Temperature, phenology, and turf macroalgae drive seascape change: Connections to mid-trophic level species

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Abstract.   Landscape patterns created by the structure and form of foundational species shape ecological processes of community assembly and trophic interactions. In recent years, major shifts in foundation species have occurred in multiple ecosystems. In temperate marine systems, many kelp beds have shifted to turf macroalgae habitats with unknown consequences on seascape patterns or changes in the ecological processes that maintain communities. We investigated the effect of turf macroalgae on seascape patterns in three habitats dominated by kelp and turf macroalgae and those that have mixed species composition. We also examined decadal elevations in temperature with known growth and reproductive phenology of kelp and turf macroalgae to provide a mechanistic understanding of the factors that will continue to shape these seascapes. Our results indicate that turf macroalgae produce a more heterogeneous habitat with greater primary free space than those that are mixed or dominated by kelp. Further, we examined the relationship between seascape patterns and richness and abundance of fishes in each habitat. Results showed that patch size was positively related to the abundance of fish in habitat types, suggesting that turf-induced heterogeneity may lead to fewer observed fishes, specifically the mid-trophic level species, cunner, in these habitats. Overall, our results suggest that persistence of this habitat is facilitated by increasing temperature that shorten the phenology of kelps and favor growth and reproduction of turf macroalgae that make them poised to take advantage of free space, regardless of season.

Key words: fish; foundation species; Gulf of Maine; invasive; kelp; landscapes; macroalgae; phenology; reproduction; seascapes; temperature; turf.

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INTRODUCTION

Determining ecological generalities of foundational changes in species composition presents a particular challenge as its effects on community processes may be viewed at multiple scales ranging from that of an individual to a landscape. Previous studies indicate that at an individual-level, functional traits related to architecture, height, and complexity of habitats change with shifting species composition (Asner et al. 2008, McIntyre et al. 2015, Dijkstra et al. 2017a). These traits have been shown to modify abundance and biodiversity of inhabitant species as well as species interactions (Warfe and Barmuta 2004, Desmond et al. 2018, Ware et al. 2019). However, it is unclear how regime shifts will affect the ecological processes that shape landscapes or in turn how a novel landscape will effect the ability of inhabitant species to forage or seek refuge. Previous studies indicate that landscape patterns influence multiple ecological processes including succession and diversity (Hubbell et al. 1999, Teixido et al. 2002). Given that landscape patterns are central

components of ecological processes (Chesson 1997), it is important to understand how fundamental shifts in the composition of foundation species will affect community processes. In this study, we investigated the effect of turf macroalgae on seascape patterns and examined the relationship between seascape patterns, richness, and abundance of fishes in different macroalgae communities. We then determined decadal seasonal elevations in temperature and coupled this with known reproductive phenology of kelps and dominant turf macroalgae to provide a mechanistic understanding of the factors that will continue to shape these seascapes.

The spatial organization of foundation species is important at multiple levels that range from processes of community assembly to the network of feeding interactions. Number, size, and diversity of patches can affect diversity and succession (Connell et al. 1997, Hughes and Connell 1999, Dijkstra and Harris 2009), as well as population numbers (Wiens 1976, Wethey 1984), and movement of species (Heck and Crowder 1991). For example, it has been shown that greater heterogeneity can increase temporal and spatial variability and size of patches within a landscape which act to offset or reset successional stages (Clark 1991, Teixido et al. 2007). Landscape patterns, particularly related to fragmentation and patchiness, also influence diversity (Sale and Douglas 1984, Kadmon and Allouche 2007), recruitment dynamics (Gilbert and Levine 2013, Livernois et al. 2017), and the movement and density of species (Heck and Crowder 1991). For example, Livernois et al. (2017) demonstrated that *Zostera marina* had greater recruitment in continuous, rather than fragmented, eelgrass beds. The strength of these effects on processes that regulate community assembly and ultimately landscape pattern will depend on environmental forces that shape demographic processes of individual foundation species and the interactions among them (Petraitis et al. 1989, Hubbell et al. 1999). Senescence, predation, disturbance, and temperature among other factors transform spatial patterns within a landscape by freeing up primary substrate for colonization by other species. As abiotic factors such as temperature and the composition of foundational species concurrently change, the influence of these processes on landscape patterns will also likely change.

There have been regime changes in kelp communities around the globe (see Filbee-Dexter and Wernberg 2018 for review). These changes are mirrored in the Northwestern Atlantic where a suite of introduced species have become established in shallow rocky subtidal areas (Harris and Tyrrell 2001, Newton et al. 2013), many of which are turf macroalgae (Dijkstra et al. 2017a, Newton-Ramsay et al. 2017). This has led to a more structurally complex habitat that supports greater abundance and diversity of meso-invertebrates (Dijkstra et al. 2017a, Ware et al. 2019). Additionally, water temperatures are rising and have affected the phenology, growth, and reproduction of species (Dijkstra et al. 2011, 2017b, Pershing et al. 2015). Combined these changes are likely affecting ecological processes that shape the seascapes which in turn affect the abundances of fishes and other mobile species (e.g., crabs and lobsters) that search it for suitable refuge and foraging.

In this study, we examined the influence of decadal temperature changes and turf-forming species on seascape patterns at ecologically relevant spatial scales of 100 m^2 in three distinct foundational habitats that are dominated by turf, kelp, and mixed species. We then examined turf-induced changes in pattern on abundance and richness of fishes that visually navigate over the canopy in search of food or refuge. Here, turf algae refers to short (<20 cm), filamentous species that have more than one thallus and can densely cover the seafloor (Connell et al. 2014). As kelp beds in the Gulf of Maine can form a dense, layered canopy over the seafloor, we predict greater habitat fragmentation in mixed and turf-dominated assemblages, which will influence the distribution of upper trophic level species.

METHODS

To understand the effect of turf macroalgae on seascape metrics, high-resolution underwater video footage was collected at 12 sites (Fig. 1) using a calibrated GoPro Hero 2 and 3+. Divers moved along transects on the seafloor in a lawnmower pattern at an almost constant height above the seafloor (1.5–2.5 m) and a speed appropriate for generating contiguous images. Video transects of each site were stitched together into a single composite image (100 m^2)
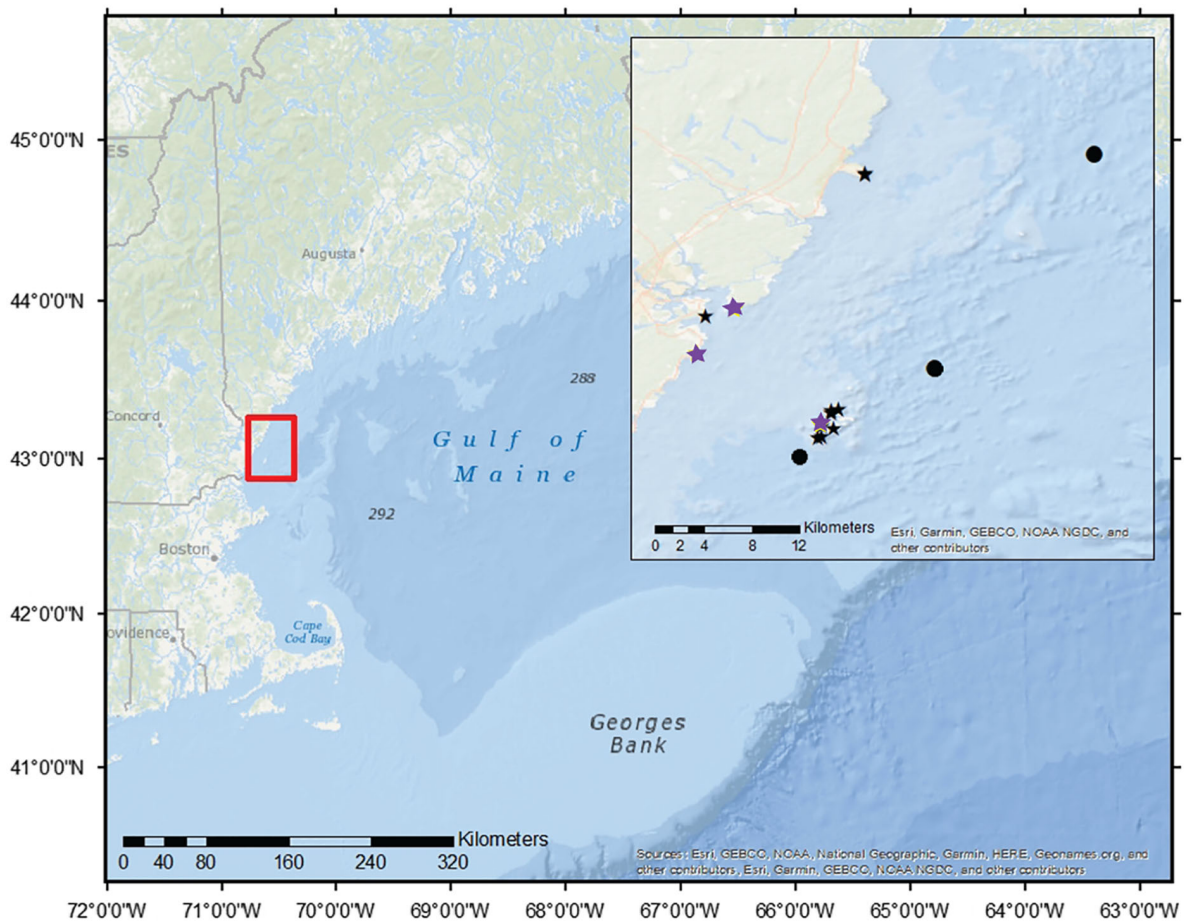
Fig. 1. Location of sites (stars) and buoys (circles) used for this study. Purple stars indicate sites that were excluded from the multiple regression analysis between fishes and seascape parameters.

of the entire site using texture-based video mosaic (e.g., scene, shape) assembly (Rzhanov et al. 2006). Still images (or video frames) were co-registered and positioned in a common frame of reference. Overlapping images were blended (feathered) to minimize seams between the frames so they would not affect the appearance of entities (e.g., seaweeds, substrate, etc.; Gu and Rzhanov 2006). To create a species map for each site, each mosaic was viewed on a high-resolution computer screen and imported into Adobe Photoshop. Using a combination of collected species, notes on individual species while diving at each site and still images extracted from the video, species and substrate were identified to the lowest taxonomic entity and manually delineated within each site. The resultant map was georeferenced, converted to a Geotiff file, and imported into ArcMap 10.3 for spatial modeling of seascape metrics using the Arc extension Patch Analyst (Rempel et al. 2012).

To examine differences in seascape metrics (Appendix S1: Table S1) among seaweed habitats, each site was classified as turf-, kelp-dominated, or a mixed seaweed assemblage. Habitat assignment was based on whether the assemblage was dominated (>50%) by turf algae, kelp, or a number of seaweed species (mixed). Each habitat was isolated (closest seaweed habitats were 1000 m apart) from the others in order to eliminate the influence of habitat connectivity as that may influence fish abundance (Irlandi and Crawford 1997).

To examine relationships between seascape spatial pattern metrics and in situ fish richness and abundance, a GoPro Hero 3+ was deployed

for one hour at the edge of each seaweed assemblage type (turf-dominated, mixed, and kelp-dominated). The camera was attached to the top of a 0.5 m metal frame. All deployments were conducted in the morning. All sites ranged in depth between 8 and 12 m. Video footage was later analyzed, and the length of all videos was standardized by using only the first 50 min of footage. All fishes sighted in the video were identified to species. Species richness was counted for each assemblage type, and the maximum number of fish observed in the frame at any point in time was recorded (MaxN).

To establish phenological changes in kelps, decadal temperature trends of degree days of 16°C, 20°C, and above were determined as these temperatures represent thermal limits for growth (20°C) and reproduction (16°C) of many kelp species, including the dominant kelp, *Saccharina latissima* (e.g., Brinkhuis et al. 1983, Redmond 2013, Simonson et al. 2015). Combined water temperatures recorded from the Western Gulf of Maine buoy, B01, and ones located at Appledore Island were used for all possible years from 1981 to 2018. The southernmost buoy around Appledore Island was discontinued. Temperatures from these buoys were combined to form a more complete temperature record for this time period, and temperatures between buoys were very similar. For example, mean summer (May–October) ocean temperatures in 2015 at the Western Maine Shelf buoy and Appledore Island were 14.72°C and 14.60°C, respectively; temperatures in 2017 at the Western Maine Shelf and Appledore C02 buoy were 14.47°C and 14.30°C, respectively. Only years with a complete temperature record between the months of May and October were used in the analysis. These buoys represent a conservative estimate of nearshore warming as offshore temperatures are more stable than nearshore temperatures (Dijkstra et al. 2017b). Growth and reproduction limits were determined by averaging the number of degree days above 16°C and 20°C for each decade, beginning in 1981.

Statistical analysis

Data were analyzed using JMP 13.0©. Seascape patterns and ocean temperature data did not conform to the assumptions of parametric statistics; therefore, nonparametric tests (Kruskal–Wallis) were used to detect differences in temperature among decades and seascape metrics among macroalgae assemblage types. On finding a significant difference in seascape patterns among habitats, Wilcoxon paired tests of significance were used to assess pairwise differences. To examine the relationship between seascape metrics, fish species richness, and maximum density of fishes, seascape metrics were first reduced to a few linear combinations using principle component analysis (PCA). Representative variables that contributed the most to each component were then used as predictors in a multiple regression for species richness and density.

Results

Over 23 genera of macroalgae were identified in the mosaics (Fig. 2), with higher species richness observed in turf and mixed assemblage habitats than those dominated by kelp. *Polysiphonia* spp. and *Neosiphonia* spp. were included in the group URFM (unidentified red filamentous macroalgae). There was a trend of declining, yet insignificant (df = 2, $P < 0.23$), free primary space from turf- to kelp-dominated assemblages (Fig. 2). Spatially, turf, kelp, and mixed habitats were quite different (Figs. 3 and 4). Turf-dominated assemblages had a greater mean shape index (df = 2, $P < 0.01$), number of patches (df = 2, $P < 0.008$), seascape fractal dimension (df = 2, $P < 0.01$), and Shannon's diversity index (df = 2, $P < 0.01$) than kelp-dominated seascapes ($P < 0.05$, Fig. 4), but were similar to mixed habitats. Smaller mean patch edge (df = 2, $P < 0.02$) and mean patch size (df = 2, $P < 0.01$) were observed in turf-dominated than kelp-dominated seascapes. There were no significant differences in evenness (df = 2, $P < 0.25$), total edge (df = 2, $P = 0.39$), and mean perimeter–area ratio (df = 2, $P = <0.81$), among seaweed assemblages.

Cunner (*Tautogolabrus adspersus*) was the most commonly observed fish species in our video surveys, making up 72% of the abundance of fishes. This is similar to other fish studies within the Gulf of Maine (Witman and Lamb 2018). Other fishes observed in the video footage included pollock, flounder, striped bass, lumpfish, and tautog. PCA grouped seascape metric variables into three components of which the factors contributing the greatest to each component
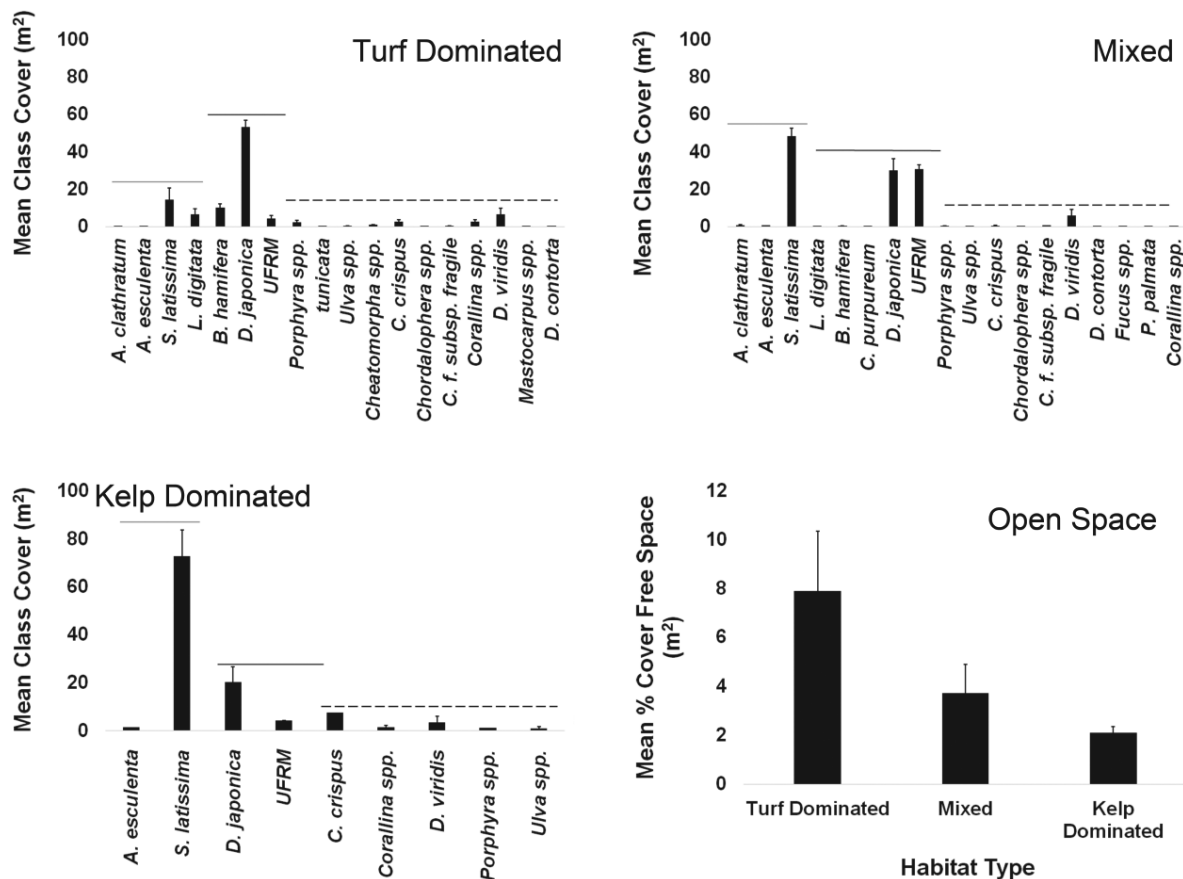
Fig. 2. Class cover of macroalgae and bare space in turf-, mixed-, and kelp-dominated habitats. The area of open space observed in each of the habitats. Declining trend in open space was observed with more open space observed in turf-dominated than kelp-dominated habitats. Kelp: light gray line; turf: darker gray line; other: dashed line. URFM (unidentified red filamentous macroalgae) indicates macroalgae that could not be identified to species in the underwater video footage.

were retained (number of patches, mean patch size, and total edge) for regression against abundance and richness of fishes (Table 1). Three sites were excluded from the multiple regression analysis as fishes could not be identified due to poor visibility. No seascape terms significantly correlated to fish species richness. Mean patch size was the only significant term that explained the abundance of fishes in the multiple regression with an adjusted R^2 value of 0.74 (Table 2, MS = 477.1, F_5^3 = 8.65, $P < 0.02$).

Decadal average number of degree days above the thermal growth limit for kelp (20°C) has risen to 13.5 ($\pm$2.48 SE) in 2010–2018 (Fig. 5). Degree days at or above 20°C in previous decades were 0.33 ($\pm$0.21 SE; 1980–1989), 7.14 ($\pm$2.35 SE; 1990–1999), and 3.33 ($\pm$1.18 SE; 2000–2009). Significant differences in decadal temperatures were observed (χ^2 = 14.07, df = 3, P = 0.003). Specifically, differences were found between 1980s and 2010s (P = 0.003), and between 2000s and 2010s (P = 0.002). Decadal average number of degree days above the reproductive limits for kelps (16°C) rose to 81.56 ($\pm$2.34 SE) in 2010–2018 (Fig. 6). Previous decades experienced 48.4 ($\pm$6.92 SE; 1980–1989), 58.83 ($\pm$4.08 SE; 1990–1999), and 56.89 ($\pm$6.20 SE; 2000–2009). Significant differences in number of degree days above 16°C were found between 2010 and 2018 and all other decades (χ^2 = 16.64, df = 3, P = 0.0008).
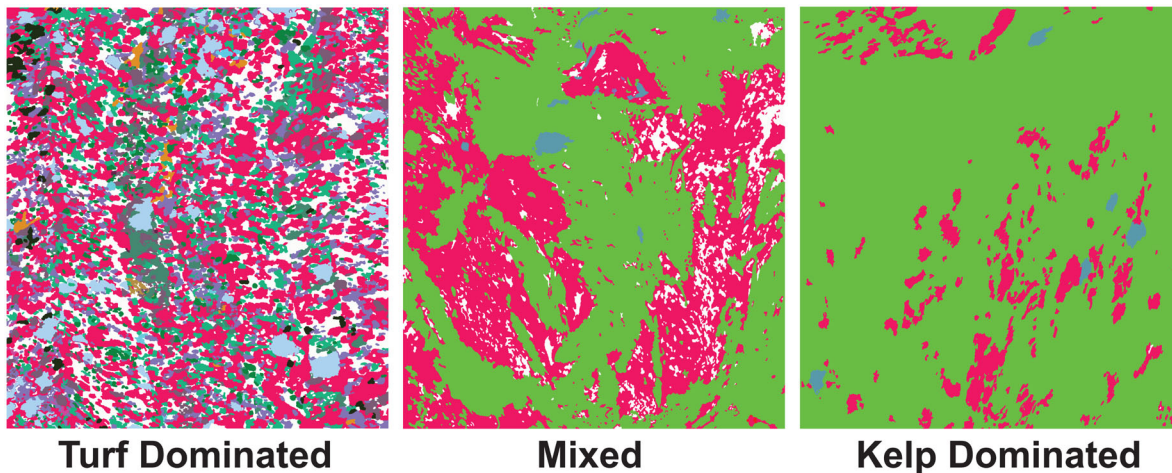
Fig. 3. Visual examples of seascape patterns in turf/kelp-dominated, and mixed macroalgae assemblages. Turf-dominated is the most heterogeneous habitat, followed by mixed and kelp-dominated assemblages.

No significant differences in number of degree days equal to or above 16°C were observed among the 1980s, 1990s, or 2000s.

Discussion

Our study demonstrates that turf macroalgae create a more heterogeneous, spatially complex seascape as indicated by the greater number and smaller sized patches in these seaweed assemblages. In this study, patches within seascapes are represented by individual species that have varying life-history characteristics that differentially respond to exogenous forces such as temperature or disturbance. Shallow rocky macroalgae assemblages are often disturbed by storm events that rip the holdfast or blades of kelp from the substrate (e.g., Lambert et al. 1992). However, for turf and other macroalgae (i.e., *Codium* spp.), storm events will disproportionately affect them as their holdfasts are not as strongly attached to the substrate as kelp holdfasts (Mathieson and Dawes 2017). These storm events are increasing in intensity, frequency, and duration, particularly during the fall and winter months in the Northwest Atlantic (IPCC 2018). A recent study found that *S. latissima* sporophytes in a turf-dominated ecosystem were settling on turf algae instead of rocky substrate. When attached to turf instead of rock, kelp growth rates were reduced, and kelp mortality was higher

due to dislodgement of the turf during storm events (Feehan et al. 2019).

Concurrently, our study indicates that temperatures are regularly above the critical thermal growth and reproductive thresholds for kelps in which reproduction of the dominant kelp species, *S. latissima*, is limited above 16°C with 0% reproduction and high mortality occurring above 20°C (Chapman and Craigie 1977, Fortes and Lüning 1980, Brinkhuis et al. 1983). The pattern of low growth and reproduction at temperatures above 16°C and 20°C is also true for other native kelps (*Laminaria digitata*, *Agarum clathratum*; Bolton and Lüning 1982, Simonson et al. 2015). These elevated temperatures likely shorten the kelps growth and reproductive season, but not that of dominant forms of turf macroalgae. For example, *Dasysiphonia japonica* and *Polysiphonia* spp. have the capacity to grow and reproduce year-round in the Gulf of Maine as their thermal growth and reproductive ranges are between 0°C and 25°C (Fralick and Mathieson 1975, Baerke and Rueness 2004, Husa and Sjøtun 2006). Further, these and many other turf-forming macroalgae are capable of reproducing vegetatively by producing fragments or other structures that facilitate rapid colonization of open space which increases their local and ultimately regional populations (Cecere et al. 2011). Reproduction and growth of *D. japonica* and *Polysiphonia* spp., among others, will likely not be cold or warm limited as winters and
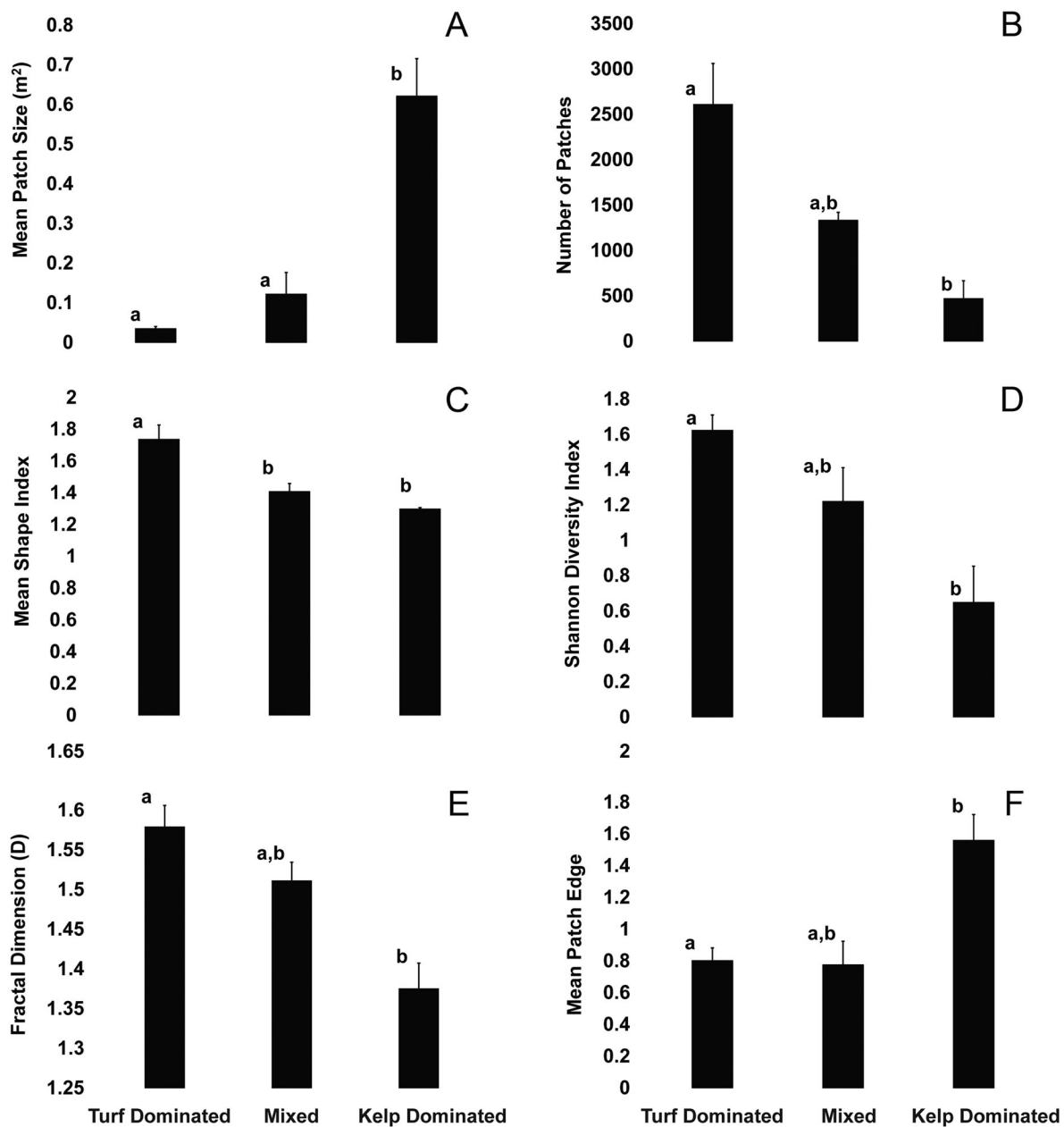
Fig. 4. Seascape metrics in turf, kelp and mixed macroalgae assemblages. Turf-dominated habitats were more complex with greater number and diversity of patches (A–D), smaller and greater variation of patch sizes (A,C), and greater seascape complexity (E). Total amount of edge was less in turf than kelp-dominated habitats (F). Letters denote significant differences in seascape features among habitats.

summers are still within their potential growth and reproductive thermal range. The greater frequency of storm-induced assemblage disturbance that frees up primary space throughout the year coupled with increasing water temperatures will likely favor primary space occupation by turf macroalgae and not kelps due to their thermal limitations and slow life cycle.

Patch size was positively related to the abundance of fish. Previous studies of the relationship

Table 1. Summary of principle component analysis of landscape metrics describing the relationship between maximum number of fish and the first three components.

Components	Eigenvalues	Representative variable	Cluster proportion of variation explained	Total variation explained
1	4.99	Number of patches	0.74	0.37
2	2.08	Mean patch size	0.62	0.22
3	1.26	Total edge	1	0.1

Table 2. Multiple regression analysis of MaxN of fishes vs. the factors that were most representative of the top three components in the PCA.

Independent variables	SS	P value	Adj. r^2
Mean patch size	765.2	0.01	0.74
Number of patches	0.003	0.99	
Total edge	0.046	0.84	

Note: Mean patch size was the only significant predictor in the model with a combined adjusted R^2 of 0.74.
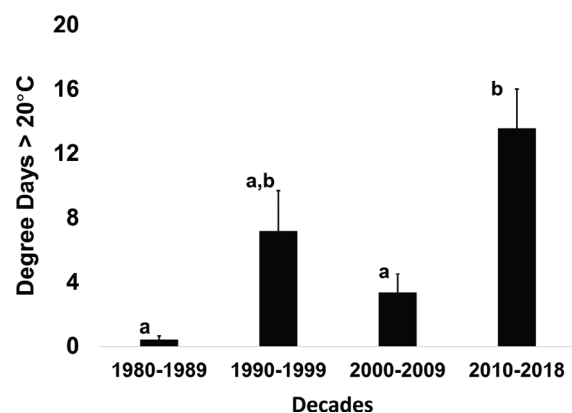

Fig. 5. Degree days above growing temperatures of kelp (20°C). Growing season of kelp has shortened by 10 d between 2010 and 2018 compared with the average of the last three decades.
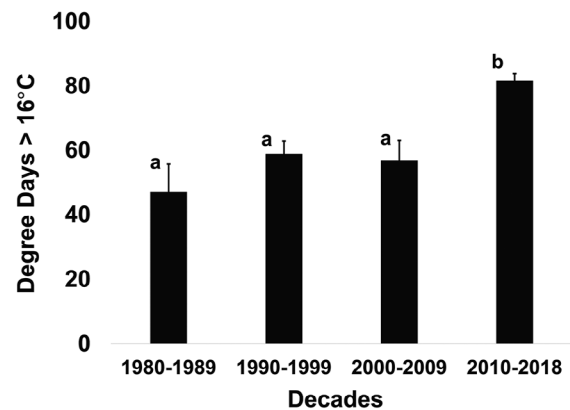

Fig. 6. Degree days above reproductive temperatures of kelp (16°C). Reproductive season of kelp has shortened by 28 d between 2010 and 2018 compared with the average of the last three decades.

between fish abundance and patch size are ambiguous with studies reporting negative and positive relationships (Boström et al. 2006, Yeager et al. 2016). Kelp-dominated habitats had the largest patch sizes. In our region, the dominant kelps, *Saccharina latissima*, *Laminaria digitata,* and *Agarum clathratum*, have long flat blades that provide a canopy over the seafloor. Previous studies demonstrate that the large blades of kelp are used as shelter for the dominant residential fish, cunner (Vasquez et al. 2014, O'Brien et al. 2018). Shelter is critical to the survival of this

species as it goes into torpor after dark and below temperatures of 5°C (Haugaard and Irving 1943, Dew 1976). If exposed while in torpor, the fish is likely to be preyed upon by migratory species such as pollock, striped bass, sculpins, and harbor seals (Dew 1976, Nelson et al. 2003). Further, Tupper and Juanes (2017) demonstrated that cunner spent more time and energy defending their shelter as their densities increased, limiting the relative number of shelters/individual. A more heterogeneous habitat dominated by turf forms of macroalgae may lead to fewer shelters and increase the time and energy that cunner spend seeking and defending their shelter. Additionally, limited shelter availability may cause cunner to occupy less desirable shelters in which the risk of predation is greater.

Migratory fish species such as pollock may not be as vulnerable to seascape patterns as they use the habitat for only brief periods of time (Bender et al. 1998), and studies indicate that migratory species are not as sensitive to seascape features

as residents (Yeager et al. 2016). However, they may experience indirect effects of turf-induced changes in seascape patterns as they prey on juvenile fishes and decapods found in this habitat (e.g., juvenile cunner or crabs). Pollock are mostly pelagic, but they sometimes feed on benthic prey and, thus, may be indirectly affected by changes in the seascape, particularly if these changes result in less shelter for their prey. If prey for pollock and other pelagic predators becomes more easily accessible due to a loss of kelp canopy (O'Brien et al. 2018), it may be a temporary boon to those predators.

Decapods and lobsters may be sensitive to changes in species composition that alter the seascape. Previous studies indicate they prefer sheltering in spaces with overlying cover (Wahle and Steneck 1992, Blamey and Bolton 2018), analogous to the canopy provided by kelp for cunner. This is especially important for juvenile and adult lobsters and crabs that may not fit into smaller crevices of boulders or ledge. The patchiness of turf-dominated habitats coupled with their short filamentous forms will leave adult individuals exposed to predators. New recruits, however, that navigate under or through the turf habitat may be more protected as the dense bushy forms of the algae may conceal prey from predators (Steneck et al. 2013, Ware et al. 2019). Overall, the effect of this changing seascape on associated decapods and lobsters will likely depend on the size and ability of an individual to navigate through it.

Conclusion

Changes from kelp- to turf-dominated habitat occurring in the subtidal rocky shores of the Gulf of Maine (Dijkstra et al. 2017a) are reflective of global changes in kelp forests (Connell et al. 2008, Wernberg et al. 2016, Filbee-Dexter and Wernberg 2018). This creates novel habitats in which the inhabitant foundation species are differentially influenced by environmental parameters. Our study indicates that turf macroalgae produce a heterogeneous community and provide a mechanism for continued persistence of this habitat. Increasing temperatures combined with more frequent, intense, and variable storm-induced fluctuations of available resources of

primary space favor turf macroalgae whose thermal ranges for growth and reproduction are well within the temperature ranges observed and predicted for this region. However, alterations and maintenance of seascape patterns in other regions will likely depend on the complex interactions between environmental variables and life-history characteristics of the inhabitant foundation species as well as the morphology of novel species. For example, alterations in overall seascape pattern may be limited where foundation species share life-history and morphological characteristics (e.g., Pessarrodona et al. 2019). These environmentally induced changes in the maintenance of species composition drive and sustain the overall increase in seascape patchiness. Our study indicates that in cases of foundational induced transformation of seascape patterns, these changes will likely propagate up the food web, specifically affecting those species that are residential and seek refuge and food within the seascape.

Acknowledgments

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SUPPORTING INFORMATION

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