Notes from the Past Show How Local Variability can Stymie Urchins and the Rise of the Reds in the Gulf of Maine

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Supplemental Materials

- Supplementary Materials 1: Extended Methods
- Supplementary Tables S1-S2
- Supplementary Figures S1-S15
- Supplementary Code and Data File
- Supplementary Web Application

Abstract

The impacts of global change — from shifts in climate to overfishing to land use change — can depend heavily on local abiotic context. Building an understanding of how to downscale global change scenarios to local impacts is often difficult, however, and requires historical data across large gradients of variability. Such data are often not available — particularly in peer reviewed or gray literature. However, these data can sometimes be gleaned from casual records of natural history — field notebooks, data sheet marginalia, course notes, and more. Here, we provide an example of one such approach for the Gulf of Maine, as we seek to understand how environmental context can influence local outcomes of region-wide shifts in subtidal community structure. We explore a decade of hand-drawn algal cover maps around Appledore Island made by Dr. Art Borror while teaching at the Shoals Marine Lab. Appledore's steep wave exposure gradient — from exposed to the open ocean to fully protected — provides a living laboratory to test interactions between global change and local conditions. We then recreate Borror's methods two and a half-decades later. We show that overfishing-driven urchin outbreaks in the 1980s were slowed or stopped by wave exposure and benthic topography. Similarly, local variation appears to have curtailed current invasions by filamentous red algae. Last, some formerly dominant kelps have disappeared over the past forty years — an observation verified by subtidal surveys. Global change is altering life in the seas around us. While underutilized, solid natural history observations stand as a key resource for us to begin to understand how global change will translate to the heterogeneous mosaic of life in a future Gulf of Maine and other ecosystems around the world.

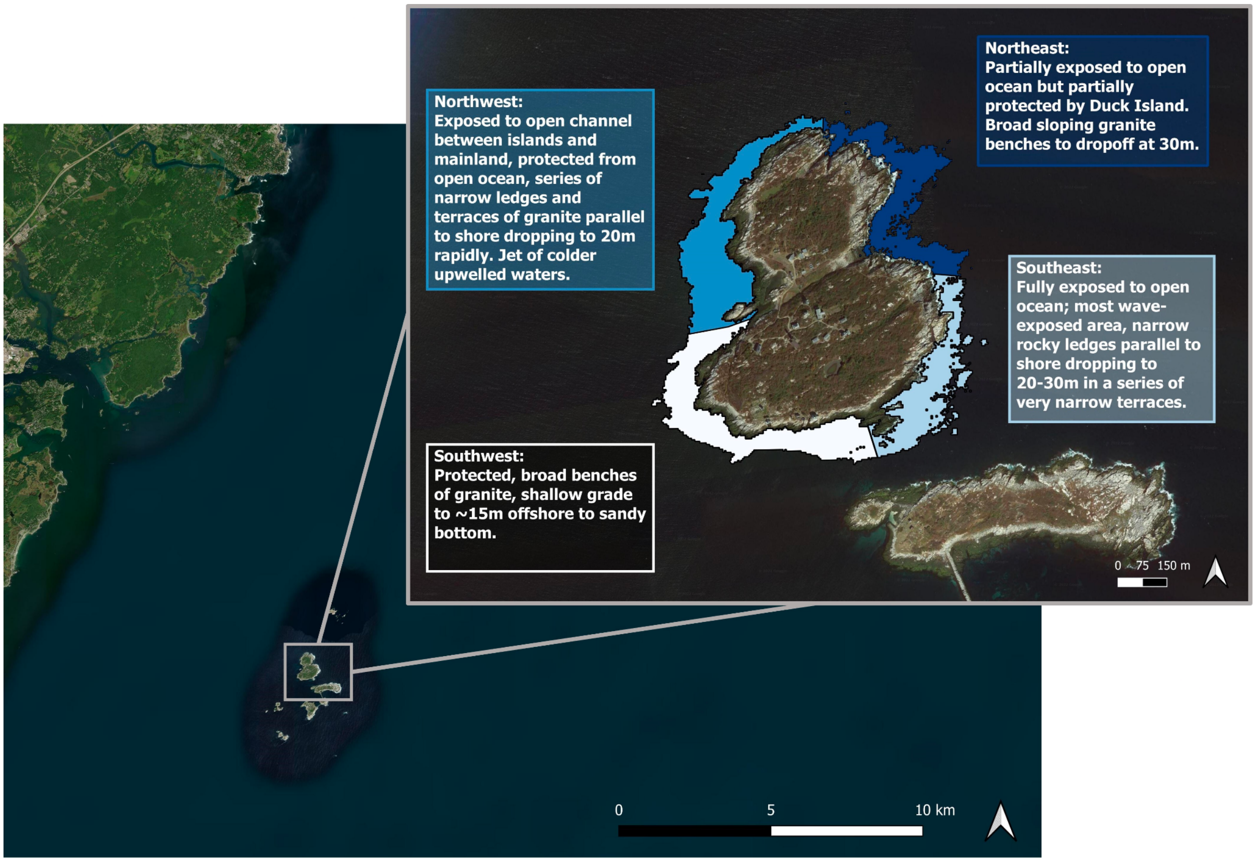
Introduction

Ecologists and managers are constantly challenged to understand how global and regional human change translates to changes at local scales (Wilbanks and Kates 1999; Knowlton and Jackson 2008; Potter et al. 2013; De Boeck et al. 2015; Gonzalez et al. 2016; Blowes et al. 2019; Chase et al. 2019). This ability to translate from the global to the local is crucial information, as resilient and resistant communities can seed recovery and adaptation (Laborde et al. 2008; Bongaerts et al. 2010; Reis et al. 2010; Rinde et al. 2014; Eger et al. 2022). As we confront the changes to come, some of the most useful data on how local spatial variation in abiotic drivers can modify the impacts of global and regional human-driven change come from the past. Yet, these data are often rare — even within the past few decades — and typically are not taken at a fine enough spatial grain to provide meaningful insights. Such data are particularly lacking for temperate subtidal macroalgal communities where, until recently, one needed to be in the water to see communities and colder waters limited access to even casual observers. Yet, the notebooks and ephemera of great and passionate natural historians can provide a key to unlocking this knowledge. Here we show that informal notes by faculty teaching at a marine lab can help us understand how local-scale variation can reduce the effects of past runaway trophic cascades and current-day bioinvasions.

Temperate macroalgal communities have experienced drastic changes both at the global (Krumhansl et al. 2016) and regional (Steneck et al. 2013) scale over the past century. These changes include radical shifts in abundance (e.g., Wernberg et al. 2012, 2016) as well as shifts in species ranges and composition (Steneck et al. 2013; Dijkstra et al. 2017; Filbee-Dexter and Wernberg 2018; Smale 2020). Macroalgal communities serve as the foundation for rocky shallow-water benthic ecosystems; changes to these systems have immense implications for associated species and their ability to provide ecosystem services, including harvesting of commercial species. Local conditions, however, can alter the effects of global and regional environmental change on these communities. Moreover, these local modifications to species trajectories can even lead to improved trajectories of recovery after massive disturbances. When kelps were subjected to massive overgrazing by sea urchins in Norway in the 1980s, for example, local variation in wave exposure allowed for kelp persistence in some areas, which then served as nuclei for recovery (Sivertsen 1997; Norderhaug and Christie 2009; Rinde et al. 2014).

The subtidal rocky reefs of the Gulf of Maine have experienced massive human-driven changes over the past half-century. Aside from one of the fastest rates of warming in the ocean (Pershing et al. 2015, 2021), we have seen a loss of predatory cod and other finfishes in the 1970s and 80s as a result of overfishing (Estes et al. 2013) creating runaway overgrazing of kelps by sea urchins (Steneck and Wahle 2013; Steneck et al. 2013). This urchin boom was followed by overfishing of urchins (Steneck et al. 2013), massive increases in mesopredatory crab and lobster abundances (Steneck and Wahle 2013; Steneck et al. 2013), and some urchin disease (Caraguel et al. 2007; Steneck et al. 2013), the latter of which was more prevalent in Nova Scotia than the Gulf of Maine itself (Scheibling 1986; Scheibling and Lauzon-Guay 2010; Feehan and

Scheibling 2014). Alongside the resulting urchin declines, we have seen increases in crustacean shell disease (Castro et al. 2012; Steneck and Wahle 2013), a rolling series of species invasions (Harris and Tyrrell 2001; Mathieson et al. 2003; Bullard et al. 2007; Newton et al. 2013; Dijkstra et al. 2017), changes in ocean color and pH due in part to increases in river runoff from strong storms driven by climate change (Aiken et al. 2012; Balch et al. 2012; Huntington et al. 2016), region-wide die-offs of mussels (Sorte et al. 2017), sea star wasting disease (Bucci et al. 2017; Van Volkom et al. 2021), and likely more. The sequence of urchin overgrazing followed by species invasions and increases in temperature, particularly in the southern Gulf of Maine (Harris and Tyrrell 2001), has had profound influences on the composition and abundance of subtidal habitat forming species (Steneck et al. 2013; Dijkstra et al. 2017, 2019). In particular, introduced seaweed species have increased by 90% in the Gulf of Maine since the 1970's, reducing canopy height and providing refuge for meso-invertebrate communities (Dijkstra et al. 2017). While we have built up a wealth of knowledge looking at the consequences of regional changes in the subtidal Gulf of Maine (see review in Steneck et al. 2013), few studies have examined how small-scale environmental variability has moderated the impacts of regional anthropogenic change across large spatial scales (but see Witman and Lamb 2018 for onshore-offshore comparisons of fishing pressure and climate change). Without this information, we can only begin to understand the factors that could impede, mitigate or facilitate adaptation to human-driven ecological change in the Gulf of Maine subtidal zone.



Northwest: Exposed to open channel between islands and mainland, protected from open ocean, series of narrow ledges and terraces of granite parallel to shore dropping to 20m rapidly. Jet of colder upwelled waters.

Northeast: Partially exposed to open ocean but partially protected by Duck Island. Broad sloping granite benches to dropoff at 30m.

Southeast: Fully exposed to open ocean; most wave-exposed area, narrow rocky ledges parallel to shore dropping to 20-30m in a series of very narrow terraces.

Southwest: Protected, broad benches of granite, shallow grade to ~15m offshore to sandy bottom.

Figure 1. The Isles of Shoals off the coast of New Hampshire and Maine with Appledore Island featured in the inset. In the inset, we highlight the four quadrants of the island considered in this manuscript and describe their broad differences in swell exposure and subtidal topography.

Starting in 1974, Dr. Arthur Borror taught a variety of courses in ornithology, zoology, and ecology at the Shoals Marine Lab on Appledore Island (Fig. 1). Borror, a phenomenal naturalist, recorded his observations each summer at the field station in a series of notebooks now archived at the University of New Hampshire (Borror 2016). As part of one class, students surveyed intertidal transects scattered around the whole island at low tide while Borror would circle the island by boat to check on them. Between 1982 and 1990, he also brought along a bathyscope, and would regularly lean over the side of the boat to observe the dominant subtidal habitat — either a species or functional group of algae or rocky urchin barren. He recorded five hand-drawn maps in his field notebooks of these habitats around the entire island. These maps span a huge gradient of wave exposure — from completely protected to fully exposed to the open ocean — as well as bottom topography. As a curiosity, along with Dr. James Coyer, one of the authors of the present manuscript (Byrnes) repeated this observation in 2014, producing a comparable map. While these are casual natural history observations, they provide an unparalleled look at how the regional urchin boom of the 1980s and the rise of red algae in the 2010s played out against a backdrop of local environmental variability. Here we digitize these maps and use the products to explore temporal and spatial patterns of macroalgae at Appledore Island in order to understand how local variability can modify regional change within the Gulf of Maine.

Methods

Digitization of maps

We recorded handwritten metadata and took digital photos of all maps and their legends (Fig. 2, S1–S6, Supplementary Materials 1 for details of digitization), adjusted images with Adobe Photoshop and then imported them into QGIS (QGIS Development Team 2022). In QGIS, we georeferenced seven distinct points which were consistent across all maps based on the more precise 2014 map (Fig. 2A). We overlaid the georeferenced photos on a Google Satellite base map (obtained through QuickMapServices QGIS plugin Map data ©2015 Google) with transparency at 50%. We manually added polygons matching maps and labeled them corresponding to a single species or mix of species (Fig. 2B,C for 1984 map), which we will refer to as communities or habitats. To account for changes in taxonomy across years and lack of specificity for some groups, we identified communities based on a standardized taxonomy across maps (Table S1). Using a bathymetry layer (Ward et al. 2021), we clipped polygons to areas shallower than 5m below mean low low water. We then drew a perimeter line at 1.5m around the island to create a gapless island perimeter from which to determine the percent cover of habitats.

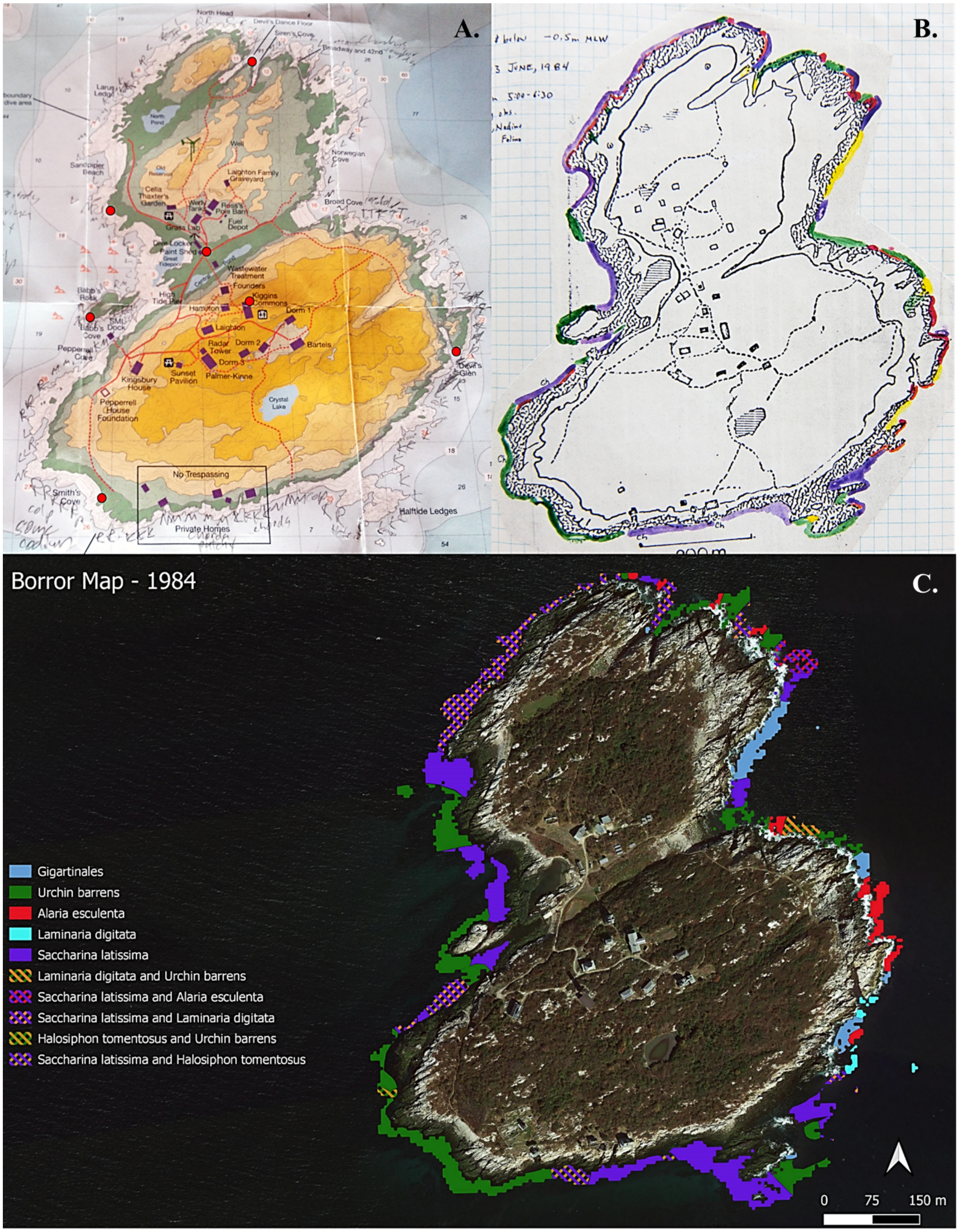


Figure 2. Appledore Island maps depicting the various habitats (often species) occupying the coastline. **A.** The 2014 map with seven red circles showing the points used for georeferencing all six maps and satellite maps in QGIS. Each habitat is represented by a different letter along the

coast. **B.** The original 1984 map where each habitat is represented by a different color along the coast. **C.** The final 1984 digitized map showing habitats present between 0–5 meters depth.

Percent cover of each habitat type

To obtain the area covered by each habitat, we imported all six map shapefiles into R (version 4.1.1, R Core Team 2020) and split polygons representing more than one habitat into multiple overlapping polygons for each unique habitat. On the original Borror maps, some labels included details such as "kelp and sparse *Saccharina*", but we were unable to quantify "sparse" or other qualitative descriptors and therefore ignored these details for consistency. We determined the intersection between the 1.5-meter perimeter around Appledore Island and polygons for each habitat in each year and used the proportion of perimeter intersected as our measure of cover. For overlapping polygons, we evenly divided the percentage of the perimeter between them. We then repeated the process with habitats grouped into "pure kelp", "mixed kelp & reds", "mixed red algae", and "urchin barrens".

Assessing local modification of urchin barren formation and red algal dominance

To evaluate how local environmental variation around the island might have impacted urchin barren formation and the rise of red algae across Appledore, we split the island into four quadrants due to substantial subtidal variation in these areas (see Fig. 1). Each quadrant had unique properties of wave exposure and benthic topography (Supplementary Materials 2). Going clockwise, these quadrants were: southwest, characterized by minimal wave exposure and wide shallow sloping benches; northwest, characterized by exposure to swell coming from the mainland and narrow fast-dropping ledges; northeast, characterized by moderate exposure to the open ocean shielded by nearby Duck island and wide sloping benches, canyons; and the southeast, characterized by direct exposure to the open ocean and fast-dropping ledges parallel to shore.

To evaluate how quadrant affected urchin barren cover and kelp cover, we analyzed each using beta regression with a logit link — ideal for bounded data (Cribari-Neto and Zeileis 2010; Douma and Weedon 2019) — with quadrant, year (as a categorical variable), and their interaction as predictors for data from 1980–1990. Based on the results, we ran *post-hoc* contrasts between quadrants in each year, correcting p-values for False Discovery Rate

(Benjamini and Hochberg 2000). We did not use 2014 data for these analyses given the shift in the subtidal community from an urchin-dominated to non-urchin-dominated state. Instead, we used 2014 data to qualitatively compare the abundance of coarse taxonomic groups in different quadrants, as n=1.

Results

Digitized maps (Fig. 2, S7–S12, Supplementary Data 1,2) clearly show several trends in composition of dominant space holders over time (Fig. 3, Figure S13 for maps). First, urchin barrens were a dominant habitat type around Appledore in the 1980s (22.8–34.1% of total habitat), although kelps comprised the majority of habitat around the entire island (49.9–63.0%). Second, we see the expansion of *Saccharina latissima* between 1990 and 2014 and the absence of urchin barrens in 2014. Notably, in 2014 red algae composed 35% of the perimeter versus less than 12% in the 1980s. More subtly, *Laminaria digitata* is absent in 2014 and *Alaria esculenta*, while abundant in 1982, is greatly diminished in abundance (Fig. 3).

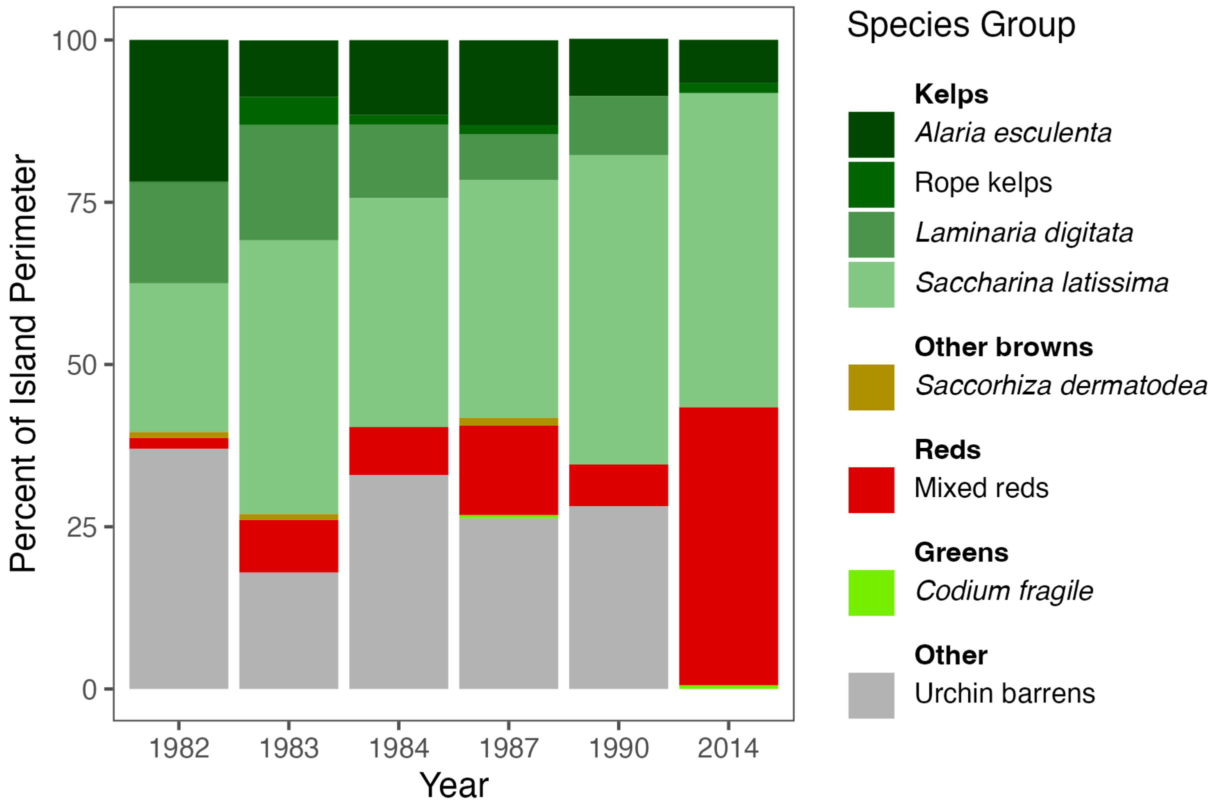


Figure 3. Change in percent of perimeter at 1.5m depth covered by each habitat or community type over time.

Looking at these trends spatially and aggregating groups into kelps, red algae (or "reds"), and barrens, we can see that the impact of urchins in the 1980s and putative impact of red algal expansion in the 2010s was unevenly distributed over Appledore (Figure 4, Fig. S14), reflecting local variability in abiotic conditions. In the 1980s, the southwest quadrant of the island was characterized by an extensive urchin barren, which persisted into the early 2000s (Siddon and Witman 2004, J. Byrnes pers. obs.). The northeast also appears to have developed two urchin barrens — one in a cove known as Devil's Dancing Floor at the north and the other at the back of Babb's Cove further to the south. These barrens eventually joined by 1987, although the most exposed tip of the northeast had begun to revert back to kelp by 1990. Barrens were rare in the northwest and southeast. This trend in urchin barrens is supported by an interaction between year and quadrant ($df = 3$, $\chi^2 = 25.8$, $p < 0.001$ Supp. Table 2) and post-hoc test results showing the trends described above (Fig. S15).

Curiously, 2014 looks similar to 1990, but red algae replaced barrens (Fig. 4). The protected southwest was dominated by stands of reds, the partially-protected northwest and partially-exposed northeast hosted a combination of kelps and reds, and the fully-exposed southeast was largely dominated by kelps.

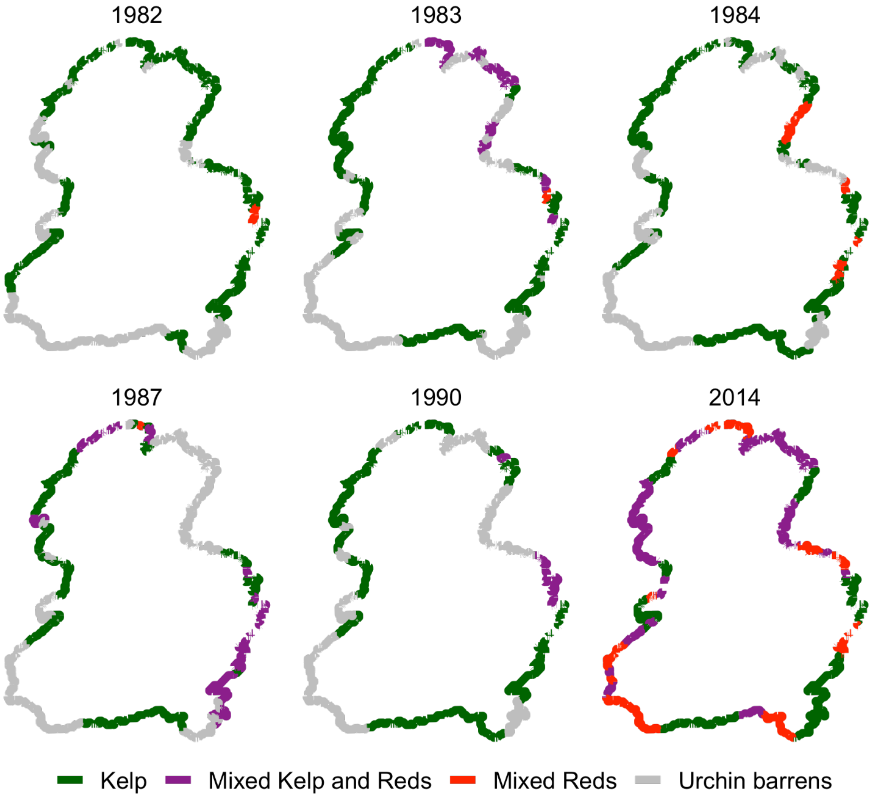


Figure 4. Maps of the perimeter of Appledore over time showing kelp, stands of mixed kelp and red algae, red algae, and urchin barrens over time.

Discussion

Our analysis of these natural history observations supports long-term trends observed in other studies (Harris and Tyrrell 2001; Steneck et al. 2013; Dijkstra et al. 2017). First, we can see the major island-wide macroalgal community responses due to two important major regional shifts in the Gulf of Maine, the explosion of urchins in the 1980s and the rise of — often invasive — red algae in the 2010s. Yet, these two observations are by no means uniform, and the substantial spatial variation suggests that local environments can play a strong role in mediating the impacts of global or regional change. Second, informal natural history observations such as these hand-drawn maps are an invaluable source of data that can contribute meaningful insight into how the local variation of a region is shaping the response of biotic communities to global patterns and even direct how we approach future management.

Borror's maps from the 1980s show strong correlation with known regional trends. By the 1980s, cod catches had declined due to overfishing (Sosebee and Cadrin 2006) and urchins were likely already on the rise (Steneck et al. 2013). Urchin barrens increased notably on the northeast and southwest of the island, where they were most abundant, while fluctuating stochastically in other quadrants. In 1990, the last survey where barrens were observed , they had notably decreased. The urchin fishery in Maine started in 1987 and peaked in 1993 (Johnson et al. 2012). *Cancer* crab abundance — a current major predator of juvenile urchins — did not begin to rise until the mid 1990s (Steneck et al. 2013). After urchin declines across the Gulf of Maine, many former barren grounds turned over multiple times between different waves of invasive algae (Harris and Tyrrell 2001). In particular, the last decade has witnessed the rise of the invasive red turf alga *Dasysiphonia japonica* in New England (Newton et al. 2013; Dijkstra et al. 2017, 2019; Ramsay-Newton et al. 2017). Indeed, much of the red algae (hereafter reds) in 2014 on the west side of the island are confirmed *Dasysiphonia*, while those in the northeast are primarily other native reds mixed with some *Dasysiphonia* (J. Byrnes, pers. obs). This expansion of red algae around Appledore Island matches both a regional and global turf-i-fication of temperate rocky reefs (Dijkstra et al. 2017; Filbee-Dexter and Wernberg 2018) driven globally by invasions, climate change, and more.

The role of local environmental variation in temperate rocky reefs

Within these broad temporal trends, however, we see substantial spatial variation. One of the features that makes Appledore Island such an excellent living lab is the variation in the abiotic environment around its rocky shores, from exposure to the open ocean to protected by the natural harbor formed by the Isles of Shoals as well as substantial variation in benthic topography. Island quadrants with narrow ledges and moderate to strong exposure to waves had the fewest barrens (NW and SE Appledore). These trends follow what we know of the biomechanical limits on urchins and their ability to form barrens under the stress of higher flows from storms or even regular strong sublethal wave velocities (Siddon and Witman 2003; Rinde et al. 2014). Curiously, the partially-exposed northeast also hosted a large barren, seeming to contradict the exposure hypothesis. However, this area has relatively simple smooth descending benches whose lack of complexity could have played a role in providing good habitat for barren formation (Randell et al. 2022). Further, the barren in the northeast quadrant grew from two protected embayments, which could have served as urchin refuges during periods of intense wave action.

Variation by quadrant seems to also play a role in the expansion of red algae, seen on the 2014 map (Fig. S12). As urchins declined in the 1990s, a series of invasive algae moved into former barren grounds (Harris and Tyrrell 2001; Levin et al. 2002; Mathieson et al. 2003; Dijkstra et al. 2017). In 2014, the protected southwest quadrant — a former barren — is largely covered with red algae that we verified in the field as the invasive *Dasysiphonia japonica. Dasysiphonia* also has a strong presence in the more protected northwest, as verified by divers (J. Byrnes, pers obs.). Red algae were also common in the shallow subtidal in the partially exposed northeast, but field identification revealed a mix of native *Polysiphonia* and *Chondrus crispus,* with *Dasysiphonia* composing only a small percentage thereof. The fully-exposed southeast remained largely kelp-dominated, and, indeed, is the only place around the island to still hold the high-wave energy tolerant *Alaria esculenta*. Aside from the southwest, red macroalgal communities in all quadrants are typically mixed with kelp rather than being a large red shag-carpet-like monoculture (J. Byrnes, *pers. obs.).*

Local variation appears to be key to understanding the ubiquity and composition of the rise of reds around Appledore, as well as where kelps are able to persist. Many rocky reefs around the globe are undergoing similar shifts from kelp forests to dominance by turf macroalgae (Connell et al. 2014; Filbee-Dexter and Wernberg 2018). Our results suggest these regime shifts, rather than being characterized by complete dominance, are more like patchworks determined by local conditions at the seascape scale. Around Appledore, wave exposure and seafloor topography create refuges for kelp from both sea urchins and red algal dominance. With respect to urchins, the results are strikingly similar to results from Norway (Sivertsen 1997; Norderhaug and Christie 2009; Rinde et al. 2014). The combination of exposure and benthic topography set the stage for oceanographic conditions such as current speed, upwelling, and wave energy, all of which could act to facilitate kelp persistence and dominance. For example, steep slopes around islands in the Gulf of Maine, such as those seen at Appledore's north head, can facilitate local upwelling (Townsend et al. 1983) bringing colder nutrient-rich waters to fast-growing kelps. We see a similar example at Cashes Ledge, an underwater mountain range with steep slopes ~140km from Appledore with a dense healthy kelp forest (Witman and Lamb 2018). Our work suggests that there might be a suite of predictable characteristics that can strengthen kelp forests' resistance to and resilience from ongoing trends of global change that warrant deeper exploration.

Natural history observations and global change

These results, garnered from informal notebooks, provide key insights into the larger field of global change ecology. Solid natural history observations and notes are an unparalleled and largely untapped resource for the field. The old field notebooks and observations from generations past floating around in archives, bookshelves, and file cabinets deserve preservation and ought to be digitized to provide us with an ecological time-machine that could open new chapters in our understanding of long-term change. Even informal large-scale observations can provide incredible clarifying insight into the ability of the local environment to modify global impacts.

Ultimately, our work shows a striking concordance with literature around the globe attempting to grapple with the importance of local-scale drivers in modifying global and regional-scale human-driven change (Wilbanks and Kates 1999; Knowlton and Jackson 2008; Potter et al. 2013; De Boeck et al. 2015; Gonzalez et al. 2016; Blowes et al. 2019; Chase et al. 2019). Patterns in the spatial variability of urchin barrens over time echo patterns seen in Norway (Sivertsen 1997; Norderhaug and Christie 2009; Rinde et al. 2014) and Southern California (Harrold and Reed 1985; Randell et al. 2022), and show how small-scale observations in the Gulf of Maine (Siddon and Witman 2003) scale up to whole coastlines. Further, large-scale patterns in the rise of reds highlight that the same types of variation — high wave and current energy — can mediate other forms of global change as well. We suggest that similar broad-scale low-taxonomic resolution approaches — whether from formal or more informal sources — might provide incredible insight as ecologists grapple with how global changes will manifest locally. That, and it makes for some fun boat (or road) trips.

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