp and then lost it [Time by Habitat: LRT,  $\chi^2_{(1)} = 18.3$ ,  $P < 0.001$ ; Fig. S5C]. Additionally, the territorial grazer *P. unifasciata* increased significantly through time at both habitats [Time: LRT,  $\chi^2_{(1)} = 20.2$ ,  $P < 0.001$ ; Fig. S5D].

## Discussion

This study demonstrates that climate-mediated increases in fish herbivory can lead to the deforestation of temperate kelp communities. It confirms, for the east coast of Australia, the global model of herbivore “tropicalization” of temperate seaweed communities proposed by Vergés et al. (16). Using a 10-y video dataset, field experiments, and a simulation model, we demonstrate that increases in the proportion of tropical herbivores and an overall intensification of herbivory led to the loss of ecologically and economically important kelp forests in a warming tropical–temperate transition zone. Our results point toward changing herbivory contributing to the decline and disappearance of kelp populations via the direct consumption of adult kelps and via grazing of the EAM (which contains the microscopic juvenile stages of kelp). This climate-mediated loss of kelp happened gradually over a decade, rather than being induced by a single extreme warming event as has recently been found on the west coast of Australia (15).

In tropical coral reef systems, grazers play a pivotal role by maintaining the EAM in a cropped state and by consuming macroalgal recruits, thereby preventing the establishment of canopy algae and facilitating coral dominance (23). In contrast, grazers are comparatively rare in temperate systems, with this ecological



function being mostly limited to territorial damselfish such as *Parma* spp. The abundance of the main grazer in the Solitary Islands, the subtropical surgeonfish *P. microlepidotus*, markedly increased at sites that experienced kelp declines. The mean grazing rates observed in our bioassay experiments by this species ( $85.6 \text{ bites} \cdot \text{h}^{-1} \cdot \text{m}^{-2}$ ) and by the entire grazing community ( $122.3 \text{ bites} \cdot \text{h}^{-1} \cdot \text{m}^{-2}$ ) fall well within the range observed in low-latitude systems such as the northern Great Barrier Reef (21). The magnitude of increase in grazer abundance and in overall bite rates observed here is consistent with a functional shift of fish herbivory toward a tropical-like system. This guild of grazing herbivorous fishes was also recently implicated in the prevention of kelp recovery following an acute warming event in temperate western Australia (21).

Evidence for the direct consumption of adult kelp came from the increase in bite marks quantified on remaining kelp and from experimental bioassays that identified two tropical/subtropical species as the main consumers: the rabbitfish *S. fuscescens* and the drummer *K. biggibus*. These species have also been identified as important consumers of kelp in southern Japan, where they have contributed to the recent deforestation of *Ecklonia kurome* (24). These results are also consistent with numerous studies that show that consumption of canopy-forming brown seaweeds is a highly specialized function within the herbivorous fish guild, with only a handful of taxa driving consumption patterns globally (25–27).

In contrast to the clear increase in EAM consumers, we did not detect a similar increase in the abundance of macroalgal browsers, *S. fuscescens* and *K. biggibus*, as kelp declined. These browsers were, however, rare in our BRUV samples, constraining the statistical power to detect temporal changes in their abundance. Moreover, the use of pilchards (as opposed to brown macroalgae) as bait in the BRUVs can underestimate the abundance of *S. fuscescens* in particular (25).

Modeling showed that the striking increase in herbivore bite marks observed on kelp was greater than would be expected solely from the concentration of feeding on fewer remaining kelp, indicating that the intensity of herbivory increased as kelp populations declined. Such an increase in consumption may occur in the presence of relatively stable herbivore populations when consumption rates per capita rise in response to warming, especially over the winter months. These findings are consistent with results from southern Japan, where the recent overgrazing of algal beds has been linked to increased herbivore activity in the winter months by the same species identified in our assays as the main consumers (*S. fuscescens* and *K. biggibus*), rather than an increase in overall browser abundance (24).

Urchins also consumed some of the kelp in our bioassays. In particular, the tropical urchin *T. gratilla* showed a clear attraction to kelp, with several individuals moving at considerable speeds to reach and consume kelp fronds (Movie S3). Although this urchin species is capable of overgrazing algal/seagrass beds when present in high densities (28), it is highly unlikely that the decline of kelp was mediated by this species. It was never viewed on any of the historical BRUVs and was only present in the two northernmost offshore sites of the Solitary Islands (Fig. S4). Nevertheless, our results do suggest that this tropical species may contribute to overgrazing of temperate algal forests if it expands its range poleward and becomes more abundant in higher latitudes.

The black urchin *C. rodgersii* also consumed some of the tethered kelp, was abundant at all offshore sites, and was occasionally viewed in the historical BRUVs. This species is well known for deforesting kelp beds in cooler latitudes along eastern Australia (29). Although the impacts of urchin grazing are highly context dependent (30, 31), all data available from eastern Australia indicate that the density of black urchins observed offshore (mean  $\pm$  SE =  $2.5 \pm 0.4 \text{ individuals} \cdot \text{m}^{-2}$ ) is too low to initiate a phase shift and cause barren formation (estimated at 4–10 individuals  $\cdot \text{m}^{-2}$ ) (32). Thus, although it is possible that these urchins are contributing to the maintenance of kelp-free areas, it is highly unlikely they triggered the initial shift.

Although SSTs increased by  $0.6^\circ\text{C}$  during the study, we found no evidence that warming was a direct physiological cause of

kelp mortality. This is not surprising, as *Ecklonia* is well known for its ability to metabolically adjust and acclimatize to a broad range of temperatures, including temperatures within the range recorded in this study (33, 34). Moreover, the overall warming trend observed was gradual, with no temperature anomalies such as the marine heat waves that have caused localized seaweed extinctions elsewhere (15) (see Fig. S6 for monthly average SST decomposition). Storms are a major physical disturbance for kelp (24) including *Ecklonia* (35), but here the most damaging storms occurred after the disappearance of kelp in 2009. Kelp decline also appeared unaffected by nutrients, although this should be interpreted with caution as the chlorophyll  $\alpha$  proxy used here only correlates coarsely with biologically important nutrients such as nitrates and ammonia. The lack of a relationship between kelp abundance and nutrients is nevertheless not surprising, given that *Ecklonia* generally thrives in clear oligotrophic waters like those in the Solitary Islands (34) and several studies have failed to find compelling relationships between nutrient concentrations and growth of *Ecklonia* (36, 37).

Ocean warming can have synergistic effects by simultaneously increasing disturbance regimes while also reducing the ability of communities to recover following a disturbance (38). Experimental studies have shown that *Ecklonia* populations near the warm edge of their distribution have a reduced capacity for recovery following canopy loss, because of low abundances of recruits, reduced physiological responsiveness, and increased reliance on surviving adults to maintain canopy recovery (34). We propose that a reduction in resilience, combined with increased consumption rates of adult kelp and growing populations of grazers targeting lower abundances of kelp recruits, led to the observed phase shift in benthic community structure. Although such synergistic effects of warming remain to be confirmed, these findings are consistent with a growing body of literature that shows how the full suppression of large seaweeds on reefs is mediated by increases in herbivore functional diversity and feeding complementarity among herbivores (18, 21, 27).

Biotic homogenization is a well-described consequence of anthropogenic activities, as habitat modification leads to the local disappearance of some species (e.g., kelp-dependent species) while invasive species expand beyond their historical ranges, often inflating species diversity at the local scale (39). Using the historical BRUV dataset allowed us to quantify detailed changes in fish community structure concurrent with warming and the loss of kelp habitat. We recorded an increase in species diversity in the region and a homogenization of the fish community composition through time, as tropical and subtropical fishes increased in abundance at sites that initially had kelp but lost it. These findings contribute to a growing number of studies that provide empirical evidence linking a warming climate to community homogenization, so far described for land vegetation and birds (40, 41).

Kelp forests are among the most productive and diverse ecosystems in the world, acting as a biological engine that provides the habitat and trophic foundation for complex food webs, also underpinning important inshore commercial fisheries (42). In Australia, kelp forests support a range of tourism ventures, recreational and commercial fisheries worth over AU\$10 billion per year (7). Climate projections estimate that ocean isotherms will continue to shift poleward at a rate seven times faster in the 21st century than the 20th century (43). As tropical and warm-temperate herbivores respond to these isotherm shifts worldwide (16, 44), climate-induced increases in herbivory are emerging as a new threat of global proportions to valuable algae-dominated temperate reefs and the important ecosystem functions they support.

## Methods

**Study Location and Data Collection.** Time series data (2002–2011) were derived from BRUVs deployed at 12 sites along 25 km of coast within and adjacent to the Solitary Islands Marine Park (SIMP), Australia (Fig. S4). At each site, three replicate BRUVs (separated by  $\sim 200 \text{ m}$ ) were deployed annually around August at a depth of 15–21 m ( $17.9 \pm \text{SD } 1.7$ ) (45). Each BRUV

was baited with mashed pilchard (*Sardinops neopilchardus*) and deployed for 30 min. BRUV surveys were originally designed to monitor temporal and regional changes in the overall fish community structure. Although RUVs baited with brown algae would have been more efficient for surveying browsing fishes (25), pilchard-baited RUVs produce similar estimates of herbivorous fish biomass to unbaited RUVs (46) and diver-operated videos (47).

The full BRUV footage was viewed to quantify the relative abundance of all fish species using MaxN, that is, the maximum number of fish of each species in the frame at any one time, a measure that eliminates the chance of recounting the same fish (48). Only replicates with a full field of view were retained for analysis. We classified fishes according to their latitudinal distribution and trophic group as detailed in Table S1.

The presence/absence of the dominant kelp *Ecklonia radiata* (hereafter *Ecklonia*) was quantified in the total field of view of the BRUVs during the first 5 min of each video. Evidence of herbivory on kelp (presence/absence) was quantified using a conservative approach, whereby replicates were only considered to suffer herbivory when obvious bite marks were observed on kelp fronds (Fig. S1). The loss of some videotapes reduced the number of samples in 2002, 2003, and 2008 from 36 to 15, 17, and 12 replicates, respectively.

SST (in degrees Celsius) and chlorophyll  $\alpha$  (in milligrams per cubic meter) data were sourced from National Aeronautics and Space Administration's GES-DISK Interactive Online Visualization and Analysis (MODIS) at 4-km<sup>2</sup> resolution (49). Chlorophyll  $\alpha$  was used as a proxy for nutrient conditions. Data were quantified for five locations spanning the survey sites every month from July 2002 until December 2011.

Hourly wave data (significant wave height,  $H_s$ , in meters, and associated period,  $T$ , in seconds) recorded by a wave rider buoy stationed within the SIMP (30°21'41"S, 153°16'11"E) for the entire sampling period was provided by Manly Hydraulics Laboratory. Wave power ( $P$ , in newtons per meter per second) was calculated for all data and storm events following linear wave theory using the following:  $P = EC$ , where  $E$  is wave energy [ $E = (1/8)\rho g H_s^2$ , where  $\rho$  refers to water density and  $g$  is the gravitational acceleration] and  $C$  is wave celerity, calculated using the wave period ( $T$ ) as  $gT/4\pi$ . Orbital wave velocities at the seabed ( $U$ , in meters per second) were obtained using Soulsby's (50) approximation  $U = \pi H_s / (T \sinh(2\pi h/L))$ , where  $h$  is the water depth (17 m) and  $L$  is the wavelength (in meters) calculated using linear wave theory  $L = gT^2/2\pi$ . Water velocities required to break or dislodge *Ecklonia* have been estimated to range from 2–5 m·s<sup>-1</sup> for large kelps (19), although exact velocities depend on individual kelp size, which varies with phenology (35). We quantified the number of storms generating bottom wave orbital velocities above >2 m·s<sup>-1</sup> for the SIMP for the period before annual BRUVs deployment as an approximate metric of potential kelp dislodgement events (Fig. S7).

**Temporal Patterns in Kelp Decline and Potential Explanatory Variables.** Our study sites included six sites where kelp was never recorded between 2002 and 2011, and six sites where kelp was recorded at least once; these sites were interspersed within and adjacent to the SIMP (Fig. S4). To analyze how the presence of kelp varied over time, we used a generalized linear mixed-effects model (GLMM) ("lme4" R package; ref. 51), using kelp presence as the binomial response variable, year as the continuous predictor, and sites as the random intercept. Only sites with kelp present at the beginning of the study were included in the analysis.

To predict the effects of multiple environmental drivers on kelp presence, we used a separate GLMM with kelp presence as the binomial response variable and average SST (in degrees Celsius), chlorophyll (in milligrams per cubic meter), and frequency of wave energy >2 m·s<sup>-1</sup> from the 12 mo preceding the BRUVs sampling point as fixed predictors, with sites nested in year as the random intercept. Year was incorporated as a random effect to include the temporal autocorrelation structure when predicting the effects of environmental drivers on kelp distribution. SST, chlorophyll  $\alpha$ , and wave energy were centered by their mean to make their effects comparable. Data from 2002 were not included in this analysis because temperature and chlorophyll  $\alpha$  satellite data only begin in July 2002 at a 4-km<sup>2</sup> resolution, and therefore artificially reduced the annual temperature and chlorophyll  $\alpha$  for that year. Because BRUVs were deployed annually, we used annual average SST data to assess the direct impacts of temperature on kelp, and, as such, a limitation of our study is that we are unable to account for finer-scale influences of temperature.

The temporal pattern of evidence for herbivory on kelp fronds was analyzed using video samples with kelp present, as kelp cannot be consumed when it is not present (replicate count detailed in Fig. S1). For each year, replicates from all sites were combined. Temporal trends were analyzed using a generalized linear model, using the presence of "consumed kelp" as the binomial response variable and year as the continuous predictor. Statistical significance for all

models was based on comparisons between full and reduced models using LRT ( $\chi^2$ )  $P$  values.

To identify whether there was a warming trend between 2003 and 2011 in the study region, we used a linear mixed-effects model following Crawley (52), with mean monthly SST averaged from five sites (see details in Fig. S6) and incorporating year as random effect (52).

#### Herbivory Simulation Model: Observed vs. Expected Levels of Proportional Herbivory.

A simulation model was run to estimate temporal changes in the probability of BRUV replicates displaying signs of herbivory due to all feeding being concentrated on fewer kelp sites as kelp populations declined. We considered that the number of sites with evidence of bites at the start of the surveys reflects the intensity of kelp consumption in the whole system, and assumed this number remained constant at the decadal scale of the survey. A simulation-based inference of herbivory prevalence was done by generating samples for every year from a binomial distribution with the number of samples taken that year and the probability of observing bitten kelp in 2002 ( $P_{\text{kelp consumed}} = 0.0945$ ). We performed in parallel a random resampling of sites with kelp present from binomial distributions specified by the annual number of samples and associated probability of observing kelp. By doing this, we generated two hypothetical, independent surveys of kelp and herbivore intensity. Although the probability of observing kelp consumption in the BRUV surveys was conditional to observing kelp, the actual levels of herbivory—not their detection—are independent from the presence of kelp resources. Then, for each year, we estimated the ratio between the number of "kelp consumed sites" and the number of "kelp present sites." Ratios greater than 1 were forced to 1 under the assumption that herbivory reallocates to those sites where kelp is still present. This process was repeated 1,000 times and the resulting grazed-to-kelp ratios were averaged for each year.

**Temporal Analysis of Fish Communities.** The composition of the total fish and herbivorous fish communities were analyzed using year as an ordered continuous predictor and kelp presence as a fixed categorical factor, with sites as a random effect nested in kelp presence. Fish abundances were  $\log(x + 1)$  transformed to meet assumptions of multivariate homogeneity (analyzed using PERMDISP) and to reduce the influence of highly abundant species. Permutational multivariate analysis of variance (PERMANOVA) was calculated with Bray–Curtis similarity matrices as our metric. Analyses used 999 permutations under a reduced model (53) and were done in the PERMANOVA+ add-on in Primer, version 6 (Primer-E, Plymouth, UK).

A tropicalization index was calculated as the proportion of fishes with tropical and subtropical distributions, and the proportion of herbivorous fishes of the entire community was also calculated (Table S1). Species richness was calculated as the total number of fish species in any given BRUV replicate and analyzed using a Poisson distribution. Proportion data were analyzed using binomial distributions. Temporal changes in the proportion of subtropical and tropical herbivorous fishes were analyzed using a GLMM with year as a continuous predictor and site as a random factor. Finally, separate analyses tested for changes in the abundance of the main consumers of kelp and EAM via filmed *Ecklonia* assays (see below). Fish abundance data for these key species were analyzed with GLMMs using Poisson or negative binomial variance structure, determined by the best-fit model using the Akaike information criterion. Temporal changes in species richness and proportion of herbivorous fishes were tested using GLMM with year and kelp presence as fixed factors and sites random and nested in kelp presence. All analyses were conducted using the "lme4" R package (51).

**Spatial Patterns in Herbivory in Neighboring Sites With and Without Kelp.** The role of herbivory as a driver of kelp distribution in the SIMP was tested using tethered kelp assays at seven sites where kelp is absent and at five nearby sites where kelp populations still remain (inshore; Fig. S4). Experiments were conducted in December 2012 and April 2013, with assays randomized among both times to remove any potential temporal bias between habitats. *Ecklonia* fronds with minimal epiphyte growth (<5% cover) were collected from inshore sites. The maximum length of each individual was measured before ( $47 \pm \text{SD } 14$  cm) and after each assay. Three to eight kelp assays ( $4.9 \pm \text{SD } 1.5$ ) were attached to a small lead weight and deployed at a depth of 10 m within each site, with adjacent assays being separated by  $\geq 4$  m. Assays were conducted between 10:00 AM to 3:00 PM, for 70–250 min ( $168 \pm \text{SD } 61$  min), and filmed for their entire duration using GoPro video cameras placed 1 m away from the tethered kelp. A total of 68 replicate bioassays spanning 191 h of video footage were watched by a single viewer (M.G.-P.), to quantify herbivore identity and bite rates on the tethered kelp and surrounding EAM.

The proportion of kelp consumed and the number of bites by different fish species on the kelp and on the EAM were standardized to 60 min. Kelp consumption was standardized per hour by using either the entire assay time when the entire kelp was not fully consumed or the amount of time it took for the entire kelp tether to be consumed. Tape measures were placed in front of each EAM camera at the beginning of filming for a few seconds to provide a scale, and EAM bite rates were converted to bites per hour per square meter. The presence of sea urchins in the field of view of each tethering assay was recorded, and the proportion of times they fed on kelp was quantified.

Underwater visual censuses of herbivorous fishes and urchins were conducted at three of the kelp-dominated inshore sites and six of the offshore sites by a single observer (A.S.H.) in April 2013 (Fig. S4). Four replicate 25 × 5-m (125-m<sup>2</sup>) belt transects were laid at each site, swam at a constant rate, and

the abundances and sizes (in 5-cm size classes) of all roving and territorial herbivorous fish species were quantified (total of 15 taxa). Density estimates were converted to biomass using published allometric length–weight regressions (FishBase; [www.fishbase.org/](http://www.fishbase.org/)). On the return swim, the same observer quantified urchin abundance within a 1-m band (i.e., 25 × 1 m).

**ACKNOWLEDGMENTS.** We thank the Manly Hydraulics Laboratory for providing wave data. We thank G. Roff and T. Wernberg for providing constructive comments on the manuscript. This research was funded by a University of New South Wales (UNSW) Early Career Researcher Award and a New Opportunities Funding Initiative from the Evolution and Ecology Research Centre (UNSW) (to A.V.). This research was undertaken under Research Permit 2012/006 from the New South Wales Marine Parks Authority. This is contribution 192 from the Sydney Institute of Marine Science.

- Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Glob Ecol Biogeogr* 12(5):361–371.
- Ockendon N, et al. (2014) Mechanisms underpinning climatic impacts on natural populations: Altered species interactions are more important than direct effects. *Glob Change Biol* 20(7):2221–2229.
- Blois JL, Zarnetske PL, Fitzpatrick MC, Finnegan S (2013) Climate change and the past, present, and future of biotic interactions. *Science* 341(6145):499–504.
- Urban MC, Tewksbury JJ, Sheldon KS (2012) On a collision course: Competition and dispersal differences create non-analogous communities and cause extinctions during climate change. *Proc Biol Sci* 279(1735):2072–2080.
- Alexander JM, Diez JM, Levine JM (2015) Novel competitors shape species' responses to climate change. *Nature* 525(7570):515–518.
- Steneck RS, et al. (2002) Kelp forest ecosystems: Biodiversity, stability, resilience and future. *Environ Conserv* 29(4):436–459.
- Bennett S, et al. (2016) The "Great Southern Reef": Social, ecological and economic value of Australia's neglected kelp forests. *Mar Freshw Res* 67(1):47–56.
- Estes JA, Duggins DO (1995) Sea otters and kelp forests in Alaska—generality and variation in a community ecological paradigm. *Ecol Monogr* 65(1):75–100.
- Hughes AR, Williams SL, Duarte CM, Heck KL, Waycott M (2009) Associations of concern: Declining seagrasses and threatened dependent species. *Front Ecol Environ* 7(5):242–246.
- Poore AGB, et al. (2012) Global patterns in the impact of marine herbivores on benthic primary producers. *Ecol Lett* 15(8):912–922.
- Sala E, Boudouresque CF, Harmelin-Vivien M (1998) Fishing, trophic cascades, and the structure of algal assemblages: Evaluation of an old but untested paradigm. *Oikos* 82(3):425–439.
- O'Connor MI (2009) Warming strengthens an herbivore-plant interaction. *Ecology* 90(2):388–398.
- Alsterberg C, Eklof JS, Gamfeldt L, Havenhand JN, Sundbäck K (2013) Consumers mediate the effects of experimental ocean acidification and warming on primary producers. *Proc Natl Acad Sci USA* 110(21):8603–8608.
- Dayton PK, Tegner MJ, Edwards PB, Riser KL (1999) Temporal and spatial scales of kelp demography: The role of oceanographic climate. *Ecol Monogr* 69(2):219–250.
- Wernberg T, et al. (2016) Climate-driven regime shift of a temperate marine ecosystem. *Science* 353(6295):169–172.
- Vergés A, et al. (2014) The tropicalization of temperate marine ecosystems: Climate-mediated changes in herbivory and community phase shifts. *Proc Biol Sci* 281(1789):20140846.
- Sala E, Kizilkaya Z, Yildirim D, Ballesteros E (2011) Alien marine fishes deplete algal biomass in the Eastern Mediterranean. *PLoS One* 6(2):e17356.
- Vergés A, et al. (2014) Tropical rabbitfish and the deforestation of a warming temperate sea. *J Ecol* 102(6):1518–1527.
- Thomsen MS, Wernberg T, Kendrick GA (2004) The effect of thallus size, life stage, aggregation, wave exposure and substratum conditions on the forces required to break or dislodge the small kelp *Ecklonia radiata*. *Bot Mar* 47(6):454–460.
- Dayton PK, Tegner MJ (1984) Catastrophic storms, El Niño, and patch stability in a southern California kelp community. *Science* 224(4646):283–285.
- Bennett S, Wernberg T, Harvey ES, Santana-Garcon J, Saunders BJ (2015) Tropical herbivores provide resilience to a climate-mediated phase shift on temperate reefs. *Ecol Lett* 18(7):714–723.
- Wilson SK, Bellwood DR, Choat JH, Furnas MJ (2003) Detritus in the epilithic algal matrix and its use by coral reef fishes. *Oceanogr Mar Biol Annu Rev* 41:279–309.
- Hughes TP, et al. (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr Biol* 17(4):360–365.
- Yamaguchi A (2010) Biological aspects of herbivorous fishes in the coastal areas of western Japan. *Bull Fish Res Agen* 32:89–94.
- Gilby BL, Tibbetts IR, Stevens T (April 6, 2016) Low functional redundancy and high variability in *Sargassum* browsing fish populations in a subtropical reef system. *Mar Freshw Res*, 10.1071/MF15386.
- Hoey AS, Bellwood DR (2009) Limited functional redundancy in a high diversity system: Single species dominates key ecological process on coral reefs. *Ecosystems* (N Y) 12(8):1316–1328.
- Rasher DB, Hoey AS, Hay ME (2013) Consumer diversity interacts with prey defenses to drive ecosystem function. *Ecology* 94(6):1347–1358.
- Eklof JS, et al. (2008) Sea urchin overgrazing of seagrasses: A review of current knowledge on causes, consequences, and management. *Estuar Coast Shelf Sci* 79(4):569–580.
- Andrew NL, Underwood AJ (1993) Density-dependent foraging in the sea urchin *Centrostephanus rodgersii* on shallow subtidal reefs in New South Wales, Australia. *Mar Ecol Prog Ser* 99(1–2):89–98.
- Filbee-Dexter K, Scheibling RE (2014) Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. *Mar Ecol Prog Ser* 495:1–25.
- Ling SD, et al. (2015) Global regime shift dynamics of catastrophic sea urchin overgrazing. *Philos Trans R Soc Lond B Biol Sci* 370(1659):20130269.
- Hill NA, Blount C, Poore AG, Worthington D, Steinberg PD (2003) Grazing effects of the sea urchin *Centrostephanus rodgersii* in two contrasting rocky reef habitats: Effects of urchin density and its implications for the fishery. *Mar Freshw Res* 54(6):691–700.
- Staehr PA, Wernberg T (2009) Physiological responses of *Ecklonia radiata* (Laminariales) to a latitudinal gradient in ocean temperature. *J Phycol* 45(1):91–99.
- Wernberg T, et al. (2010) Decreasing resilience of kelp beds along a latitudinal temperature gradient: Potential implications for a warmer future. *Ecol Lett* 13(6):685–694.
- De Bettignies T, et al. (2015) Phenological decoupling of mortality from wave forcing in kelp beds. *Ecology* 96(3):850–861.
- Bearham D, Vanderklift MA, Gunson JR (2013) Temperature and light explain spatial variation in growth and productivity of the kelp *Ecklonia radiata*. *Mar Ecol Prog Ser* 476:59–70.
- Mabin CJ, Gribben PE, Fischer A, Wright JT (2013) Variation in the morphology, reproduction and development of the habitat-forming kelp *Ecklonia radiata* with changing temperature and nutrients. *Mar Ecol Prog Ser* 483:117–131.
- Bozec Y-M, Mumby PJ (2015) Synergistic impacts of global warming on the resilience of coral reefs. *Philos Trans R Soc Lond B Biol Sci* 370(1659):20130267.
- Sax DF, Gaines SD (2003) Species diversity: From global decreases to local increases. *Trends Ecol Evol* 18(11):561–566.
- Davey CM, Chamberlain DE, Newson SE, Noble DG, Johnston A (2012) Rise of the generalists: Evidence for climate driven homogenization in avian communities. *Glob Ecol Biogeogr* 21(5):568–578.
- Savage J, Vellend M (2015) Elevational shifts, biotic homogenization and time lags in vegetation change during 40 years of climate warming. *Ecography* 38(6):546–555.
- Bertocci I, Araújo R, Oliveira P, Sousa-Pinto I (2015) REVIEW: Potential effects of kelp species on local fisheries. *J Appl Ecol* 52(5):1216–1226.
- Sen Gupta A, et al. (2015) Episodic and non-uniform migration of thermal habitats in a warming ocean. *Deep Sea Res Part II Top Stud Oceanogr* 113:59–72.
- Bates AE, et al. (2014) Resilience and signatures of tropicalization in protected reef fish communities. *Nat Clim Chang* 4(1):62–67.
- Malcolm HA, Schultz AL, Sachs P, Johnstone N, Jordan A (2015) Decadal changes in the abundance and length of snapper (*Chrysophrys auratus*) in subtropical marine sanctuaries. *PLoS One* 10(6):e0127616.
- Harvey ES, Cappo M, Butler JJ, Hall N, Kendrick GA (2007) Bait attraction affects the performance of remote underwater video stations in assessment of demersal fish community structure. *Mar Ecol Prog Ser* 350:245–254.
- Watson DL, Harvey ES, Fitzpatrick BM, Langlois TJ, Shedrawi G (2010) Assessing reef fish assemblage structure: How do different stereo-video techniques compare? *Mar Biol* 157(6):1237–1250.
- Harvey ES, et al. (2012) Comparison of the relative efficiencies of stereo-BRUVs and traps for sampling tropical continental shelf demersal fishes. *Fish Res* 125–126:108–120.
- Acker JG, Leptoukh G (2007) Online analysis enhances use of NASA earth science data. *Eos Trans AGU* 88(2):14–17.
- Soulsby R (1997) *Dynamics of Marine Sands* (Thomas Telford Publications, London), p 249.
- Bates D, Maechler M, Bolker B, Walker S (2014) lme4: Linear mixed-effects models using Eigen and S4. R package version 1(7).
- Crawley MJ (2013) *The R Book* (Wiley, West Sussex, UK).
- Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecol* 26(1):32–46.
- Green AL, Bellwood DR, eds (2009) *Monitoring Functional Groups of Herbivorous Reef Fishes as Indicators 511 of Coral Reef Resilience—A Practical Guide for Coral Reef Managers in the Asia Pacific Region* (IUCN, Gland, Switzerland).