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

Adriana Vergésa,−c,1, Christopher Doropoulosd,e, Hamish A. Malcolmf, Mathew Skyea,−b, Marina García-Piza,−b, Ezequiel M. Marzinellia,b,c,g, Alexandra H. Campbella,−b,c, Enric Ballesterosb, Andrew S. Hoeyj, Ana Vila-Concejolj, Yves-Marie Bozece,l, and Peter D. Steinbergc,−f,g

*Centre for Marine Bio-Innovation, School of Biological, Earth, and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia; bEvolution and Ecology Research Centre, School of Biological, Earth, and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia; cCommonwealth Scientific and Industrial Research Organization Oceans and Atmosphere, Dutton Park, QLD 4102, Australia; *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; 1Marine Ecosystem Research, Fisheries NSW, Department of Primary Industries, Coﬀs Harbour, NSW 2450, Australia; *Singapore Centre for Environmental Life Sciences Engineering, Nanyang Technical University, Singapore 637751, Singapore; 2Centre d’Estudis Avançats de Blanes (Consejo Superior de Investigaciones Científicas), 17300 Blanes, Girona, Spain; 3Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia; and 4Geocoastal Research Group, School of Geoscience, The University of Sydney, Sydney, NSW 2006, Australia

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.

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.


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

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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. L4]. 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. L4]. 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. L4). 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 $a$ 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 $a$ [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$^{-1}$ (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 35% 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. 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$^{-1}$, at the depth of kelp observations (18 m); Right $y$ axis (in green) average chlorophyll $a$ concentration (in milligrams per cubic meter); (E) exemplary BRUV screen shots from 2002 to 2011.

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.
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 declines in 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 community 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. 3 A 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 fuscescens* and *Prionurus unifasciata*, and the presence of *Johnsia 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% (±0.09 SEM) of the initial kelp frond area offered 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. fuscescens* 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 *Tripneustes gratilla*, 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 (±SE) 86.58 ± 9.96 bites·h⁻¹·m⁻², eightfold higher than *S. fuscescens*, 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. fuscescens* from two occurrences, and 3 bites for *P. microlepidotus* from one individual (average ±SE: 0.45 ± 0.09 and 0.05 ± 0.01 bites·h⁻¹·m⁻², respectively).

The two main consumers of kelp fronds in the filmed assays, *S. fuscescens* 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. S5 A and B). In contrast, the grazer *P. microlepidotus* 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 Vergès 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 bites h$^{-1}$ m$^{-2}$) and by the entire grazing community (122.3 bites h$^{-1}$ 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 then, indicating that the intensity of herbivory remained as high as from experimental bioassays that identified two tropical/subtropical species as the main consumers: the rabbitfish *S. fuscescens* and the drummer *K. bigibbus*. 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. bigibbus*, 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. 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. bigibbus*), rather than an increase in overall browser abundance (24).

EAM 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 temperate algal forests if it expands its range poleward and becomes more abundant in higher latitudes. The black urchin *C. rogersii* also consumed some of the tattered 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 ± SE = 2.5 ± 0.4 individuals m$^{-2}$) is too low to initiate a phase shift and cause a large overall browser abundance (4–10 individuals 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 °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 acclimateize 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 anomaly, and such a warming event in the past may 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 or 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/subtropical fishes increased in number, and 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, and serve as a source of carbon credits for coastal carbon projects (43). 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 ~200 m) were deployed annually around August at a depth of 15–21 m (17.9 ± 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 same fish in the overall fish community structure. Although BRUVs baited with brown algae would have been more efficient for surveying browsing fishes (25), pilchard-baited RVUs produce similar estimates of herbivorous fish biomass to unbaited RVUs (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 in the overall fish community structure. Although BRUVs baited with brown algae would have been more efficient for surveying browsing fishes (25), pilchard-baited RVUs produce similar estimates of herbivorous fish biomass to unbaited RVUs (46) and diver-operated videos (47).

To identify whether there was a warming trend between 2003 and 2011 in the study region, we used a linear mixed-effects model following Cravely (52), with mean monthly SST averaged from five sites (see details in Fig. S5) 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 feeding being concentrated on fewer kelp sites as kelp populations declined. We concluded that the nearshore 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 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(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 sites “kelp consumed sites” vs. 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 Patterns of 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 and after each assay. Three to eight kelp assays (4.9 ± SD 1.5 cm) were attached to a small lead weight and deployed at a depth of 10 m within each site, with adjacent assays being separated by ≥4 m. Assays were conducted between 10:00 AM to 3:00 PM, for 70 min (∼300 wave cycles) and incorporating year as random effect (52).

**Spatial 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) (“*lm4*” R package; ref. 51), using kelp presence as the binomial response variable, year as the continuous predictor, and site 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⁻¹ 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 α, 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 α satellite data only begin in July 2002 at a 4-km² resolution, and therefore artificially reduced the annual temperature and chlorophyll α 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. Wave energy was curtailed in Fig. S1. For each site, data 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 (χ²) P values.
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 X 5-m (125-m²) belt transects were laid at each site, swam at a constant rate, and the abundances and sizes (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/). On the return swim, the same observer quantified urchin abundance within a 1-m band (i.e., 25 X 1 m).

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