

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

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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.

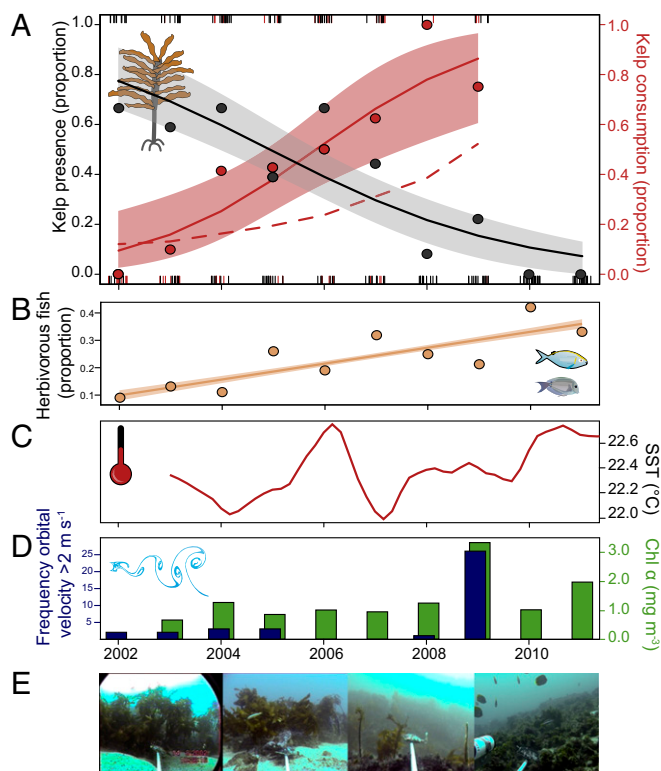
Author contributions: A.V., H.A.M., E.M.M., A.H.C., and P.D.S. designed research; A.V., C.D., H.A.M., M.S., M.G.-P., E.M.M., A.H.C., E.B., A.S.H., A.V.-C., and Y.-M.B. performed research; A.V., C.D., M.S., E.M.M., A.H.C., A.V.-C., and Y.-M.B. analyzed data; and A.V., H.A.M., M.S., E.M.M., A.H.C., E.B.,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

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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).



**Fig. 1.** Ten-year loss of kelp and potential biophysical drivers behind its decline at the Solitary Islands, eastern Australia. Temporal trends in (A) decline of kelp (gray) and increase on the incidence of herbivory (red). Solid circles are the observed mean values, solid lines represent mean of the model fits for presence/absence in the frame of individual BRUVs using binomial regression, and shading is the SEM of model fits. Dashed red line represents the result of a simulation model of a predicted intensification in herbivory due to the concentration of stable herbivory levels on less kelp. Small strokes on the top (kelp presence) and bottom (kelp absence) axes represent individual BRUV replicates; (B) proportional increase of tropical herbivorous fishes within the herbivore community in sites where kelp disappeared, based on MaxN data; (C) trend of average SST (in degrees Celsius); (D) Left y axis (in blue): number of occurrences per year of storms with enough energy to detach kelp holdfasts, that is, wave orbital velocity > 2 m s<sup>-1</sup>, at the depth of kelp observations (18 m); Right y axis (in green) average chlorophyll  $\alpha$  concentration (in milligrams per cubic meter); (E) exemplary BRUV screen shots from 2002 to 2011.

We used a 10-y (2002–2011) baited remote underwater video (BRUV) dataset, collected initially to monitor fish populations, to quantify temporal changes in kelp abundance and kelp–herbivore interactions along reefs spanning 25 km in a tropical–temperate transition zone near the warm edge of distribution of the dominant kelp *Ecklonia radiata* in eastern Australia. Kelp forests completely disappeared from all of the study sites during this period. To understand the mechanisms underlying this deforestation, we quantified three abiotic variables likely to influence kelp distribution: water temperature (6), nutrients (14), and wave action (19, 20), and assessed the role of temperate and tropical herbivores as potential biotic drivers of kelp loss.

Herbivory was quantified through direct measures of bite marks on kelp fronds and temporal changes in herbivore fish community composition. An inshore–offshore gradient in kelp abundance within this tropical–temperate transition zone was further used as a space-for-time substitution to experimentally test the role of herbivores on forested vs. kelp-free reefs. We compared herbivory between the offshore sites (now devoid of kelp) and inshore reefs, the nearest sites where kelp forests still remain. Specifically, we asked, (i) Is kelp decline related to changes in biotic and abiotic variables through time?

(ii) Does fish community composition change as kelp disappears and, specifically, is there evidence of an increase in tropical herbivorous species? (iii) What is the role of herbivores in modulating the contemporary inshore–offshore zonation of kelp communities?

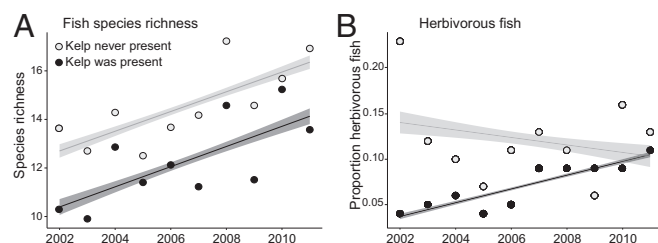
## Results

There was a complete loss of kelp within the BRUV study sites from 2002 to 2011 [likelihood ratio test (LRT),  $\chi^2_{(1,167)} = 57.3$ ,  $P < 0.001$ ; Fig. 1A]. Six of the original 12 sites monitored did not host kelp populations at any stage during the study. At the other six sites, kelp presence declined from ~70% in 2002 to <20% from 2008, with no kelp observed from 2010 onward. The proportion of kelp with obvious feeding marks (Fig. S1) increased significantly throughout the study period [LRT,  $\chi^2_{(1,62)} = 15.8$ ,  $P < 0.001$ ; Fig. 1A]. Herbivory was evident in <10% of BRUV deployments at reefs with kelp in 2002–2003, increased to ~50% by 2004, and to >70% in 2008–2009 (Fig. 1A). Concurrently, the proportion of tropical and subtropical herbivorous fishes within the total herbivorous fish community assemblage at these sites increased from <10% in 2002 to >30% by 2010 [LRT,  $\chi^2_{(1,156)} = 55.3$ ,  $P < 0.001$ ; Fig. 1B].

Average sea surface temperature (SST) increased from 22.1 to 22.7 °C [LRT,  $\chi^2_{(1,107)} = 5.7$ ,  $P = 0.017$ ], with two distinct periods of warming from 2004 to 2006 and from 2007 to 2011 (Fig. 1C). Although kelp presence tended to decrease with increasing average SST (coefficient = -1.2, SE = 1.0; Fig. S2A), multiple-regression analysis showed that kelp decline was not significantly related to average SST [LRT,  $\chi^2_{(1,149)} = 1.92$ ,  $P = 0.166$ ].

Potentially destructive wave energy was 10 times higher in the winter of 2009 than in other periods, and chlorophyll  $\alpha$  was also highest at this time (used here as a proxy for nutrient levels; Fig. 1D). Kelp decline was not related to changes in the concentration of chlorophyll  $\alpha$  [LRT,  $\chi^2_{(1,149)} = 1.84$ ,  $P = 0.175$ ; Fig. S2B] or to the occurrences of storm events capable of dislodging kelp [i.e., wave orbital velocities > 2 m s<sup>-1</sup> (21); LRT,  $\chi^2_{(1,149)} = 0.380$ ,  $P = 0.537$ ; Fig. S2C].

Fish species richness per BRUV deployment increased from 2002 to 2011 at all sites, and was consistently higher at sites where kelp was never present [Time: LRT,  $\chi^2_{(1,336)} = 37.4$ ,  $P < 0.001$ ; Habitat: LRT,  $\chi^2_{(1,336)} = 8.7$ ,  $P < 0.01$ ; Fig. 2A]. Notably, the proportion of herbivorous species within fish assemblages increased over time at sites that experienced kelp decline (i.e., sites where kelp was present in 2002) reaching levels comparable to sites that never had kelp [herbivorous fish: Time by Habitat: LRT,  $\chi^2_{(1,336)} = 249.4$ ,  $P < 0.001$ ; Fig. 2B]. Increases in herbivorous fish abundance in sites where kelp declined were mostly attributable to a rise in the abundance of the grazing surgeonfish *Prionurus microlepidotus*, from an average of 9% in 2002 to 33% in 2011. The proportion of herbivorous fishes decreased marginally over time on kelp-free reefs; however, this trend is strongly influenced by a single data point and should be interpreted with caution (2002; Fig. 2B).



**Fig. 2.** Observed temporal changes in (A) fish species richness, and (B) relative abundances of herbivorous fishes at six reefs where kelp was never present (light gray) and six reefs where kelp was present at the beginning of the study (dark gray). Circles represent the mean values, solid lines represent model fits, and gray bands represent the SE of the model.



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.

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