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ARTICLE

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Ocean warming undermines the recovery resilience of New England kelp forests following a fishery-induced trophic cascade

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Abstract

Ecological theory predicts that kelp forests structured by trophic cascades should experience recovery and persistence of their foundation species when herbivores become rare. Yet, climate change may be altering the outcomes of top-down forcing in kelp forests, especially those located in regions that have rapidly warmed in recent decades, such as the Gulf of Maine. Here, using data collected annually from 30+ sites spanning >350 km of coastline, we explored the dynamics of Maine's kelp forests in the ~20 years after a fishery-induced elimination of sea urchin herbivores. Although forests (*Saccharina latissima* and *Laminaria digitata*) had broadly returned to Maine in the late 20th century, we found that forests in northeast Maine have since experienced slow but significant declines in kelp, and forest persistence in the northeast was juxtaposed by a rapid, widespread collapse in the southwest. Forests collapsed in the southwest apparently because ocean warming has—directly and indirectly—made this area inhospitable to kelp. Indeed, when modeling drivers of change using causal techniques from econometrics, we discovered that unusually high summer seawater temperatures the year prior, unusually high spring seawater temperatures, and high sea urchin densities each negatively impacted kelp abundance. Furthermore, the relative power and absolute impact of these drivers varied geographically. Our findings reveal that ocean warming is redefining the outcomes of top-down forcing in this system, whereby herbivore removal no longer predictably leads to a sustained dominance of foundational kelps but instead has led to a waning dominance (northeast) or the rise of a novel phase state defined by "turf" algae (southwest). Such findings indicate that limiting climate change and managing for low herbivore abundances will be essential for preventing further loss of the vast forests that still exist in northeast Maine. They also more broadly highlight that climate change is “rewriting the rules” of nature, and thus that ecological theory and practice must be revised to account for shifting species and processes.

KEYWORDS
herbivory, *Laminaria digitata*, phase shift, range shift, *Saccharina latissima*, species on the move, top-down vs. bottom-up

INTRODUCTION

Historically, the presence or absence of large predators (and a resultant trophic cascade [Ripple et al., 2016]) shaped the trajectories of many kelp forest ecosystems (Steneck et al., 2002). This ubiquity and power of top-down forcing allowed ecologists to reliably understand and predict patterns of kelp forest community structure and ecosystem resilience for several decades (Dayton, 1985; Steneck et al., 2002). More recently, however, the direct and indirect effects of ocean warming and marine heatwaves have increasingly altered kelp performance, especially at the “warm edge” of their geographic ranges (Arafeh-Dalmau et al., 2019; Cavanaugh et al., 2019; Filbee-Dexter & Wernberg, 2018; McPherson et al., 2021; Smale et al., 2019; Smale & Wernberg, 2013; Wernberg et al., 2016). Thus, there is now considerable scope for climate change to alter the distribution of kelp in today’s oceans, but such effects will depend on the relative power of, and interaction between, top-down and bottom-up forces in a given region. In line with this notion, while some kelp forests have declined over the past 50 years, others have been in stasis, and still others have recovered or expanded (e.g., Beas-Luna et al., 2020; Krumhansl et al., 2016). Yet, to date, the effects of trophic cascades and climate change on kelp forests have largely been studied separately (but see, e.g., [Ling et al., 2009; Rasher et al., 2020; Smith et al., 2021]), leading to a limited understanding of how top-down forcing (predator–prey interactions) and bottom-up forcing (environmental stress) interactively shape modern forests. This knowledge gap is compounded by a general lack of large-scale, long-term data for kelp forest ecosystems (Krumhansl et al., 2016).

For example, the Gulf of Maine coastal ecosystem incurred striking ecological changes during the 20th century because of overfishing, and has since experienced rapid ocean warming. It remains unclear, however, how these factors have jointly impacted Maine’s kelp forests and altered their distribution, abundance, and community composition. During the 20th century, the collapse of predatory finfish populations (Atlantic cod and wolf fish) corresponded with a proliferation of sea urchins (*Strongylocentrotus droebachiensis*) whose grazing deforested coastal reefs in the region (Steneck et al., 2004, 2013). Humans then harvested sea urchins until the fishery collapsed; by the early 2000s sea urchins had become “ecologically extinct” (sensu [Soulé et al., 2003]) on the outer coast of Maine (Steneck et al., 2013). In the wake of the fishery, kelp forests rapidly recovered (Steneck et al., 2013), first in the southwest by the mid 1990s (where the sea urchin fishery was first exhausted) and then in the northeast by the late 1990s to early 2000s (as the fishery shifted northward and serially waned). Kelp forest recovery, and overfishing, resulted in an increase in benthic invertebrate predators (crabs) that consumed incoming juvenile sea urchins, thereby reinforcing the shift back to kelp (Steneck et al., 2013). Since then, however, ocean temperatures have rapidly risen (Pershing et al., 2015), with summer seawater temperatures in southwest Maine beginning to resemble those south of the Gulf of Maine, where forests have recently collapsed (Feehan et al., 2019; Filbee-Dexter et al., 2020). Therefore, in the absence of large-scale data, it remains unknown (a) where, and to what degree, sea urchins have remained scarce in Maine’s coastal ecosystem, (b) if Maine’s kelp forests persisted or continued to recover over the past ~20 years concurrent with modern sea urchin dynamics and rapid warming, (c) if recent forest trajectories and compositions have varied between oceanographically colder (northeast) versus warmer (southwest) subregions, or (d) where, and to what degree, ecological processes (sea urchin herbivory) versus abiotic stressors (rising temperatures) have governed kelp abundance and distribution in recent decades.

To answer these questions, each year from 2001 to 2018 we surveyed between 31 and 67 forests—spanning >350 km of coastline in Maine (USA)—and then modeled how temperature change and sea urchin density influenced kelp abundance using causal techniques hailing from econometrics (Antonakis et al., 2021; Bell et al., 2018, 2019). Notably, the time period we studied was marked by rapid regional warming and several marine heatwaves, allowing us to explore the emergent effects of climate change in this “natural laboratory.” Additionally, the vast stretch of ocean that we studied (Figure 1) spans both the Eastern and Western Maine Coastal Currents, oceanographic features that together produce a more than 6°C difference in summer seawater temperatures from

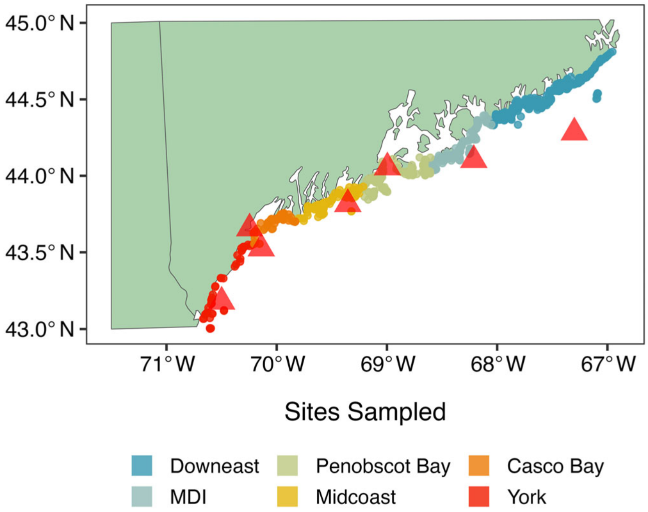

FIGURE 1 A map of reef sites surveyed between 2001 and 2018 (dots), colored by subregion. Red triangles denote the locations of oceanographic buoys that were used to derive NSSTs.

north to south (Appendix S1: Figures S1 and S2). Our approach thus allowed us to quantify (and predict, over the near-term) how ocean warming is differentially impacting kelp populations in cooler (northern) versus warmer (southern) subregions of the Gulf of Maine.

METHODS

Quantifying kelp forest trajectories through time and space

To quantify changes in Maine's kelp forests through time and space, we conducted in situ surveys (via scuba) of rocky reefs every year from 2001 to 2018 (via long-term monitoring by the Maine Department of Marine Resources; hereafter "ME-DMR"). From May to June of each year, ME-DMR divers visually surveyed up to 140 randomly selected sites, some of which were sheltered from waves and/or in rivers or estuarine environments and were subsequently excluded from our analysis (see below). At each site, the diver began their survey at 15 m depth (mean lower low water, hereafter "MLLW") and swam perpendicular to the shore, placing a 1 m^2 quadrat at predetermined intervals (associated with 15, 10, and 5 m depth isobaths). The diver recorded aggregate percent cover of subsurface canopy-forming macroalgae and understory macroalgae (respectively) within the quadrat ($n = 10$ quadrats per depth per site, except three sites where $n = 3$–10). Subsurface canopy-forming macroalgae included the kelps *Saccharina latissima*, *Laminaria digitata*, *Alaria esculenta*, and *Agarum clathratum* (order Laminariales) as well as two *Desmarestia* species. However, because *Desmarestia* accounted for a very small amount of macroalgae surveyed (percent cover in all species-specific surveys from 2016 to 2018: mean: 2.6; SD: 4.2; range: 0.0 to 26.3; Appendix S1: Figure S3), we hereafter refer to the ME-DMR canopy-forming macroalgae data as "kelp." To specifically align ME-DMR survey data with the focal areas of past studies (i.e., wave-exposed reefs located at the ends of peninsulas and offshore islands), we scored the wave exposure of each site and its distance from shore (using a scale of 1–5 for each metric), then removed all sheltered sites (exposure score of 2 or less) and inland sites (coastal score of 2 or less). To classify the wave exposure of each site, we estimated the total arc (in degrees) where a site was exposed to the open ocean (i.e., a "fetch" of more than 10 km). Sites with a score of 1 had no open ocean fetch whereas those with a score of 5 had close to 180° of exposure to open ocean. To classify distance from shore, we set the exposed mainland coast at a level of 3 and then assigned offshore islands with higher scores and sites within rivers or estuaries with lower scores. Site classifications including location, exposure score, and distance from shore score are available to the reader in the open-access data (Rasher et al., 2024). While rare, any quadrats conducted in soft-bottom or unstable (i.e., pebble) habitats were excluded.

For analysis, we divided the coast into six subregions based on hydrology, geographic breaks (e.g., embayment) and local convention. From southwest to northeast these are York, Casco Bay, Midcoast, Penobscot Bay, Mount Desert Island (hereafter "MDI") and Downeast (Figure 1). Casco Bay subregion extends from Cape Elizabeth to Cape Small and is a well defined embayment. Likewise, Penobscot Bay extends from Port Clyde to Isle au Haut and is another large, well defined embayment. Downeast Maine extends from the Schoodic Peninsula to the US–Canadian border. The Midcoast and MDI subregions are interspersed between these bays. The York subregion extends from Cape Elizabeth to the Maine–New Hampshire border (Figure 1). These subregions also broadly follow existing state fishery management zones (e.g., Downeast and MDI correspond to zones A and B for the American lobster fishery, respectively).

Excluding sites for analysis—based on the aforementioned criteria—produced a filtered ME-DMR dataset containing $n = 3$–31 sites per subregion per year (except 2015–2018, when York and Casco Bay were not surveyed). We then augmented this filtered ME-DMR dataset with other, species-specific algal community data collected by the authors in 2016, 2017, and 2018 from various subregions (including York and Casco Bay) that met the same criteria (see below), to bolster our analyses of the impacts of seawater temperature and sea urchins on kelp (see *Statistical analyses*). The resultant dataset contained between 31 and 67 wave-exposed, outer coastal study sites per year for analysis (see Appendix S1: Table S1 for a breakdown of site sample sizes per subregion per year). Within the dataset, we only analyzed data collected at 5 m depth, because (a) only this depth was consistently surveyed across years and programs and (b) it predictably harbors stable substrate (ledge, boulder), a prerequisite to forest development.

Quantifying changes in algal community composition

To quantify changes in algal community composition through time and space, we also conducted high-resolution in situ surveys (via SCUBA) of similar rocky reefs along the coast of Maine during the summers of 2004, 2016, 2017, and 2018. Survey sites in 2004 ($n = 6$ to 31 sites per subregion; 100 total) were selected using a random-number generator to determine the site's longitude within a predetermined segment of coastline; the most wave-exposed point closest to this longitude became the dive site. In 2016, 2017, and 2018, we randomly resampled a subset of the 2004 sites. In 2016, we resurveyed five sites in three subregions (Midcoast, MDI, and Downeast) and in 2017, we resurveyed 22 sites in three subregions (Penobscot Bay, MDI, and Downeast). In 2018, we resurveyed all subregions ($n = 29$ sites, 5 to 6 sites per subregion) except for York; data for York in 2018 were acquired from author JEKB. Each site was surveyed at 5 to 7 m depth (MLLW; hereafter "5 m depth") as well as at 10 m depth MLLW each year. However, when analyzing changes in community composition, we focused only on data from 5 m depth (for the reasons described above). The one deviation from this approach was for York, where surveys were conducted at 7 to 10 m depth; we included these data despite the depth difference because no other 2018 data were available. As with ME-DMR data, prior to analysis we scored the wave exposure of each site and its distance from shore, then removed any surveys of inland sites, sheltered sites, and the few quadrats conducted in soft-bottom or unstable habitat, from each dataset. The resultant sample sizes of sites per subregion per year in the analysis of change in algal community composition at 5 m depth are presented in Appendix S1: Table S2.

At each site and depth, a diver quantified the species identity and percent cover of all kelps and other canopy-forming macroalgae (i.e., *Desmarestia* spp.) found within a 1 m^2 quadrat. This process was repeated at predetermined intervals along a 10 m transect ($n \geq 8$ quadrats per depth per site). In addition, within a 0.25 m^2 subsection of every quadrat, the diver assessed the identity and percent cover of all macroalgae that defined the understory. Last, within each 1 m^2 quadrat, the diver categorized the substrate type (ledge, boulder, cobble, and so forth, using the scale in Wentworth (1922)). The only deviation from this protocol was in York in 2018, where a Universal Point Contact method ($n = 80$ points along a 40 m transect) was instead used.

Kelps were identified to the species level. Understory algae were identified to genus or species level, except for filamentous red algae, which were grouped. For the kelp time series analysis and associated driver model (see *Statistical analyses*), percent cover estimates of each kelp species were aggregated as the total percent cover of kelp and combined with the ME-DMR data. In models assessing changes in algal community composition, percent cover estimates were left at the species level or grouped at the genus or higher level for those that could not be resolved in the field. Changes in algal community composition were evaluated between years 2004 and 2018, the only years when all six subregions were surveyed at this higher taxonomic resolution.

Quantifying sea urchin density through time and space

We enumerated the density of adult green sea urchins (*S. droebachiensis* with a test diameter > 20 mm) found within each 1 m^2 quadrat sampled during the annual ME-DMR survey, as well as during the species-specific algal surveys conducted from 2016 to 2018 (but not 2004). As with algal data, we filtered the combined sea urchin density dataset to include data only from 5 m depth and from those sites that met our aforementioned criteria.

When sea urchins were found, we also measured their size (test diameter, to the nearest mm) in a subset of the ME-DMR quadrats ($n = 2$ per depth per site) or all of the quadrats censused during the high-resolution algal surveys from 2016 to 2018 ($n \geq 8$ per depth per site). A summary of sea urchin sizes through time and space can be found in Appendix S1: Figure S4.

Quantifying seawater temperature changes through time and space

Kelps thrive in cool, nutrient-rich water (Hurd et al., 2014; Lüning, 1990) and rising seawater temperatures are known to—both directly and indirectly—reduce kelp abundance, reproductive success, and recovery from disturbance

(Filbee-Dexter & Wernberg, 2018; Smale, 2020; Vergés et al., 2014; Wernberg et al., 2011). To assess the possible effects of changing seawater temperatures on kelp (see *Statistical analyses*), we obtained publicly available seawater temperature data for 2001–2018 from NERACOOS and NOAA oceanographic buoys (National Buoy Data Center, 1971) located in all six subregions. Measurements were made at depths shallower than our kelp forest surveys (1 m vs. 5 m depth) but were nevertheless utilized here, because (a) in situ seawater temperature data at the reef level are lacking in this region, and (b) during summer, Maine's coastal thermocline is typically below 10 m depth (Brown & Irish, 1993). More, empirical buoy measurements are generally more accurate than satellite-derived estimates of SST (Vinogradova et al., 2009). We thus calculated daily mean "Near-Surface" Seawater Temperatures (NSSTs) from hourly measurements taken at 1 m depth. In Casco Bay, NSST data from NDBC 44007 were primarily used, whereas CASM1 provided data during several weeks when NDBC 44007 was out of service. The Downeast buoy (NDBC 44027) had multiday or month-long gaps during 8 of 18 study years. We interpolated these missing data using nearby MDI data by way of linear regression ($R^2 = 0.943$). Otherwise, data originated from a single buoy in each subregion (Figure 1). While missing daily data occurred up to 8%–12% for some subregions, we averaged data together in spring and summer, ultimately only losing 1 or 2 data points per subregion.

ME-DMR kelp forest surveys occurred primarily in May of each year from 2001 to 2018. We hypothesized that two components of annual temperature change influenced the abundance of kelp observed during each survey: (1) summer (1 June to 31 August) seawater temperatures experienced the year prior, which may have affected adult kelp biomass (via direct mortality) or impacted reproduction in the prior year, and (2) spring (1 March to 31 May) temperatures in the 2–3 months leading up to and during the survey, which may have impacted adult and juvenile kelp growth during this time—the peak of primary production—either via thermal stress or due to reduced nutrient availability. We thus calculated mean and maximum spring NSSTs, as well as 1-year time lagged mean and maximum summer NSSTs, for each subregion from 2002 to 2018. For each, we also calculated subregional means across the time series, as well as annual deviations (anomalies) from the subregional mean, for our model (see below). We considered other temperature calculations, including "heat degree days" (the cumulative number of days where temperatures exceeded known thermal tipping points for kelps, Appendix S1: Figure S5) but these alternative temperature metrics were too collinear with means to be used in our models.

We repeated this process using ¼° resolution temperature data from the National Oceanographic and Atmospheric Administration's Optimum Interpolated Sea Surface Temperature (OISST) product (Banzon et al., 2016; Huang et al., 2021; Reynolds et al., 2007) in order to evaluate if more spatially extensive modeled seawater temperature data would provide clearer answers within our models. All results (Appendix S1: Figures S1 and S2) were qualitatively the same as using buoy temperature data and thus we chose to use the buoy data for simplicity.

Statistical analyses: Patterns and drivers of change in kelp abundance

To evaluate temporal trends in kelp percent cover and whether they varied by subregion, we fit simple generalized linear models with time, subregion, and an interaction term to each response variable in R (version 4.1.1 [R Core Team and Team, 2021]), using the combined datasets from the ME-DMR survey (2001–2018) and high-resolution surveys conducted in 2016–2018. Of note, data from the high-resolution 2004 survey were not used in the time series and associated models because sea urchins were not enumerated in that survey. For kelp percent cover, we fit a beta regression with a logit link with the same three predictors using the *betareg* package (Cribari-Neto & Zeileis, 2010). We evaluated model assumptions of uniform quantile residuals using DHARMa (Hartig, 2021) and a lack of correlation between time and residuals within a subregion. In each case, the data met the model assumptions.

To assess the relationships between kelp abundance and temperature, sea urchins, and other subregional drivers correlated with both of these potential drivers, we fit a generalized linear mixed effects model with a beta error and logit link. Estimated kelp abundance in the model was described as follows for site i in subregion j and year t with α_j and α_t as site and year random effects, respectively:

$$\operatorname{logit}\left(\widehat{k_{ijt}}\right) = \beta_0 + \beta_1\left(u_{ijt} - \overline{u_j}\right) + \beta_2\left(s_{jt} - \overline{s_j}\right) + \beta_3\left(l_{jt} - \overline{l_j}\right) + \beta_4\overline{u_j} + \beta_5\overline{s_j} + \beta_6\overline{l_j} + \alpha_j + \alpha_t,$$

here k is kelp proportion cover, u is adult sea urchin density, s is subregional mean NSST in the spring, l is subregional mean NSST in the summer of the previous year, and both alphas are random effects of subregion and year. Random effects represent the influence of other, unmeasured temporal and spatial factors that were uncorrelated with the drivers of interest. We also included "group mean-centered" sea urchin density and temperature terms (in addition to subregional mean sea urchin and temperature variables, e.g., the $u_{ijt} - \overline{u_j}$ term for sea urchins). Group mean centering refers to calculating anomalies in each measurement relative to their associated subregional mean across all years, rather than an anomaly relative to the entire dataset. Employing group mean-centered terms in our model allowed us to use the longitudinal data and pull out the signal of other, unmeasured subregional drivers that are correlated with temperature or sea urchin density. This technique for handling confounding omitted variable bias is common in econometrics (Wooldridge, 2010) and using this technique allowed us to obtain cleaner estimates of causal drivers (Antonakis et al., 2021; Bell et al., 2018, 2019).

Using this type of causal model with observational data is critical, because putative drivers can be spatially confounded with other factors at the regional level. Temperature, for example, also matches a gradient in urbanization and coastal oceanography (i.e., nutrients, stratification) in this system. By including the subregional averages over time, the confounding signal from these and other unobserved variables that are correlated with subregion are accounted for in the group mean term. Subregion-level anomalies thus represent the effects of changes in the causal driver of interest, while holding subregion-level confounders constant. This method assumes that the driver anomalies (relative to their subregional means) are (1) not confounded with other, unmeasured drivers of the response variable and (2) the reason for those anomalies does not vary by subregion. We tested the first assumption by relaxing it; that is, using "year" as a fixed categorical effect in the model. We did so with the OISST data, as the buoy temperature data had too little variation in temperature for this approach. Our results did not change. We found the second assumption—that the reason for anomalies did not vary by subregion—reasonable, as biotic and abiotic processes were unlikely to vary dramatically between subregions. For a more thorough explanation of this modeling approach, see the references above and the appendices of Dee et al. (2023).

In our causal model, the lack of interaction terms was purposeful. Changes in kelp abundance from ocean warming, if starting from a cold temperature, could be small. Changes in kelp abundance from warming, if starting from moderate temperatures, might be rapid. This would not be due to an interaction effect, but rather the nonlinearity of the relationship examined. Models were fit using the *glmmTMB* package in R and assessed with diagnostics as described previously.

Statistical analyses: Counterfactual models to reveal the primacy and strength of drivers

Because the subregional anomalies in the causal model produce an inference that has been de-confounded from the influence of other factors that correlate spatially with each term, the fit model—including subregional means—can then be used to generate counterfactual predictions under different scenarios in order to understand the relative impact of each driver. We therefore used our fit models to explore several counterfactual scenarios:

1. The direct impact of spring warming under different sea urchin density scenarios: The effect of a spring temperature anomaly with a low, moderate, or high sea urchin density anomaly, relative to subregional means (and no lagged summer temperature anomaly).
2. The net effect of seawater warming: The impact of a spring temperature anomaly along with a negative, zero, or positive lagged summer temperature anomaly (and with sea urchin density anomaly held at 0).
3. The impact of ocean warming on top-down control: The effect of a sea urchin density anomaly when coupled with a negative, zero, or positive spring temperature anomaly (and with lagged summer temperature anomaly held at 0).

Statistical analyses: Patterns and drivers of change in algal community composition

Finally, we evaluated change in kelp and understory species composition (separately) between 2004 and 2018 using a generalized latent linear variable modeling (GLLVM) approach in the *gllvm* package (Niku et al., 2019, 2021) in R. We used GLLVM rather than NMDS or other approaches because we wanted to evaluate changes in different species and overall community composition parametrically while controlling for correlations between species. Using GLLVM, we were able to evaluate changes in means, which species changed and which did not, and account for correlations between species abundances using underlying latent variables. For all models, we utilized two latent variables to account for correlations between response variables. All response variables were logit transformed in order to meet assumptions of using percent cover data with a model with a Gaussian error and identity link function.

RESULTS

Ecosystem change through time and space

With the exception of Downeast and a small number of sites in the MDI and Penobscot Bay subregions, sea urchins were rare along Maine's outer coast at the turn of the 21st century (Figure 2). They remained in low abundance over the next two decades, with the exception of nine site-year combinations (mostly in the northeast) where adult densities exceeded 30 per m^2, a density threshold at which green sea urchins denude kelp forests in the Northwest Atlantic (Filbee-Dexter & Scheibling, 2014). This long-term, widespread rarity of herbivores should have led to a lasting, stable persistence (and continued recovery) of kelp forests across the entire region (Breen & Mann, 1976; Himmelman et al., 1983; Steneck et al., 2013). Yet, the long-term trajectories of kelp forests were generally negative, with the scope of decline varying markedly as a function of subregion (Figure 3; Appendix S1: Table S3).

Kelp forests were lush and widespread across northeast Maine (MDI and Downeast) from 2001 to 2004, with kelp cover averaging ~80%–85% by 2004. However, these northeast subregions then incurred slow but significant declines in kelp abundance (on average), resulting in forests remaining widespread but site-level abundances declining to ~55%–70% cover on average by 2018. Average kelp cover in the center of Maine's coast was more variable and significantly declined (from 80% to 50% in Penobscot Bay) or did not significantly change (in Midcoast). By contrast, kelp forests in the southwestern subregions had already collapsed by the early 2000s (York) or experienced rapid and precipitous declines (Casco Bay) from 2001 to 2012 (Figure 3; Appendix S1: Table S3), with average cover in York falling to less than 10% by 2014. Kelp cover across the southwest subregions was very low as of 2018.

Drivers of ecosystem change

Drivers of kelp decline could include (a) sea urchins, whose grazing can reduce kelp cover or denude entire reefs, when very abundant (Filbee-Dexter & Scheibling, 2014)

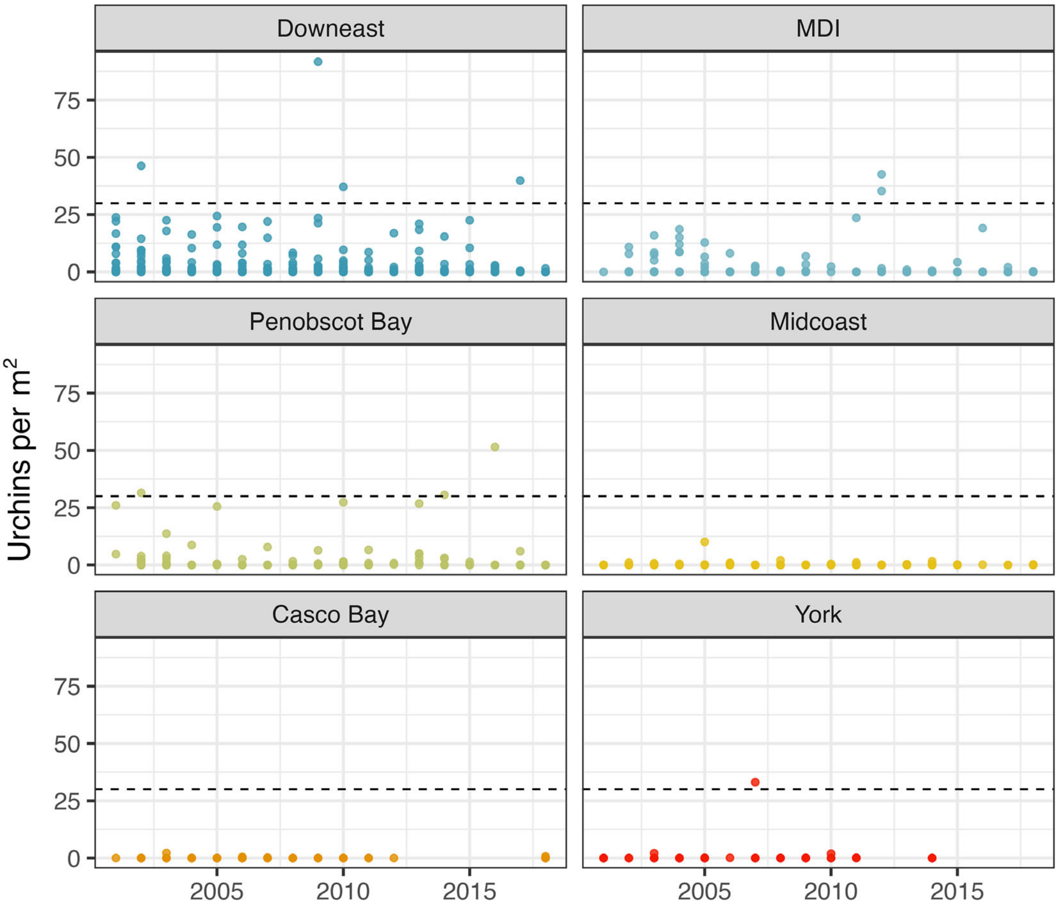

FIGURE 2 Sea urchin density (number per square meter) within each subregion of Maine, 2001 to 2018. Each dot depicts a site-level mean, derived from replicate surveys at 5 m depth. Dotted line: a known density threshold above which green sea urchins deforest reefs in the Northwest Atlantic.

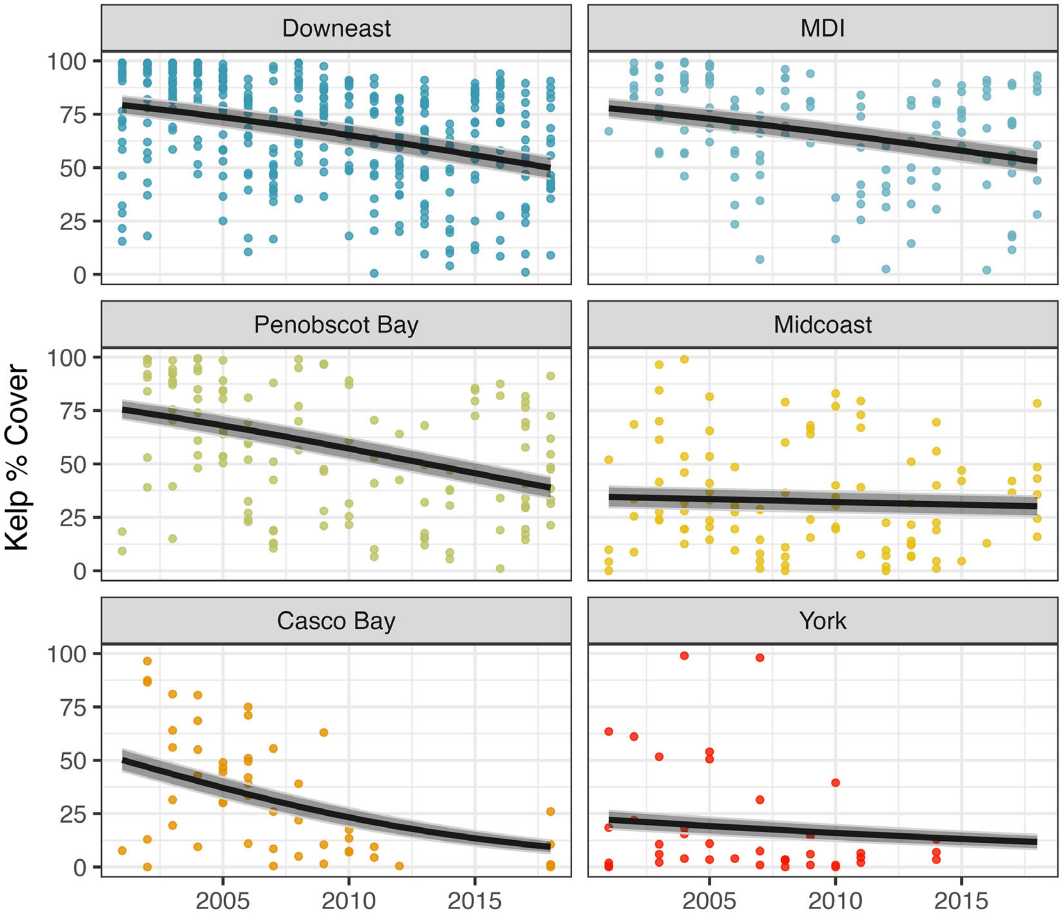

FIGURE 3 Kelp abundance (percent cover) within each subregion of Maine, 2001 to 2018. Each dot depicts a site-level mean, derived from replicate surveys at 5 m depth. See Appendix S1: Table S3 for model outputs.

and/or (b) rising ocean temperatures, which can reduce kelp reproductive success (Bartsch et al., 2013; Gauci et al., 2022; Liesner et al., 2020), reduce kelp performance via declines in nutrients (García-Reyes et al., 2022; Zimmerman & Kremer, 1984), and trigger mortality when they exceed kelp thermal tolerance limits (Hurd et al., 2014; Lüning, 1990). From 2001 to 2018, sea urchins were highly abundant across just nine site-year combinations, primarily in Downeast, MDI, and Penobscot Bay subregions (Figure 2). During this period, mean spring and summer NSSTs rapidly increased (at least ~0.05°C per year and up to ~0.1°C per year) (Figure 4; Appendix S1: Tables S4–S9), but to very different absolute levels in the Eastern versus Western Maine Coastal Currents (Brooks & Townsend, 1989), and this rapid warming was punctuated by several marine heatwaves. Recently, maximum summer NSSTs in southern Maine commonly exceeded 20°C and were, on average, ~5.6°C warmer than those observed in northeast Maine. Consequently, southwestern subregions now regularly experience temperatures (15°C) at which nitrate saturation reaches zero (García-Reyes et al., 2022; Zimmerman & Kremer, 1984) as well as temperatures (20°C) at which sugar kelp erodes faster than it grows (Lee & Brinkhuis, 1986).

Modeling of driver effects and near-term change

Modeling our data with techniques that account for other, unmeasured factors that could be confounding, we found that—over the past ~20 years—the occurrence of high sea urchin densities, unusually warm spring NSSTs, and unusually warm summer NSSTs (the year prior) each strongly and negatively influenced kelp abundance through space and time (Tables 1 and 2). Such findings suggest that environmental stress and local ecology (herbivore–kelp interactions) have both shaped forest trajectories (Figure 3) but to varying levels depending on subregion. To disentangle the relative influence of these drivers, identify their context-dependencies, and predict potential near-term changes to the ecosystem, we next modeled various counterfactual scenarios using our ~20 years of empirical data.

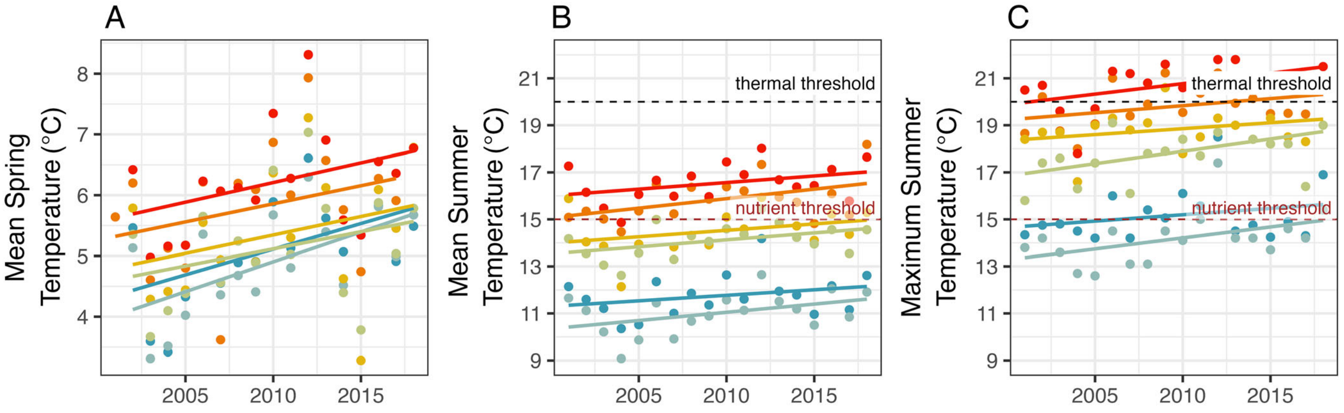

FIGURE 4 Mean spring (A), mean summer (B), and maximum summer (C) seawater NSSTs (in degrees Celsius) in each subregion of Maine, 2001 to 2018. Subregions are coded as follows: Dark blue = Downeast; Light blue = MDI; Green = Penobscot Bay; Yellow = Midcoast; Orange = Casco Bay; Red = York. Dotted lines represent known thresholds for thermal and nutrient stress for the two dominant kelp species. See Appendix S1: Tables S4–S9 for model outputs.

TABLE 1 χ^2 likelihood ratio tests of drivers of kelp abundance across the outer coast of Maine.

Term	χ^2	df	*p*
Sea urchin anomaly	54.149	1	1.859e-13
Spring temperature anomaly	4.588	1	3.219e-02
Lag summer temperature anomaly	5.349	1	2.074e-02
Mean sea urchins in subregion	44.439	1	2.624e-11
Mean spring temperature in subregion	51.701	1	6.463e-13
Mean lag summer temperature in subregion	1.169	1	2.795e-01

When modeling the effect of spring temperature anomalies across several sea urchin density scenarios (and holding lagged summer temperature anomalies at 0), our data revealed that overgrazing by sea urchins negates any temperature or subregional effect in the ecosystem (Figure 5); in this scenario, a hyperabundance of sea urchins (80 per m^2 greater than the mean) results in kelp being broadly absent and thus the impacts of rising spring NSSTs are masked (Figure 5, right). With a density anomaly of 40 per m^2 greater than the mean, sea urchins reduce kelp cover to universally low levels (5%–30% cover, depending on subregion) but then unusually high spring NSSTs further reduce kelp cover, particularly in the northeast (Figure 5, middle). Here, in the southwest, the combined effects of drivers (potentially including but not limited to temperature) hold kelp at low cover regardless. By contrast, in the scenario in which sea urchins are scarce (as exists now), spring warming anomalies reduce kelp cover, but the absolute impact of such anomalies (i.e., the start and end points of kelp cover) differ greatly by subregion (Figure 5, left) given the different temperatures that exist across subregions. Such a modeling exercise predicts that, in the absence of summer warming anomalies, the northeastern subregions would continue to host lush kelp forests over the near-term if sea urchin populations were kept in check.

Under a second set of scenarios—where spring and lagged summer seawater temperature anomalies are varied but sea urchin density anomalies are held at zero—our data revealed that these two facets of ocean warming acted in concert to reduce kelp abundance (Figure 6). Unusually high spring NSSTs reduce kelp cover under all three scenarios, while the presence of unusually warm summer NSSTs the year prior leads to notably greater reductions (Figure 6, middle to right). Importantly, however, there are geographic differences in the scope for these temperature effects, given the differing subregional conditions. This modeling exercise predicts that reoccurring warming anomalies in both the spring and summer will cause a further collapse of kelp forests in the southwest (York and Casco Bay), a novel collapse of kelp forests in the Midcoast subregion, and a continued, gradual decline of the kelp forests found in Penobscot Bay, MDI, and Downeast subregions. If so, in the face of an unusually warm summer followed by an unusually warm spring, even those forests that currently exist in the cold, far northeasterly subregions may fall to 40% cover (Figure 6, right).

Finally, when assessing the effects of gaining versus losing sea urchins under various spring warming scenarios (and no lagged summer warming anomaly), our data revealed that unusually high temperatures redefine the potential outcomes of top-down forcing on kelp cover (Figure 7). Under all three scenarios, a hyperabundance of sea urchins always drives down kelp cover due to overgrazing, but the relative impact of grazing decreases under unusually warm spring conditions (Figure 7, left to

TABLE 2 Coefficient estimates, SE, and *z* tests for the main model described in the study.

Term	Estimate	SE	*z*	*p*
Intercept	7.678	0.863	8.897	5.745e-19
Sea urchin anomaly	−0.051	0.007	−7.359	1.859e-13
Spring temperature anomaly	−0.216	0.101	−2.142	3.219e-02
Lag summer temperature anomaly	−0.204	0.088	−2.313	2.074e-02
Mean sea urchins in subregion	0.322	0.048	6.666	2.624e-11
Mean spring temperature in subregion	−1.771	0.246	−7.190	6.463e-13
Mean lag summer temperature in subregion	0.057	0.053	1.081	2.795e-01
Year SD	0.405			
Subregion SD	0.000			

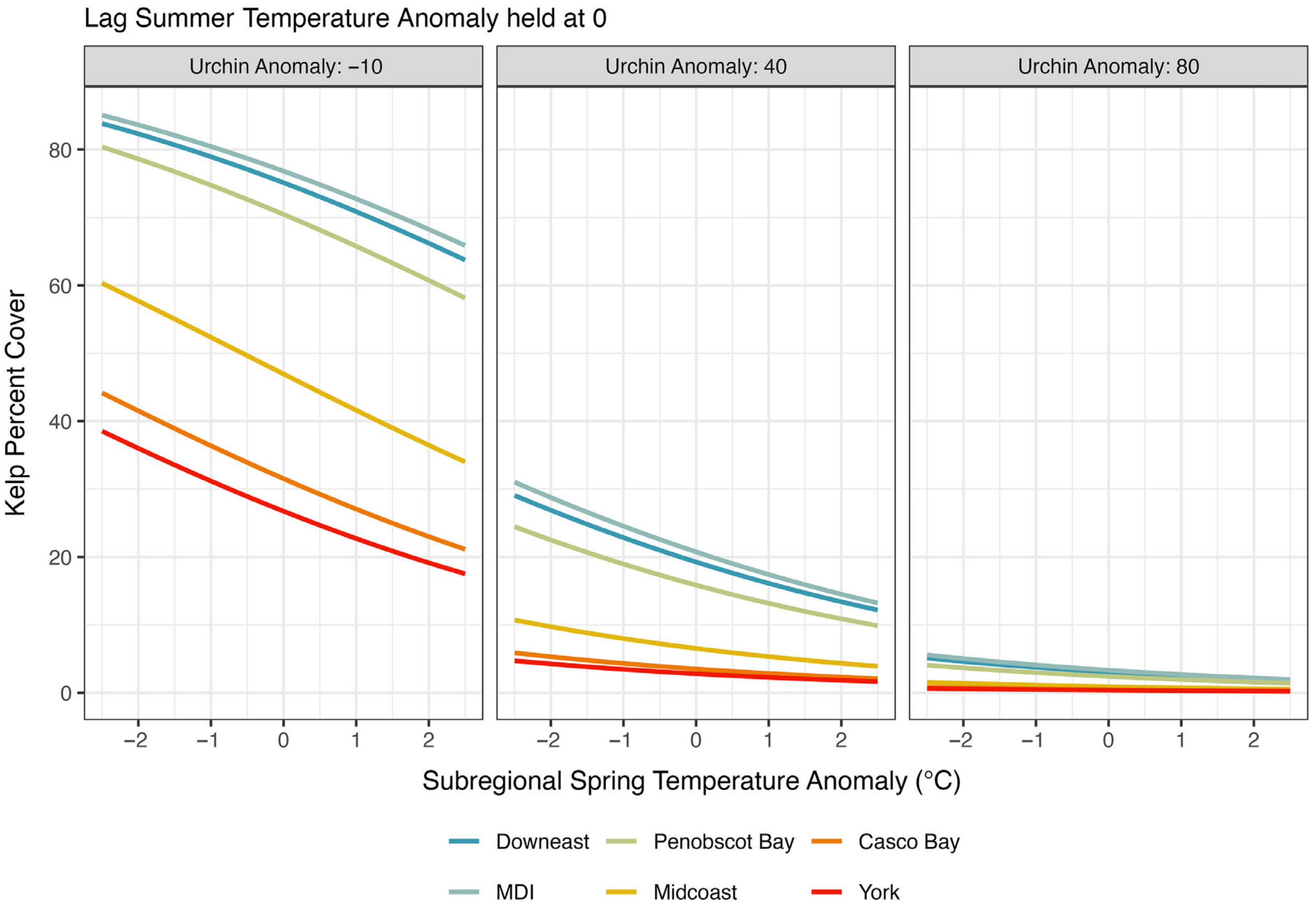

FIGURE 5 The modeled effect of changes in subregional spring temperature anomaly on percent cover of kelp, when co-occurring with various site-level sea urchin density anomalies and no lagged summer temperature anomaly (i.e., set to subregional mean). Color denotes subregion.

right). Conversely, as sea urchin densities are reduced to low levels through top-down forcing (i.e., density anomaly <30, via sea urchin harvest and/or predation), kelp cover increases, but only markedly under average to cool conditions, and much more so in the northeast. The effect of sea urchin removal on kelp weakens with warming because the maximum kelp abundance possible in each subregion—and thus the scope for kelp to dominate when herbivory is suppressed—is lower during a spring warming anomaly. This weakening impact of top-down forcing is exacerbated if the previous summer was unusually warm as well (data not shown).

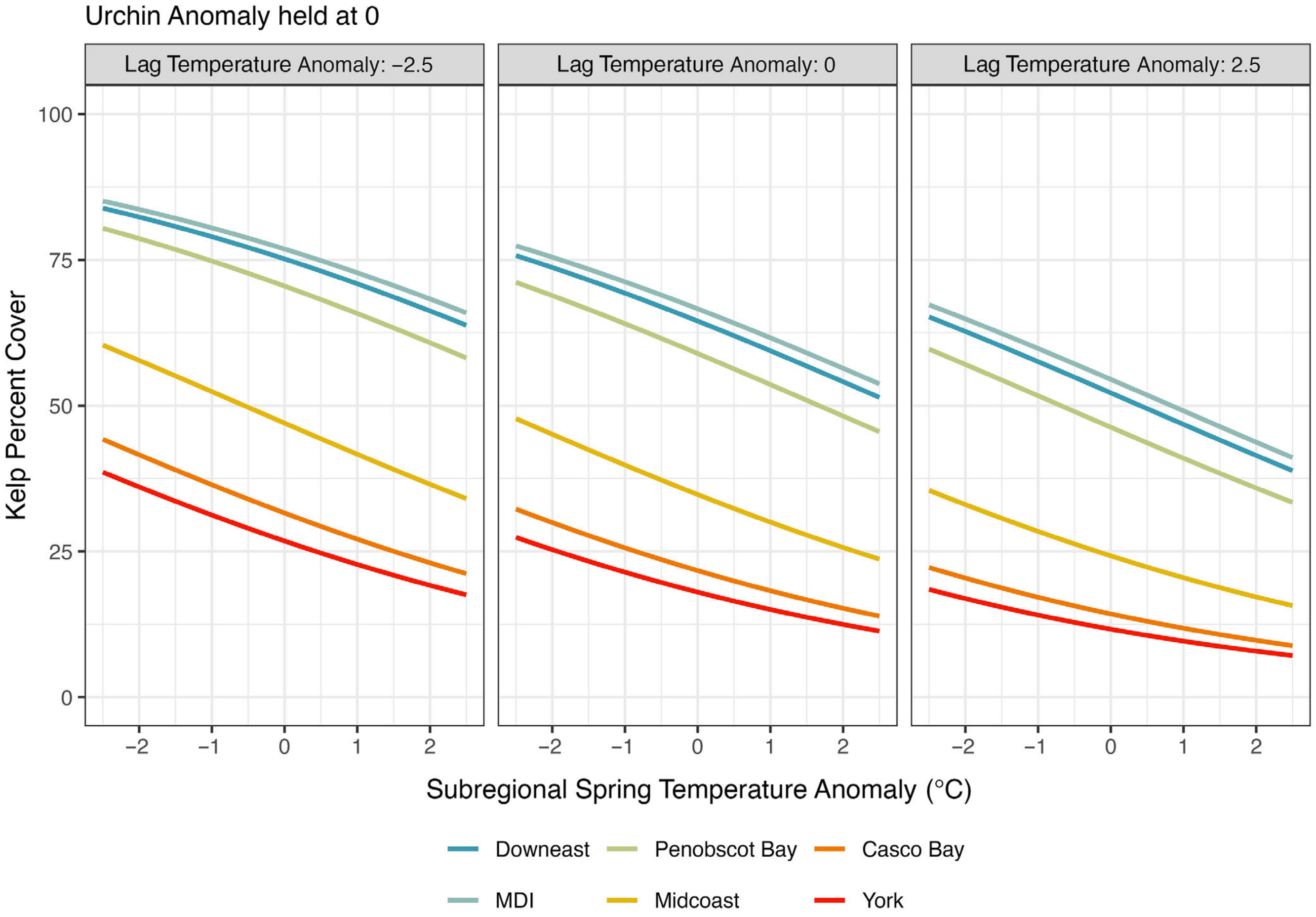

FIGURE 6 The modeled effect of changes in subregional spring temperature anomaly on percent cover of kelp, when co-occurring with various subregional lagged summer temperature anomalies and no sea urchin density anomaly (i.e., site-level density set to subregional mean). Color denotes subregion.

Changes in algal community composition

Between 2004 and 2018, Maine's reefs also experienced changes in algal community composition, even in places where forests persisted (Figure 8; Appendix S1: Tables S10–S12). While scarce at all sites, shotgun kelp (*Agarum clathratum*) declined in the one subregion in which it was previously common (MDI) to near zero. Likewise, winged kelp (*Alaria esculenta*)—a species with a subarctic to arctic distribution (Lüning, 1990)—declined in Downeast and Penobscot Bay and trended toward decline in MDI (all northeast subregions). Moreover, winged kelp was not observed in the three most southerly subregions in 2018. Sugar kelp (*Saccharina latissima*) significantly declined in Casco Bay, but remained at modest relative abundances throughout the other subregions except Downeast. By contrast, horsetail kelp (*Laminaria digitata*) significantly increased in abundance in Downeast and Midcoast subregions and stayed in high relative abundance in MDI and Penobscot Bay subregions.

With regard to understory species, Irish moss (*Chondrus crispus*) increased in four subregions (MDI, Penobscot Bay, Midcoast, Casco Bay) between 2004 and 2018, but declined in York. Irish moss, when abundant, may form an occlusive barrier to the settlement of other juvenile algae (Worm & Chapman, 1996). Acid weed (*Desmarestia aculeata* and *D. viridis*) increased in York and Penobscot Bay subregions, as did the green alga *Chaetomorpha* in York and Casco Bay. *Rhodomela* spp. increased in relative abundance across all subregions, while algae from the genus *Ulva* increased or decreased stochastically across the region. Most notably, red filamentous algae (a consortium of "turf algae" including *Polysiphonia* spp. and the invasive alga *Dasysiphonia japonica*) significantly increased in every subregion (except MDI) between 2004 and 2018, with the most dramatic increase in York (Figure 9; Appendix S1: Tables S13–S15) and the Isle of Shoals (Dijkstra et al., 2017, 2019). These turf algae, once they become abundant, are known to prevent juvenile kelp recruitment (Filbee-Dexter & Wernberg, 2018).

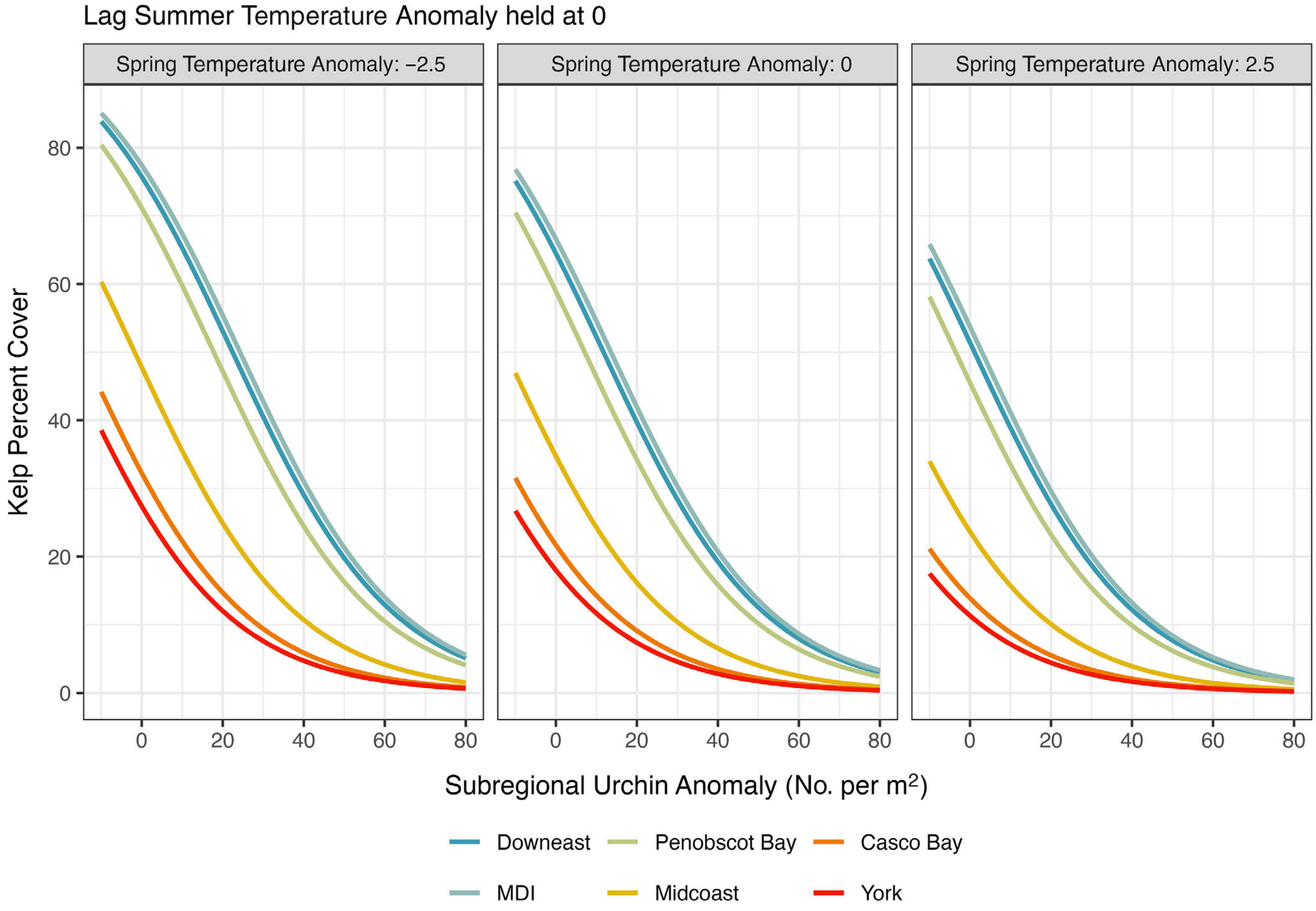

FIGURE 7 The modeled effect of sea urchin density anomaly on percent cover of kelp, when co-occurring with differing levels of spring temperature anomaly and no lagged summer temperature anomaly (i.e., set to the subregional mean). Color denotes subregion.

By contrast, the leafy red alga *Phycodrys fimbriata*—a species with a historical distribution spanning from Long Island Sound to the Canadian Arctic—declined between 2004 and 2018 in all subregions except for the most northerly subregion. Likewise, *Ptilota serrata*—a red alga with a mostly subarctic distribution that was always in low abundance—was rarer everywhere in 2018, with its greatest decline in Casco Bay.

DISCUSSION

Each year from 2001 to 2018 we surveyed between 31 and 67 kelp forests spanning >350 km of linear coast in Maine (Figure 1). The resulting data are unprecedented for the Gulf of Maine, both in their spatiotemporal scope and resolution and the standardized way in which they were obtained. Likewise, they are globally unique; long-term data are surprisingly rare for kelp forest ecosystems (Krumhansl et al., 2016) despite being critical to both scientific discovery and resilience-based management (Hughes et al., 2017). These long-term data confirmed the widespread occurrence of kelp forests across Maine's coast at the turn of the 21st century and then revealed differing trajectories among subregions in the ensuing decades—most notably, that forests persisted in the northeast versus rapidly collapsed in the southwest. Whereas the collapse of forests in southwest Maine has been described for a few well-studied sites (Dijkstra et al., 2017; Witman & Lamb, 2018), the widespread persistence of kelp forests across northeast Maine, and their gradual decline over the last ~15 years (Figure 3), were previously unknown.

Our modeling of the data revealed that ocean warming is altering the outcomes of top-down forcing in this system, such that a continued scarcity of herbivores over the last 20 years (Figure 2) did not predictably drive a lasting dominance of kelp across the region, but instead coincided with a waning dominance of kelp (northeast to central Maine) or the collapse of kelp forests and the rise of a novel state defined by "turf" algae (southwest Maine). Indeed, our models revealed that unusually high seawater temperatures and—at a few select times and places, herbivores—were the primary drivers of kelp loss in recent

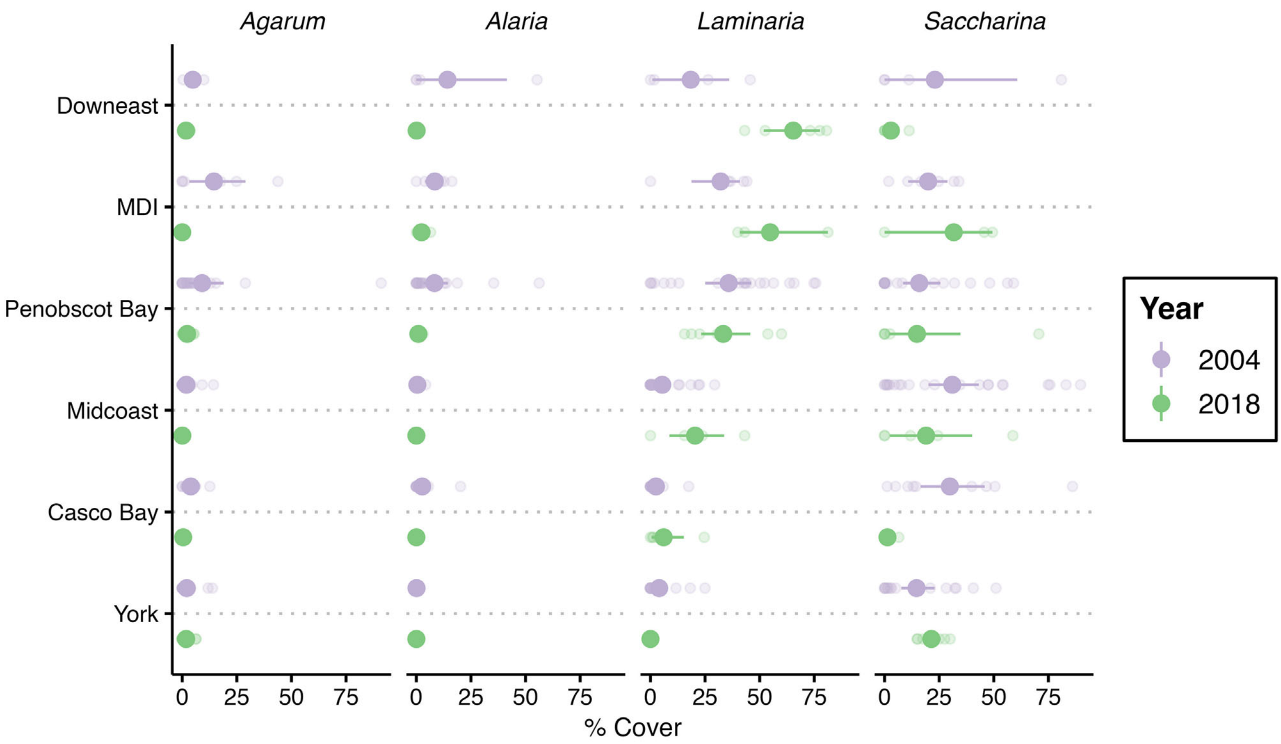

FIGURE 8 Percent cover of each kelp species (subregional mean ± 95% CI) in 2004 versus 2018. See Appendix S1: Tables S10–S12 for model outputs.

times (Tables 1 and 2), and further showed that the power and absolute impact of these drivers varied by subregion and ecological context (i.e., very high vs. low sea urchin densities) (Figures 5–7). For example, the negative effects of warming anomalies on kelp were rapid and pronounced in the southwest—which experienced much higher absolute temperatures versus their northern counterparts (Figure 4)—while in the north, declines were gradual and moderate. High sea urchin densities, in the few times and places they occurred, universally reduced kelp (irrespective of subregion). Thus, although a fisheries-induced reduction of herbivores was key to the widespread return of kelp forests in the 1990s (Steneck et al., 2013) and their persistence in northeast Maine in subsequent decades, such top-down forcing no longer predictably leads to a lasting abundance of kelp, especially in Maine's warmer locales where climate forcing now reigns supreme.

The impact of warming anomalies on kelp identified here (Tables 1 and 2) may have arisen via direct (stress) effects, indirect (ecological) effects, or a combination of pathways. Warming anomalies likely caused adult mortalities in the southwest, as such anomalies are known to trigger mass mortality via thermal stress (Filbee-Dexter et al., 2020; Smale et al., 2019). The Gulf of Maine incurred several extremely warm summers (including multiple heatwaves) during the study in which maximum NSSTs in the southwest rose to near or above presumed "thermal tipping points" of the two dominant kelp species (Bolton & Lüning, 1982) (Figure 4). Also, high seawater temperatures reduce nutrient availability to kelp, causing nutrient depletion at 15°C (García-Reyes et al., 2022; Zimmerman & Kremer, 1984); as such, kelps were likely to have experienced nutrient stress annually in York and Casco Bay, and across all subregions by the end of the study (Figure 4). Reduced nutrients during periods of maximum growth (spring) or thermal stress (summer) can accelerate kelp loss over time. Warming anomalies may have also impeded kelp reproduction—perhaps both directly and indirectly—further accelerating the collapse of southern forests. For instance, elevated summer temperatures trigger population declines through reduced germination (Bartsch et al., 2013). When kelp gametophytes experience unusually warm conditions, their sporophyte offspring—generally recruiting in the winter and early spring—are less abundant, grow more slowly, harbor fewer nutrients, and display higher sensitivities to heat stress (Gauci et al., 2022; Liesner et al., 2020). Finally, warming can also facilitate the introduction of novel species that increase adult kelp mortality (Scheibling & Gagnon, 2009) and/or inhibit recruitment (Wernberg et al., 2016); ourselves and others (Dijkstra et al., 2017) have identified the proliferation of filamentous red "turf algae" across the southwest (Figure 9). It is possible that

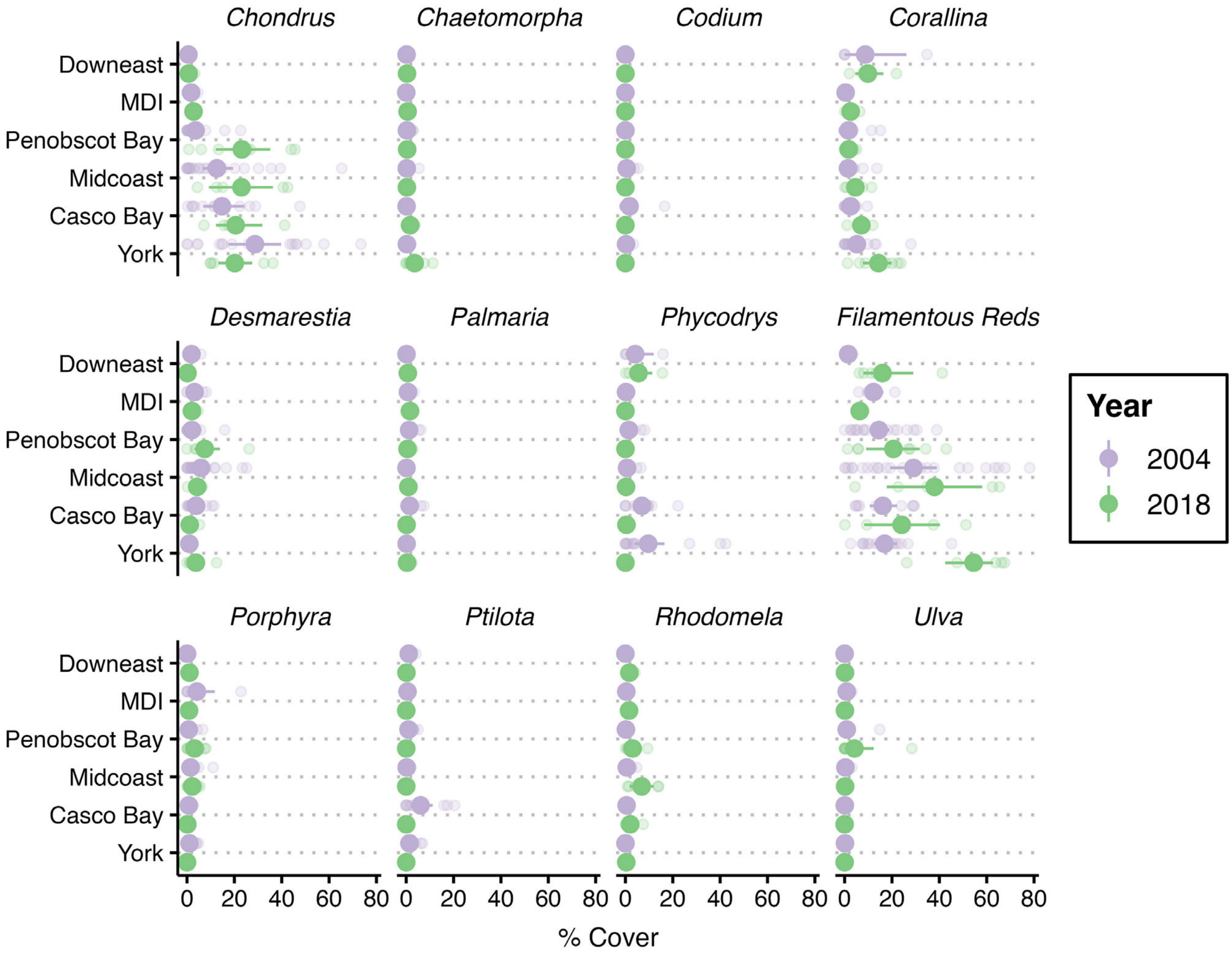

FIGURE 9 Percent cover of common understory algae species (subregional mean ± 95% CI) in 2004 versus 2018. See Appendix S1: Tables S13–S15 for model outputs.

these turf algae—which preempt space and create hostile conditions for kelp in other systems (Filbee-Dexter & Wernberg, 2018)—prevented forest recovery in the southwest.

In the northeast—which experienced much lower absolute levels of warming (Figure 4) yet nonetheless saw gradual declines in kelp abundance (Figure 3)—the impacts of warming anomalies likely manifested in similar ways, but were smaller in magnitude given cooler conditions, other subregional drivers that enhance kelp abundance, or both. For example, given the well documented relationship between seawater temperature and nutrients (Zimmerman & Kremer, 1984), rising temperatures in the north may have lessened the availability of nutrients during key periods of kelp growth and reproduction in recent years (Figure 4), which may have contributed to gradual declines over time. Also, Maine's kelp forests appear to be genetically distinct even among adjacent bays (Breton et al., 2018) as well as at larger scales (Mao et al., 2020). It has been shown elsewhere that populations with differing thermal histories (i.e., those residing in the colder vs. warmer parts of their range) have genetically-based responses to thermal stress, with lower thermal tolerance and less recovery in colder populations (King et al., 2019; Martins et al., 2020). Thus, the warming experienced in the northeast—while lower in temperature—nonetheless may have caused negative effects on kelp reproduction. Indeed, *L. digitata* germination is a cold-adapted process (Bartsch et al., 2013). Experiments have shown that, without cold seasons (and "cold priming" of gametophytes), sporophyte offspring have less success and are more heat sensitive (Gauci et al., 2022; Liesner et al., 2020). Such cross-generational impacts of warming may gradually undermine kelp populations over time.

While the effects of ocean warming were strong and pervasive in our study, it is important to note that other potential drivers of kelp abundance and composition—such as storm frequency and intensity, wave energy, ocean color and turbidity, and nutrient composition—

may also be important. Because we have little information on the roles of these drivers in this system, we could not include them in our analysis. Yet, when we included a temporal fixed effect in our temperature (OISST)-based models, our results were unchanged, indicating that our causal inferences were robust. We hope that future studies can acquire high-resolution data on these unmeasured drivers or evaluate them experimentally. Furthermore, it is important to note that our analyses indicated that factors other than temperature that are correlated with mean spring temperature influenced kelp cover in our study. As such, it was critical that we used models that were robust to omitted variable bias, as we would have otherwise likely overestimated the spring temperature effect (but not the summer temperature effect, since the two subregional means are highly correlated; Pearson's correlation = 0.83). Indeed, the relationship between subregional mean sea urchin density and kelp abundance was positive, indicating shared or correlated drivers (e.g., oceanographic forces) would have otherwise biased or confounded our results, had we not controlled for them. Our findings show that further work is needed to evaluate other drivers in this region, and more broadly highlight the importance of using models that properly adjust for omitted variable bias to produce causal estimates of climate effects from observational data.

Overall, our long-term (Figures 2 and 3) and high-resolution (Figures 8 and 9) data paint a picture of "species on the move" in the Gulf of Maine. The ecological effects of rapid kelp loss and changes in community composition—especially the rise of a novel "turf" phase state—are not well described, but evidence from York (Dijkstra et al., 2019) and other rapidly warming systems (Filbee-Dexter et al., 2020; Smale et al., 2013) suggests that the retreat of kelp forests will have considerable ecosystem-wide impacts (Smale et al., 2013, 2022). Hence, monitoring, predicting future warming and punctuated heatwaves (Jacox et al., 2022), and adopting policy frameworks that embrace species range shifts (Pinsky et al., 2018, 2020) will be essential for avoiding "ecological surprises" and managing this rapidly changing system. At the same time, regional measures that promote the persistence of Maine's remaining kelp forests in the northeast—key among them, managing for low sea urchin abundances (Figure 5)—as well as measures that slow species range shifts, such as enhanced top-down forcing via large predator restoration (Tekwa et al., 2022), may help to maintain ecosystem functions and services in the near-term. Ultimately, however, we are likely to see an additional contraction of kelp forests over the long-term unless our global carbon emissions are aggressively curbed, as ocean warming and marine heatwaves are expected to increase otherwise (Smale et al., 2019).

Last, and most broadly, our study adds to a growing body of literature showing that climate change is rewriting the rules of nature. Here, we demonstrate that ocean warming can reshape the outcomes of top-down forcing in kelp forests, to the degree that reducing herbivore abundances—whether it be by direct harvest or a predator-induced trophic cascade—no longer predictably restores the ecosystem to its historically stable state (i.e., kelp dominance) as predicted by ecological theory and past observation. In other places, climate change has transformed the ecology of kelp forests by adding new ecological processes (Wernberg et al., 2016) and/or amplifying the strength of existing species interactions, beyond critical tipping points (Rasher et al., 2020). Together, such findings highlight that traditional paradigms in ecology no longer broadly apply, and that a more nuanced, context-dependent approach is needed to understand, predict, and manage kelp forest ecosystems moving forward.

AUTHOR CONTRIBUTIONS

Thew S. Suskiewicz and Douglas B. Rasher initiated and designed the study. All authors collected the data. Jarrett E. K. Byrnes analyzed the data. Douglas B. Rasher wrote the manuscript, with contributions from all authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Rasher et al., 2024) are available in Dryad at https://doi.org/10.5061/dryad.v9s4mw73q. Code (Byrnes & Suskiewicz, 2024) is available in Zenodo at http://doi.org/10.5281/zenodo.10909623.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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