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Authors(s):	Robert Neil Jarrett (Corresponding Author), Damian Brady (Co-author), Richard Wahle (Co-author), Robert Steneck (Co-author)
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Title: Shifts in habitat use and demography of American lobsters in coastal Maine over the past quarter century

Authors: Robert N. Jarrett II*, Damian C. Brady, Richard R. Wahle, Robert S. Steneck

Darling Marine Center, University of Maine, Walpole, Maine 04573, USA

*Corresponding author: robert.jarrett@maine.edu

Running page header: Shifting lobster habitat use and demography

Abstract: Some species are so linked to specific environments that their habitat association almost becomes a species-defining character and is used by managers and policymakers to direct their conservation. The American lobster, *Homarus americanus,* is among the most valuable fisheries species in North America and among the best studied benthic marine invertebrates in the world. Its populations and habitats have been studied and detailed in publications for over 35 years. This lobster species was known to dwell in shelters and their populations had historically been concentrated in shelter-providing boulder habitat. Our study revisited 20 long-term monitored sites at 10 m depth along more than 320 km of the Gulf of Maine. Surprisingly, we recorded fundamental changes in lobster abundance, habitat use and distribution. Specifically, lobster population densities declined overall and occupancy in boulder habitats declined 60% while densities on featureless ledge and sediment habitats increased 633% and 280% respectively from 2000 to 2019. Lobster rock shelter occupancy declined in recent years, but average body size increased, due in part to declines in smaller size classes. These demographic changes may result from both reduced recruitment and intraspecific competition resulting from the lower population densities. Habitat changes at our monitored sites included declines in kelp abundance, increases in diminutive algal turfs, and nearly 3°C warming of benthic water temperature in July (1995-2021) some of which may have contributed indirectly to those shifts. While these changes in shallow water habitat and demography have implications for the lobster fishery and stock assessments, it also illustrates previously undescribed behavioral plasticity.

Keywords: Habitat selection; Population structure; Habitat complexity; Intraspecific competition; Behavior; Climate change

1. INTRODUCTION

For some species, the habitats in which they live are treated as characteristic of the species. This has implications to myriad fields from bird identification (Lin et al. 2023), conservation biology (Berg et al. 1994) to fisheries management (Kraufvelin et al. 2018). Habitat associations can be driven by a variety of processes including availability of food (Hindell & Lee 1988), mates (Lodé 2011), physiological tolerances (Cooper & Gessaman 2004) and refugia from agents of mortality (Deuel et al. 2017). Such drivers of demography are fundamental to understanding how and why species' abundance may change over time and space. How conspecific individuals interact with each other, their habitat, and the resulting dynamics can play out over a range of spatial and temporal scales (Fauchald et al. 2000, Holland et al. 2004). Habitat suitability is applied in fisheries contexts to capture habitat carrying capacity for an entire stock, but this is studied and applied over large geographic scales. Moreover, stationarity is often assumed, with relationships between the species and environment being constant over space and time. Such an approach can miss fine-scale patterns, demographic changes, and relationships that underlie patterns observed at large spatial scales (Behan et al. 2021). In a terrestrial example, fine-scale habitat data for American marten detected increased habitat selection and path tortuosity within cedar-hemlock patches of forest, when broadscale habitat data could not (McCann et al. 2014). Higher resolution, habitat-specific, sampling may be necessary to capture these individual interactions and habitat use changes that affect the way we interpret broadscale patterns, processes and the mechanism that drive the overall population dynamics (Levin 1992).

Examining patterns at the relevant scale for a particular life history of an organism is critical to understanding its ecology. Scale is particularly important with demographic patterns in patchy landscapes and seascapes (Kotliar & Wiens 1990, Ciannelli et al. 2008). Many species utilize structurally complex habitats as refugia. However, like most habitats, refugia exist as patches within a matrix of less suitable habitat (Pinsky et al. 2012). Several ecological processes may drive habitat selection of a species within heterogenous habitats often shifting with the organism's life stage. Examples of these processes include physical environmental conditions (Watt-Pringle & Strydom 2003), e.g. ice cover and size of ice floes affect habitat selection of pinniped species in Alaska (Simpkins et al. 2003); availability of resources (Beekey et al. 2004, Boyd et al. 2015); competition (Holbrook & Schmitt 2002), e.g. crayfish outcompeting benthic fishes in Europe for shelter habitat (Bubb et al. 2009); or predation (Juanes 2007, Rogers et al. 2014).

The American lobster, *Homarus americanus*, is the most productive lobster fishery in the world (Wahle et al. 2020) and has been characterized as a lucrative monoculture in the western North Atlantic (Steneck et al. 2011), with annual landed value exceeding $740 million in the state of Maine, USA in 2021 (Maine DMR 2023). As the largest benthic decapod in the region, much of the foundational ecological work on the American lobster was done in the 1970s to 1990s (Cobb 1971, Aiken & Waddy 1986, Wahle & Steneck 1991, 1992, Karavanich & Atema 1998), during and after which several fisheries independent survey programs were established that support management of the extremely valuable commercial fishery throughout Maine (i.e., American Lobster Settlement Index est. 1989, Maine-New Hampshire Inshore Trawl Survey est. 2000, Ventless Trap Survey est. 2006).

These fisheries independent surveys along with lobster landings capture the broadscale dynamics of the species within the Gulf of Maine. Landings and survey indices, as they were established, increased throughout the 1990s into the 2010s. This continued until 2016 when landings peaked after having more than quadrupled (the trap and trawl surveys also peaked around this time with preceding declines in the settlement index after 2012; Oppenheim et al. 2019, Maine DMR 2023, Reardon et al. 2023). The methodology and random stratified sampling design of the trawl and trap surveys may be well suited to capture the overall decline and broadscale trend of the stock (ASMFC 2020), but they do not necessarily characterize the fine-scale, ecological patterns of the species over the same time frame.

Over the last several decades, a paradigm of lobster's benthic ontogenetic shifts emerged (Steneck 1989, Wahle & Steneck 1991). Competent postlarvae would settle into shallow coastal cobblestone habitats (Wahle & Steneck 1991), with over 80% settling at depths less than 20 m (Wilson 1999). They then transition to early benthic phase lobsters (5-45 mm carapace length (CL)) living in small shelter providing spaces between cobblestones to avoid predation (Wahle & Steneck 1991, Palma et al. 1999). As they grow larger, adolescent phase lobsters (45-89 mm CL) move to larger boulder habitat (Lawton & Lavalli 1995, Steneck 1997, 2006), still using it as shelter though they are less vulnerable to attack (Wahle 1992). In the 1990s and early 2000s, lobsters were so concentrated in boulder habitat that densities were orders of magnitude greater than in featureless ledge and sediment habitats (Steneck & Wilson 2001). However, we are now seeing this paradigm change. Postlarval settlement has expanded to greater depth, as deep as 100 m due to the warming bottom water temperatures (Wahle et al. 2013a, Goode et al. 2019). We could expect additional alterations to this paradigm of lobster ecology as a result of the direct and indirect effects of climate change.

Here, we focused on how the distribution, abundance, habitat use, and demography of American lobster has changed over the last several decades of rapid environmental change within the Gulf of Maine. We leveraged the long-term monitoring of Steneck and Wilson (2001), by applying the same survey methods at the same sites but nearly two decades later.

2. MATERIALS AND METHODS

2.1 Quadrat Sampling

In 2019 and 2021, we revisited 20 of the long-term (1989-2000) monitored sites from Steneck and Wilson (2001). The sites span the entire coast of Maine in four regions: York, Midcoast, Mount Desert, and Jonesport (Fig. 1). Each site was located in coastal shallow zones, separated by at least 1 km. These sites were selected because they had the most extensive prior data. Following previous sampling, the sites were revisited from late June through early August.

We conducted quadrat sampling using the same methodology as Steneck and Wilson 2001. We used 1 m^2 quadrats targeting three specific substrates: boulder, ledge, and sediment. At the target depth of 10 m, quadrats were 'haphazardly' tossed without regard for the presence or absence of lobsters. Quadrats were only measured if they fell on a single substrate type. The quadrat, including any shelters within it were searched for lobsters. All lobsters within the quadrat were caught to measure carapace length (CL), determine sex, and count the number of claws. For any that escaped the diver, CL was estimated. The type of shelter, if any, the lobster was using was also recorded. This method effectively detects lobsters down to approximately 20 mm CL (Steneck & Wilson 2001).

Additionally, coverage of kelp and other macroalgae was measured. The sampling was stratified, with percent cover of kelp measured first, before kelp fronds were moved aside for the percent cover of macroalgae to be determined. In 2021, the percent cover of macroalgae was further subset into filamentous algae; the non-native, filamentous red alga, *Dasysiphonia japonica*; and the remaining other macroalgae species. A description of each of the data variables collected for each quadrat can be found in Table 1.

2.2 Analysis

This analysis included new data from 2019 and 2021, while data used from the previous sampling of Steneck and Wilson (2001) was limited to 1995-2000 (except for kelp cover data which begins in 1993). Only data from boulder substrates were reported in Steneck and Wilson (2001) due to the low lobster population densities in the other substrates, however, we used data from boulder, ledge, and sediment sampling for our comparisons. Prior years were not as consistent in sampling all sites and regions we revisited. Only the regions we revisited (York, Midcoast, Mount Desert, and Jonesport) were used, other regions were excluded. However, all sites in each region that were sampled each year were used in the analysis of overall trends.

The number of lobsters per quadrat was used to determine the population density by substrate type and (not weighted by differences in substrate area) overall. The densities were then used to calculate the variance-to-mean ratio (VMR) to understand the spatial dispersion of the population. The Kolmogorov-Smirnov test was used to compare lobster size distributions between years and a threshold of 45 mm was used to compare modes between distributions, due to transition in life phase at that size. The mean was calculated at each site for the percent of lobsters per shelter type. Given the non-normal distribution of the densities and shelter data, the non-parametric Kruskal-Wallace test was used to determine differences across all years of the sampled categories followed by Dunn's post-hoc tests, with Bonferroni correction, for multiple pairwise comparison. A t-test used to compare the VMR of each year to a random distribution and a chi-squared test was used to compare the distribution of lobsters across shelter types between years. All analyses were conducted in R (v. 4.2.3, R Core Team 2023) and R Studio (v. 2023.06.1, RStudio Team 2020).

2.3 Temperature data

Bottom water temperatures were used to characterize the rapid environmental change in the coastal shallow study sites. However, in-situ measurements of bottom water temperature are limited, therefore modeled bottom water temperature data from 1995-2022 was obtained from the Northeast Coastal Ocean Forecasting Systems (NECOFS), which is an implementation of Finite Volume Community Ocean Model (FVCOM) (Chen et al. 2006a). The closest three nodes to each study site from the model's unstructured grid were determined and the node with the closest depth to 10 m was selected. The mean coast-wide temperature in July each year was calculated using the monthly mean temperature from July of each of the nodes selected for each site. July temperatures were used to coincide with the sampling timeframe of the study, with July being when the majority of both past sampling (1995-2000) and new sampling for this study (2019, 2021) occurred. NECOFS model skill is lower in shallow coastal water, likely due to tidal cycles and stratification (Li et al. 2017). However, due to the model's low cost, high spatial resolution and broad geographic extent, it is valuable source of estimated bottom water temperature for our study sites that has been used to inform management decisions for several benthic species including lobster (Li et al. 2015, Tanaka & Chen 2016, Goode et al. 2019).

3. RESULTS

While population density of lobsters at 10 m among all substrates increased from 1995 to 2000, by 2019 and 2021 densities were significantly lower than 1997-2000 (Dunn's Test, $p < 0.008$, Table S1). Substrate-specific population densities declined 60% in boulder substrates from the 2000 to 2019 (red bars, Fig. 2). The ledge and sediment substrates increased 633% and 280% from the lowest in 2000 to 2019 respectively (orange and yellow bars, Fig. 2). In fact, there was not a significant difference in population densities across the three substrate types in 2019.

Lobster populations were highly aggregated from 1995 to 1998 but over the intervening period became randomly distributed among substrates (2019-2021) (Fig. 3). The variance to mean ratio (VMR) illustrates the trend in distribution patterns. This trend may have begun in 1999 but was not significantly different (t-test, $p < 0.05$, Table S2) from a random distribution (yellow line, Fig. 3) by 2019 and 2021.

Trends in shelter use mirrored the changes observed in habitat use with rock shelters most frequently occupied but declining after 2000 (red-purple bars, Fig. 4). The percentage of lobsters using rock shelters declined 34% from 2000 to 2019, while the lobsters observed beneath algae (green bars, Fig. 4) or not using a shelter (light blue bars, Fig. 4) increased 161% and 168% respectively during that time. The percentage of lobsters using sediment pits as shelters remained low across all years (yellow bars, Fig. 4). Pairwise comparisons using a chi-squared test between years found that differences between all comparisons were highly significant ($p < 0.001$) except for 1997 v. 1998, 1999 v. 2000, and 2019 v. 2021 which were not significantly different.

Concomitant with a reduction in specific habitat and shelter association, size frequency distributions shifted to larger lobsters in recent years (Fig. 5). Over 93% of lobsters sampled each year from 1996-2021 were smaller than 83 mm (minimum legal size of the fishery in Maine; solid yellow line, Fig. 5), except for 2019, where 85% were smaller than legal size. The size distribution of lobster shifted to the right from 2000 to 2019 (Fig. 5). The mode of the density estimate (vertical white lines, Fig. 5) increased from 35 mm in 2000 to 70 mm in 2019, overall being at or below 45 mm CL in the first time period to above 45 mm in the second period. The difference between the size distributions in both 2019 and 2021 to all previous years were highly significant (Kolmogorov-Smirnov test, $p < 0.001$, Table S4). The mean size of lobsters increased across all three substrate types between the two sampling periods (1995-2000 and 2019, 2021) and the mean size was lowest for both periods in the boulder substrate compared to ledge or sediment.

The mean number of claws for lobsters across substrate types and shelter types varied (Fig. 6). The mean number of claws was lower in the sediment substrate compared to boulder and ledge substrate; sediment was significantly lower (Dunn's test, $p < 0.05$, Table S5) in the first time period (Fig. 6a). The mean number of claws lobsters had between the two time periods were not significantly different for each substrate type. The mean number of claws was highest for lobsters using rocky shelters and lowest for lobsters using sediment pits as shelter (Fig. 6b). The mean number of claws for lobsters not using a shelter was also relatively high. There was not a significant difference in the mean number of claws across the two time periods for each shelter type (Dunn's test, $p < 0.05$, Table S6).

The biologic nature of the habitat also changed both within the late 1990's and between the late 1990's and recent years (i.e., 2019 & 2021). The most striking differences were observed in the macroalgal communities. Kelp abundance declined over 64% in percent cover from 1993 to 2000 (Fig. 7). Meanwhile, the percent cover of other macroalgae (mostly diminutive "turf" algae consisting of filamentous algae and *Chondrus crispus*) increased 119% from when measurements began in 1997 to 2000, though the overall coverage was still relatively low, below 20%. Following the sampling gap, the other macroalgae category had increased to over 50% by 2019. Kelp abundance remained low in 2019 and 2021, with similar percent coverages to the late 1990s. In 2021, filamentous algae cover made up 66% of the other macroalgae.

Finally, ocean temperatures on the sea floor surrounding our shallow study sites have increased since 1995 (Fig. 8). Modeled mean monthly temperatures in July from NECOFS ranged from 9.7 to 19.1°C across all the study sites. The coast-wide mean increased nearly 3°C from 1996 to 2021. As described in Friedland et al. (2020), Gonçalves Neto et al. (2021) and others, in 2010, there is a shift towards higher bottom water temperature that holds through the most recent years.

4. DISCUSSION

The two over-arching conclusions from our work were: 1) American lobsters have changed their habitat selection behavior. 2) These shallow coastal habitats in Maine have changed with our changing climate. These two observations may be important examples of how organisms acclimate to climate change and the importance of examining at what scale this occurs. We discuss specific details of this below.

Lobsters at our monitored sites were less abundant, with fewer occupying shelters in boulder habitats and more using featureless ledge and sediment habitats (Fig. 2). This more random selection of habitats (Fig. 3) could have larger demographic consequences since featureless habitats are more abundant than cobble or boulder fields (Wahle & Steneck 1991). Beyond lobster sheltering less than they had in the past, more lobsters were observed under algae (Fig. 4). While sheltering under kelp at one of our monitored sites was reported before (Bologna & Steneck 1993), it is unlikely this functions as a refuge from predators. Studies at some of our monitoring sites starting in the 1980s showed large predatory fishes were largely absent and lobsters larger than 20 mm (CL) were rarely attacked. By the time lobsters grew to 60 mm (CL) they were virtually immune from predation in shallow coastal zones (Wahle & Steneck 1992, Steneck 1997, Butler et al. 2006, Wahle et al. 2013b). Those experiments also showed that large predators, like Atlantic cod and wolffish were already ecologically extinct (sensu Estes et al. 1989) and since the 1990s they have only declined further. This lack of predation, that precedes the initial surveys, may have enabled subsequent changes in the ecological processes affecting lobster demography.

Drawing upon several lines of extensive survey and experimental evidence, Wahle et al. (2013b) evaluated the lobster - predatory fish interaction along the steep thermal and biogeographic transition from the cool regime of the eastern Gulf of Maine to warmer southern New England. Predation experiments conducted in 2000 revealed a significantly lower number and diversity of predatory fish, and correspondingly lower attack rates on tethered lobsters, in Maine than at the southern edge of the species range in Rhode Island. A subsequent survey in 2003 and 2004 by divers and remotely operated vehicle of nursery habitat confirmed that in the northern areas, where predatory fish were less abundant and diverse, lobsters were more weakly associated with shelter-providing habitat, and more often found on featureless habitat with no shelter. Together, the results not only underscore the relatively low predation pressure in the Gulf of Maine compared to more predator rich areas to the south, but they also indicate while the smallest early benthic phase lobsters in nursery habitats are most prone to predation and remain strongly associated with shelter, they effectively outgrow their predators at a smaller size in the northern relatively predator-free areas than in the south. These findings suggest that predation is unlikely to have played a strong role in driving the shift in habitat use by larger juvenile lobsters in Maine between 1995 and 2021.

Our study showed that lobster size frequency distributions trended towards larger size in recent years with a larger proportion above harvestable size (83 mm CL; Fig. 5). However, the mode of the 2019-2021 size density estimates are still below the minimum legal size. The shift towards larger lobsters most likely resulted from the documented decline in lobster settlement at 10 m depths over the past two decades (Goode et al. 2019, Oppenheim et al. 2019, McManus et al. 2023), which has contributed to the lower population densities we recorded (e.g. Fig. 2). However, the shift in size structure may affect other ecological processes including competition.

The observed decline in small lobsters results in fewer lobsters requiring shelter-providing habitat compared to a population of larger lobsters, which could contribute to changes in observed sheltering behavior and shelter competition. Specifically, the more recently dominant adolescent phase lobsters (45-89 mm), are behaviorally distinct from early benthic phase lobsters (5-45 mm). The ontogenetic behavioral change from obligate shelter-dwelling early benthic phase to adolescent phase is well documented (Wahle & Steneck 1991, Wahle 1992). In contrast, adolescent phase lobsters are more vagile and their size makes them less vulnerable to predation. Although proportionately fewer, adolescent phase lobsters still tend to occupy shelters due to their thigmotactic and negative phototactic behaviors (Cobb 1971) venturing out mostly at night to forage.

Adolescent phase lobsters compete for shelters, and the intensity of competition likely scales with population density and body size (i.e., about one lobster per square meter; Steneck & Wilson 2001). Experimental studies found that although larger lobsters were competitively dominant, they would vacate habitats having high population densities often going to deeper habitats where population densities were lower. This demographic effect of intraspecific competition is called “demographic diffusion” and results in populations of smaller lobsters dominating the shallows (Steneck 2006). The decline in overall population density (Fig. 2) and specifically the decline in smaller early benthic phase lobsters (Fig. 5) may have relaxed competition in shallow coastal habitats such that it is possible that demographic diffusion no longer has a controlling influence on lobster size and distribution. In this case, larger adolescent and adult lobsters may now be retained in the shallow habitats, which follows the increase in the size distribution across all three substrates. As the larger lobsters compete for space the competitively subordinate lobsters may have been forced into less preferred habitats that provide less shelter and protection.

Given the lower proportion of lobsters occupying shelters in boulder habitats, does it also follow that shelter competition has relaxed? For this question, we focus on the association between clawlessness and substrate and shelter type (Fig. 6). Previous studies determined that size differences between lobsters competing for shelters dictates the intraspecific competitive dominance in agonistic interactions, however the loss of one or both claws most significantly reduces lobster competitiveness (O'Neill & Cobb 1979). As a result, when competition is intense, subordinate lobsters missing claws would be more likely to be relegated to featureless habitats such as sediment and ledge substrates. However, finding lower lobster population density and a lower proportion of lobsters being observed in shelters in our study both suggest relaxed competition. But we found little or no habitat related differences in the proportion of one or no clawed lobsters across the 1995-2000 and 2019-2021 sampling periods (Fig. 6). The lower proportion of two clawed lobsters in sediment substrate and in sediment pit shelters suggests that those are less preferred habitats, while boulder substrate and rocky shelters had, in past and recent years, the highest frequency of lobsters with both claws and is most preferred habitat.

Changes in habitat use and sheltering behavior affect lobster catchability, both for fishers and fisheries independent surveys. Trap catchability or the distance a given lobster trap can attract a lobster increases in featureless habitats (Miller 1990). This may be due to hydrodynamic differences affecting the scent plume of bait (Tremblay & Smith 2001, Geraldi et al. 2009). Kelp and perhaps other algae may also decrease the catchability of lobsters (Miller 1989), due to hydrodynamic differences. The heterogeneity of the benthos can also affect fisheries estimates of abundance. For fisheries independent trawl surveys, complex bottom is less well sampled and results in low catch efficiency (Somerton 1999, Zimmermann 2003). Lobsters occupying boulder shelters have almost certainly been underestimated by trawl surveys as compared to the effectively sampled featureless sediment substrate. Observed increases in population densities on sediment habitats may compensate for overall decline in abundance, therefore changes in habitat use should be considered when interpreting trends in the Maine-New Hampshire Inshore Trawl Survey (Tanaka & Chen 2016) and to a lesser extent the more offshore Northeast Fisheries Science Center Bottom Trawl Survey (Chen et al. 2006b, Pinsky et al. 2021).

There is also a practical consideration for fishers in Maine. Since 1995 there has been a fixed limit to the number of traps a lobster fisher can fish. However, with the changes described above, fishing practices also may have to adapt to the more random spatial distribution of lobsters. When lobsters were concentrated in boulder fields, traps were often placed there. However, as lobster distributions become less substrate specific, more traps, more widely spaced may be required to capture them. In Maine, lobster fishing regulations have limited the number of traps fished since 1995 (Maine DMR 2023) so fishing effort cannot easily expand and contract interannually to match lobster stock distributions.

Ocean habitats are changing with climate change. The Gulf of Maine as a whole, from 2004 to 2013, warmed faster than 99% of the world's oceans (Pershing et al. 2015). Using modeled bottom water temperature from NECOFS across our study sites, we saw ~3°C increase in the mean from the start of our study and a rapid shift of increased temperature in 2010 (Fig. 8) that is driven by changing oceanography in the Gulf of Maine (Friedland et al. 2020, Gonçalves Neto et al. 2021, Townsend et al. 2023). Laboratory experiments have demonstrated that lobsters spend more time out of their shelter to forage with increased temperatures, including increased time spent doing so during the day (Wang et al. 2016). Combined with larger lobsters sheltering less and using featureless habitats that do not provide shelter, increased foraging during the day may help to explain lower proportion of lobsters observed using a shelter. With higher temperatures than in the past, even lobsters that are using shelters may be more active and out of shelter during the day when we conducted our sampling, while in the previous sampling most activity occurred would have occurred at night. Additionally, larger lobsters, that now make up more of the population, would be more affected by the temperature-limited oxygen concentrations and organisms having greater metabolic demands (Pauly et al. 2022). However, there are other ways warming seas and other ecological processes are changing lobster environments.

Algal communities have undergone several phase shifts over the past several decades, in part due to rising temperature. Following the decline in sea urchin barrens due to overfishing beginning in the late 1980s, some of our southernmost monitoring sites had already began to see the return of kelp (Steneck et al. 2013). Subsequent to that return, we saw declines of kelp from the quadrat sampling in the 1990s where it has remained low (Fig. 7).

About the same time, starting in the south, other filamentous turfs and macroalgae increased rapidly. Upon returning to the sites in 2019 and 2021, we recorded algal communities dominated by filamentous turf algal species. This algal community shift was best documented at Isle of Shoals, within sight of our southern-most York monitoring sites. *Codium fragile*, a green alga, and *Neosiphonia* spp., a filamentous red, started to dominate around in the 1990s and *Dasysiphonia japonica*, another filamentous red, dominated some sites as early as 2012 (Dijkstra et al. 2017). The change in the structure of macroalgal communities, with the shift to an alternate stable state dominated by turf algae (Filbee-Dexter & Wernberg 2018, Suskiewicz et al. 2024), is most often too diminutive to provide additional shelter for lobsters and not a big contributor for the increase in lobster observed using algae as a shelter. However, some lobsters may only be moving around beneath the higher canopy algae (e.g. *Codium*) and thus could be captured in this category without them "sheltering" under those algae.

It is tacitly assumed that the ecology and life history process of organisms within an ecosystem will not change. This stationarity is implicitly assumed in almost all fisheries stock assessments that inform fisheries management. This assumption can impact how essential fish habitat and habitats of particular concern are defined and protected for managed species. The ecosystem we describe here for the coast of Maine is highly dynamic, particularly with rapid climate change. Past sheltering behaviors do not characterize current behaviors, and behavioral plasticity provides an avenue to adapt to these rapid changes. Understanding changes in fine-scale demographic patterns provides crucial context for possible evidence of non-stationarity in life history process and the broad scale dynamics captured in fisheries-independent surveys for the assessment and management of the stock. Habitat-specific monitoring within a finer spatial scale are necessary to incorporate these continued ecological changes into decision-making processes.

Most importantly, we see evidence that organisms can change their habitat selection and occupancy over time. However, we also see that habitats have changed and will likely continue to change in the foreseeable future. Ecologists and fisheries managers may have to be less place-based and more environmentally oriented as populations and communities shift at multiple spatial scales and at ever increasing rates.

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TABLES:

Table 1: Description of data variables collected for each quadrat.

Variable	Description
Substrate	Bottom substrate where quadrat is placed: Boulder (rocky complex bottom that can provide shelter), Ledge (hard bedrock bottom that is relatively featureless), or Sediment (sand or mud bottom)
Kelp	Percent cover of kelp species
Other Macroalgae	Percent cover of other macroalgae species with kelp fronds moved aside
Number of Lobsters	Total number of lobsters found within the quadrat
Carapace Length (mm)	Length of lobster carapace measured from behind eye to where the carapace meets the tail
Sex	Sex of the lobster identified using the first set of pleopods (Male or Female)
Claws	Number of claws the lobster has
Shelter Type	Type of shelter where lobster was found: Rock (crevices between rocks and boulders), Algae (beneath kelp fronds or the canopy of other macroalgae), Sediment (a pit dug by a lobster in the sand or mud), No Shelter (the lobster is found in the open, unsheltered)

FIGURES:

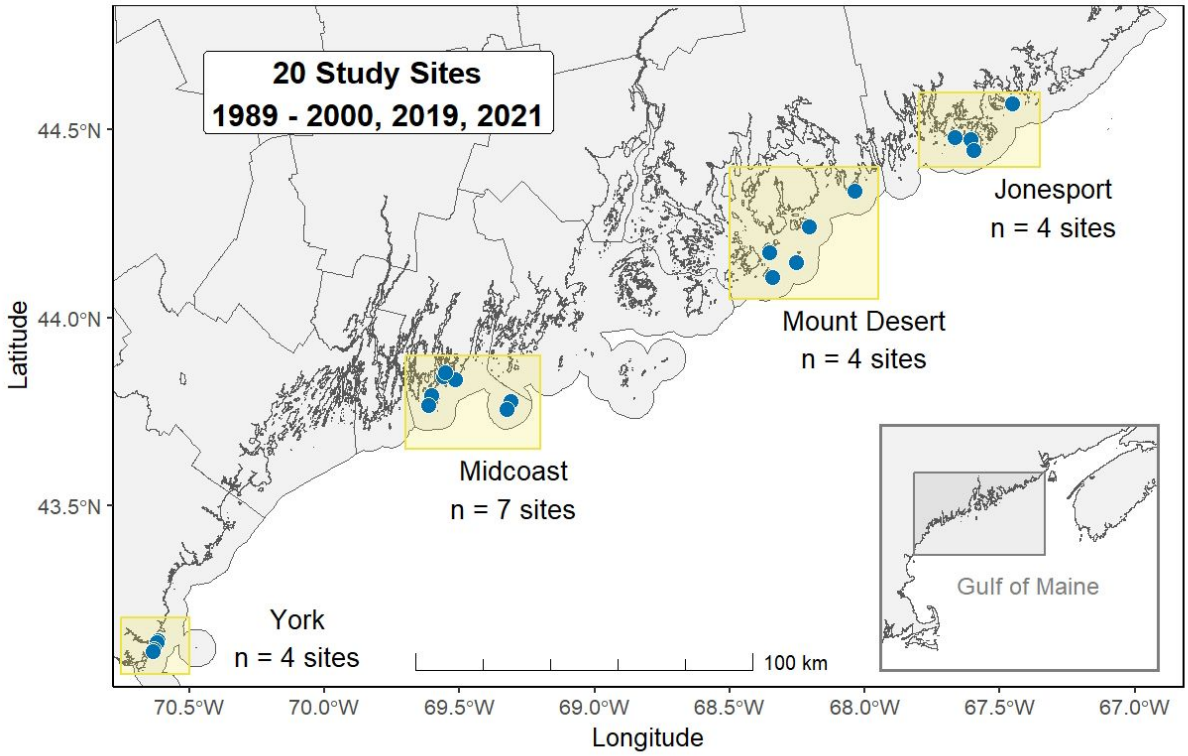

Figure 1: Map of the study sites revisited along the outer coast of Maine. The sites are spread across four regions: York (4 sites), Midcoast (7 sites including 2 at Monhegan Island), Mount Desert Island (4 sites), and Jonesport (4 sites). The quadrat sampling across the sites occurred from 1989-2000, 2019, 2021.

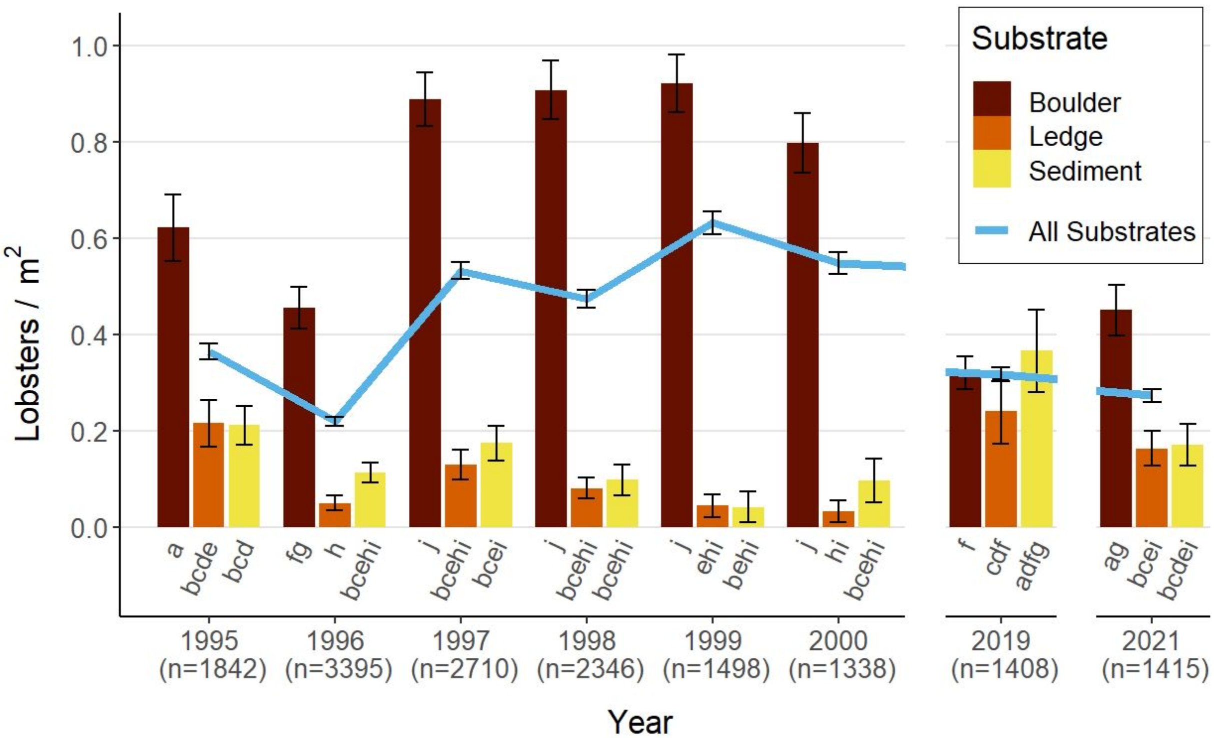

Figure 2: Mean lobster population densities from 1995 to 2021. Bars are mean density for each substrate (boulder, ledge, and sediment). The blue line is overall mean density across all substrates. Error bars are 95% confidence intervals. Letters, noted below bars, shared between years are not significantly different from one another (Dunn's test, $p < 0.05$, Table S1), the number of quadrats is beneath each year.

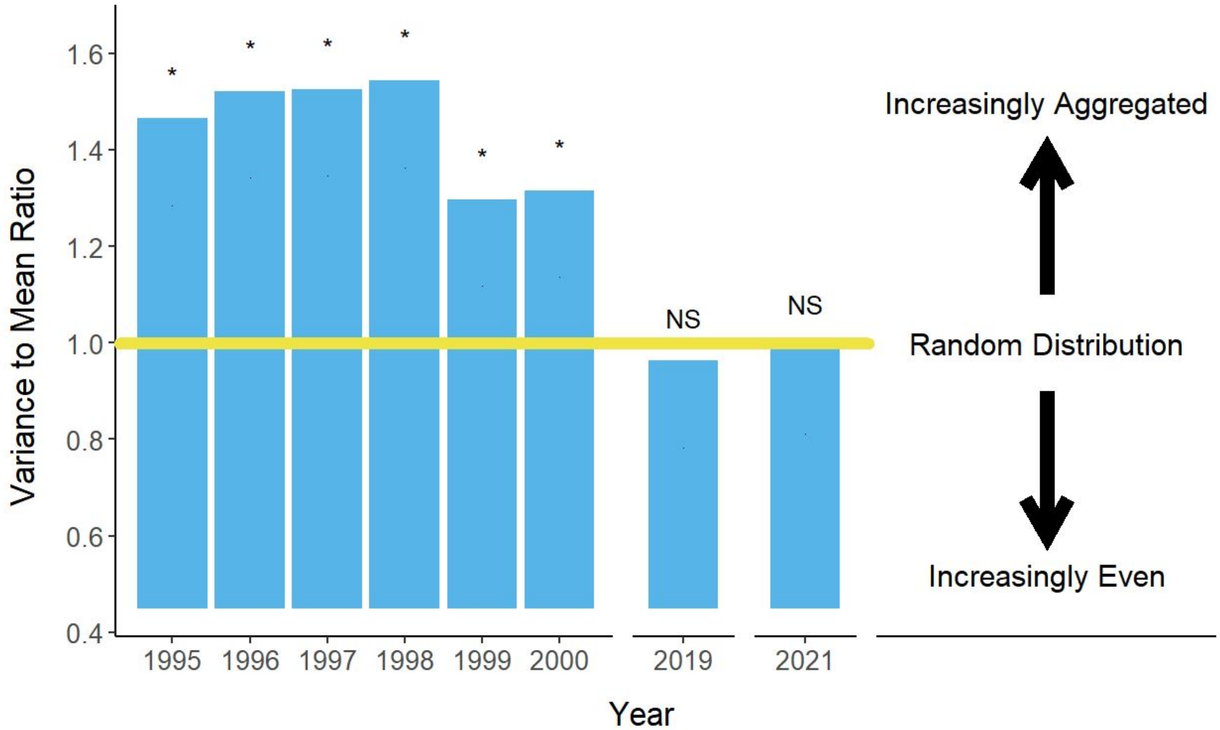

Figure 3: The variance to mean ratio (VMR) of overall lobster population densities (1995 - 2021). VMR > 1 indicates an aggregated population, VMR < 1 indicates an evenly dispersed population, VMR ~ 1 indicate a randomly distributed population (yellow line). A t-test was used to determine if the population distribution is significantly different from that of a random distribution, indicated with asterisks (Table S2).

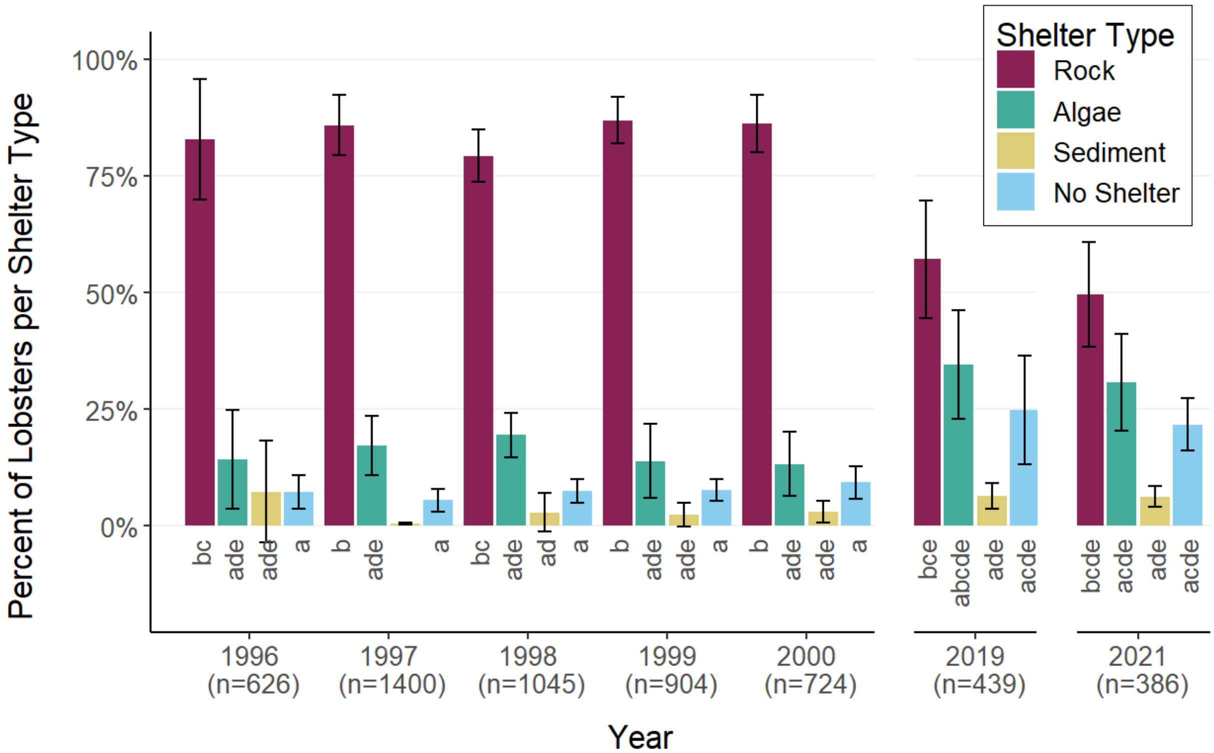

Figure 4: Shelter occupancy ranging from rock shelter, beneath algae, in sediment pit, or no shelter from 1996 to 2021. Error bars are 95% confidence intervals. Letters, noted below bars, shared between years are not significantly different from one another (Dunn's test, $p < 0.05$, Table S3), the sample size of lobsters is included beneath each year.

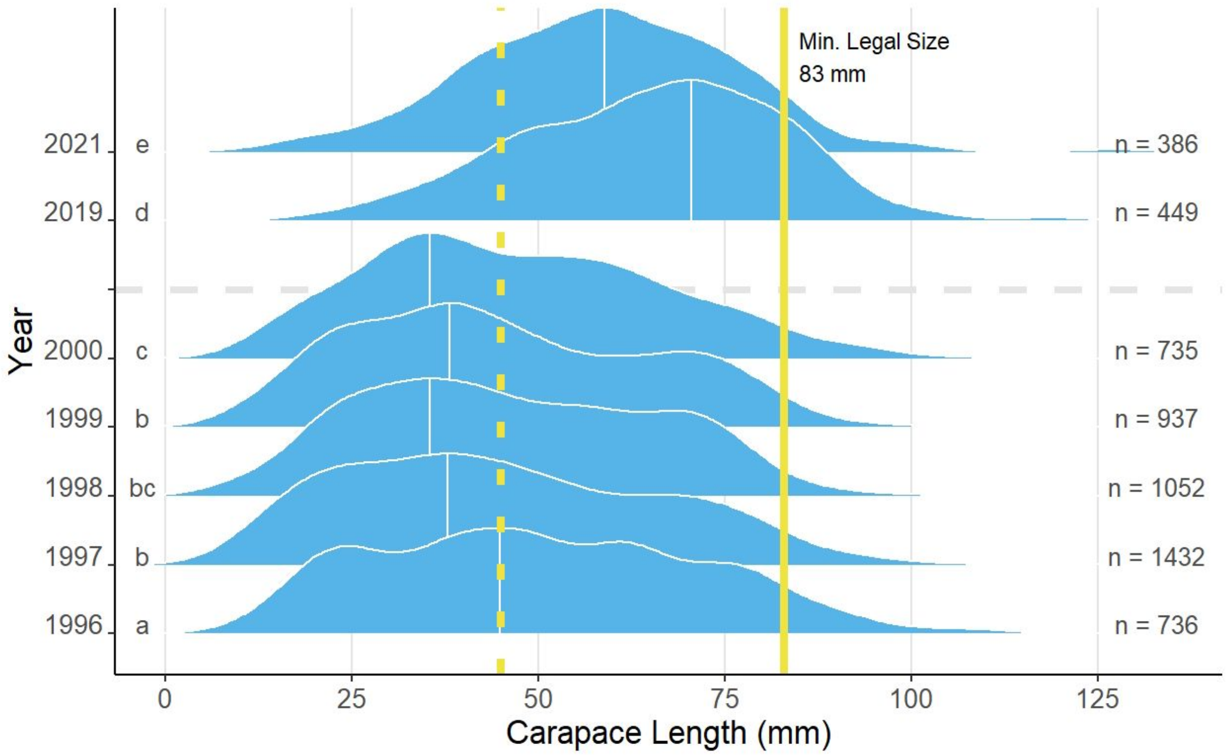

Figure 5: The relative density estimates of sampled lobster sizes for each year. The white lines indicate the mode of the estimate. The vertical dashed yellow line denotes the transition between early benthic phase and adolescent phase lobsters (45 mm CL) and the solid yellow line denotes the minimum legal size of the fishery in Maine (83 mm CL). The horizontal dashed line denotes the sampling gap between 2001 and 2018. Letters, noted to the left, shared between years are not significantly different from one another (Kolmogorov-Smirnov test, $p < 0.05$, Table S4) and the sample size of lobsters is noted on the right.

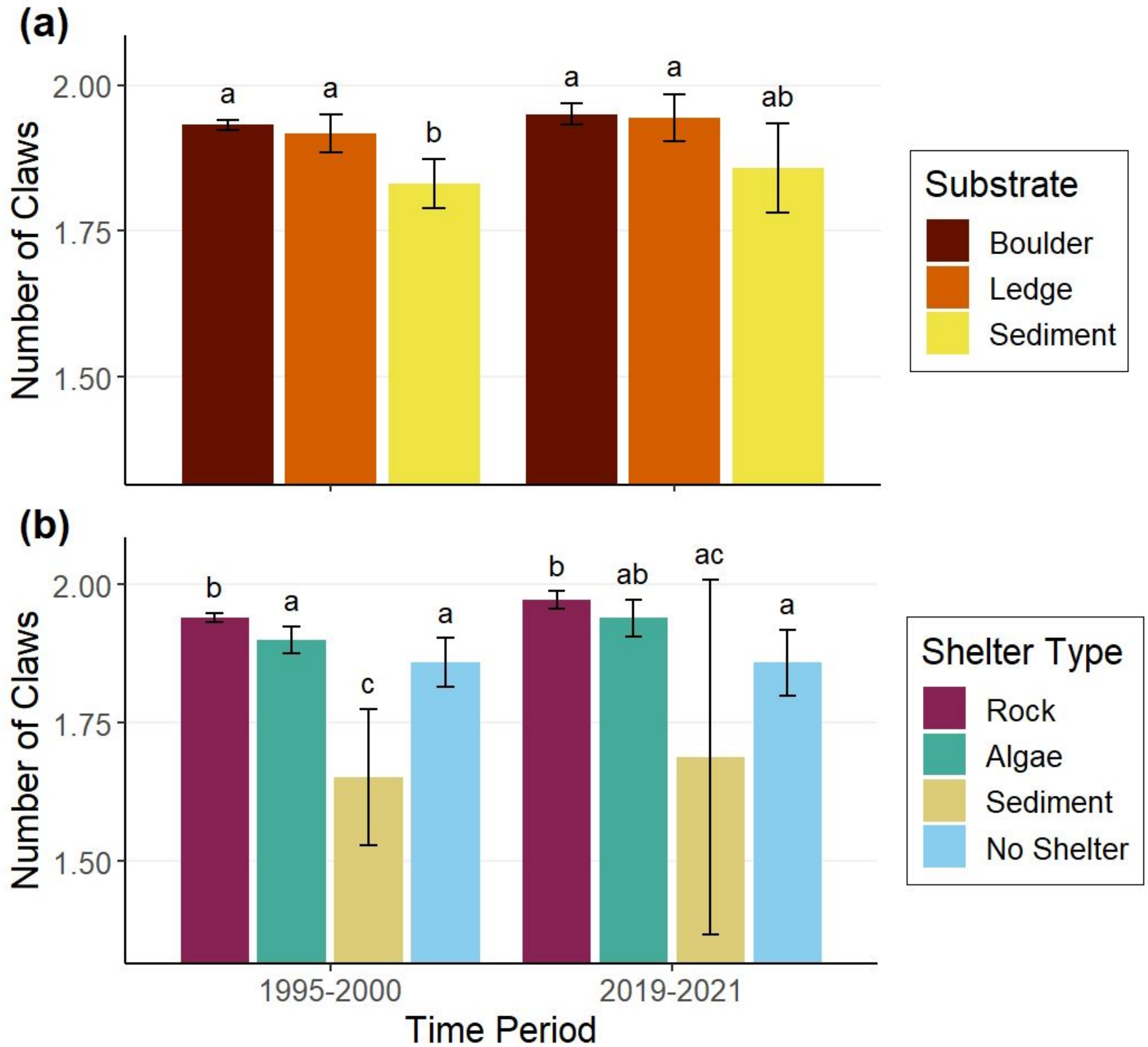

Figure 6: The mean number of claws of lobsters observed across the two sampling periods (1995-2000 and 2019-2021) compared across (A) substrate type and (B) shelter type. Error bars are 95% confidence intervals. Letters (above) shared between groups are not significantly different from one another (Dunn's test, $p < 0.05$, Tables S5 & S6) for each plot.

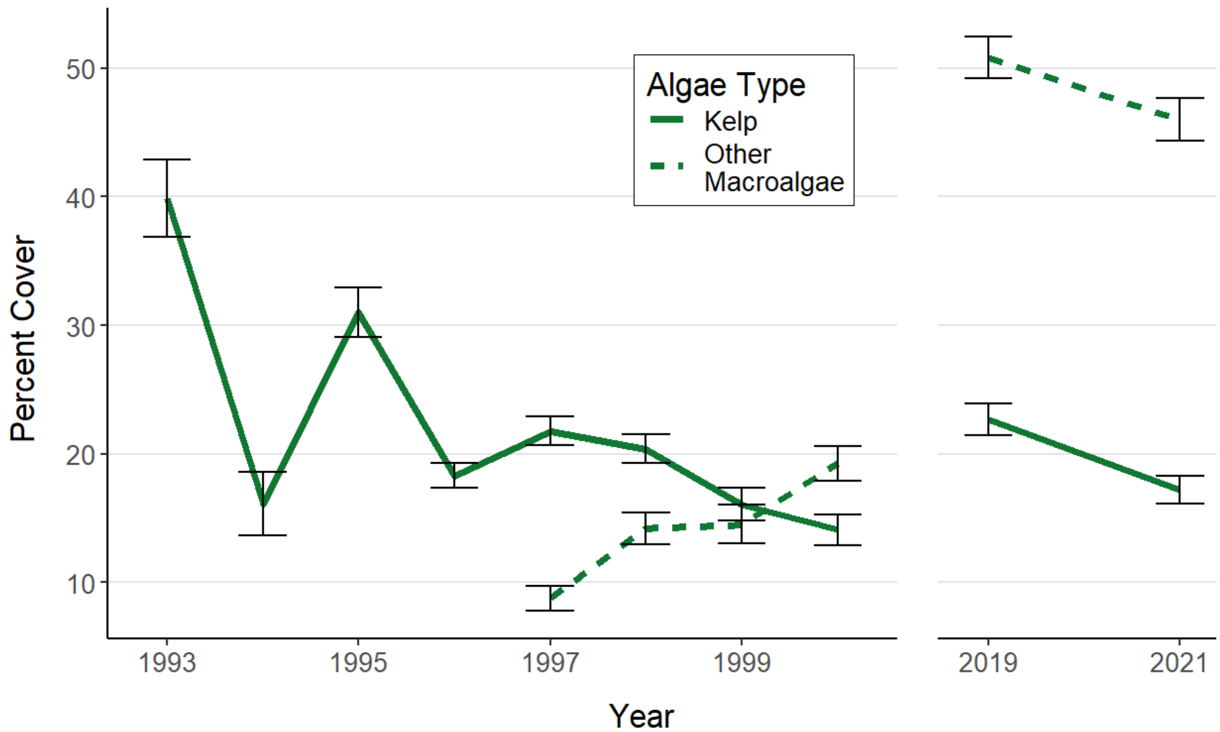

Figure 7: Mean percent cover of kelp and other macroalgae from quadrat sampling from 1993-2021. Error bars are 95% confidence intervals.

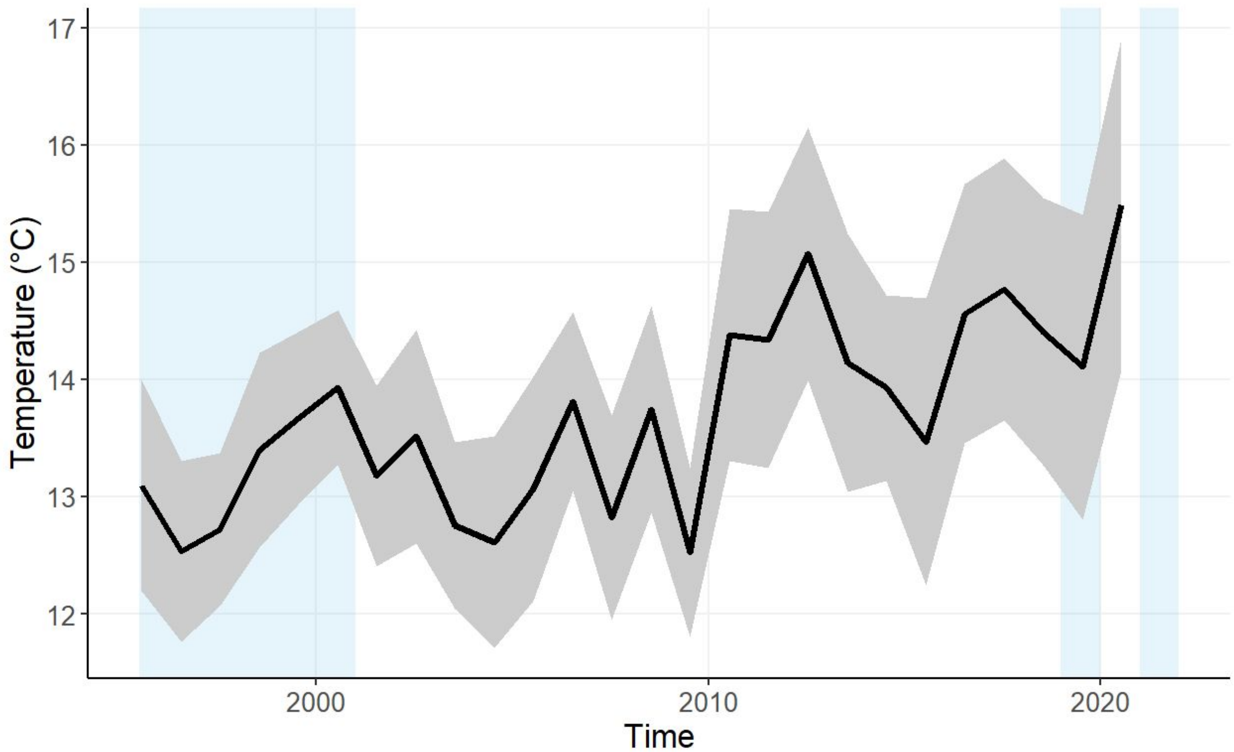

Figure 8: Coast-wide modeled mean July bottom water temperature from Northeast Coastal Ocean Forecasting Systems (NECOFS) from 1995-2020. The plotted mean was calculated across study sites. Shaded gray area is the 95% confidence interval and blue background indicates years when quadrat sampling occurred.

Table S1: Z-score and p-values of multiple pairwise comparison of lobster population density by year and substrate type (B=Boulder, L=Ledge, S= Sediment) using Dunn's test with Bonferroni correction ($p < 0.05$ sig. level).

Comparison	Z	P	Comparison	Z	P	Comparison	Z	P
1995 B - 1995 L	9.740	5.63E-20	1995 L - 1999 S	3.610	8.46E-02	1999 L - 2019 L	-3.924	2.41E-02
1995 B - 1995 S	10.571	1.12E-23	1995 S - 1999 S	3.679	6.47E-02	1999 S - 2019 L	-3.911	2.54E-02
1995 L - 1995 S	0.089	1.00E+00	1996 B - 1999 S	8.896	1.60E-16	2000 B - 2019 L	8.656	1.35E-15
1995 B - 1996 B	4.451	2.36E-03	1996 L - 1999 S	0.258	1.00E+00	2000 L - 2019 L	-4.050	1.42E-02
1995 L - 1996 B	-6.822	2.48E-09	1996 S - 1999 S	1.937	1.00E+00	2000 S - 2019 L	-2.818	1.00E+00
1995 S - 1996 B	-7.586	9.08E-12	1997 B - 1999 S	16.367	9.13E-58	2019 B - 2019 L	1.271	1.00E+00
1995 B - 1996 L	17.105	3.78E-63	1997 L - 1999 S	1.977	1.00E+00	1995 B - 2019 S	3.329	2.40E-01
1995 L - 1996 L	5.021	1.42E-04	1997 S - 1999 S	2.928	9.40E-01	1995 L - 2019 S	-3.463	1.47E-01
1995 S - 1996 L	5.367	2.21E-05	1998 B - 1999 S	16.601	1.89E-59	1995 S - 2019 S	-3.642	7.47E-02
1996 B - 1996 L	15.016	1.60E-48	1998 L - 1999 S	1.099	1.00E+00	1996 B - 2019 S	0.805	1.00E+00
1995 B - 1996 S	14.882	1.20E-47	1998 S - 1999 S	1.273	1.00E+00	1996 L - 2019 S	-7.159	2.25E-10
1995 L - 1996 S	2.788	1.00E+00	1999 B - 1999 S	17.078	6.00E-63	1996 S - 2019 S	-5.644	4.59E-06
1995 S - 1996 S	2.940	9.06E-01	1999 L - 1999 S	0.193	1.00E+00	1997 B - 2019 S	7.712	3.41E-12
1996 B - 1996 S	12.404	6.82E-33	1995 B - 2000 B	-5.241	4.42E-05	1997 L - 2019 S	-5.212	5.14E-05
1996 L - 1996 S	-2.873	1.00E+00	1995 L - 2000 B	-15.039	1.13E-48	1997 S - 2019 S	-4.373	3.38E-03
1995 B - 1997 B	-6.986	7.79E-10	1995 S - 2000 B	-16.416	4.08E-58	1998 B - 2019 S	8.081	1.78E-13
1995 L - 1997 B	-17.291	1.51E-64	1996 B - 2000 B	-10.900	3.20E-25	1998 L - 2019 S	-6.129	2.43E-07
1995 S - 1997 B	-19.127	4.13E-79	1996 L - 2000 B	-24.244	2.09E-127	1998 S - 2019 S	-5.722	2.91E-06
1996 B - 1997 B	-13.818	5.45E-41	1996 S - 2000 B	-22.033	3.86E-105	1999 B - 2019 S	8.596	2.29E-15
1996 L - 1997 B	-28.488	4.56E-176	1997 B - 2000 B	1.382	1.00E+00	1999 L - 2019 S	-6.033	4.43E-07
1996 S - 1997 B	-26.201	7.07E-149	1997 L - 2000 B	-18.782	2.94E-76	1999 S - 2019 S	-5.910	9.46E-07
1995 B - 1997 L	12.867	1.91E-35	1997 S - 2000 B	-17.730	6.83E-68	2000 B - 2019 S	6.727	4.79E-09
1995 L - 1997 L	2.302	1.00E+00	1998 B - 2000 B	2.170	1.00E+00	2000 L - 2019 S	-6.109	2.77E-07
1995 S - 1997 L	2.376	1.00E+00	1998 L - 2000 B	-20.797	1.28E-93	2000 S - 2019 S	-4.761	5.32E-04
1996 B - 1997 L	10.204	5.24E-22	1998 S - 2000 B	-18.766	3.96E-76	2019 B - 2019 S	-1.029	1.00E+00
1996 L - 1997 L	-2.690	1.00E+00	1999 B - 2000 B	3.114	5.09E-01	2019 L - 2019 S	-1.761	1.00E+00
1996 S - 1997 L	-0.241	1.00E+00	1999 L - 2000 B	-16.172	2.20E-56	1995 B - 2021 B	2.156	1.00E+00
1997 B - 1997 L	21.647	1.78E-101	1999 S - 2000 B	-14.977	2.84E-48	1995 L - 2021 B	-7.206	1.59E-10
1995 B - 1997 S	11.753	1.89E-29	1995 B - 2000 L	11.672	4.91E-29	1995 S - 2021 B	-7.777	2.05E-12
1995 L - 1997 S	1.101	1.00E+00	1995 L - 2000 L	3.811	3.82E-02	1996 B - 2021 B	-1.690	1.00E+00
1995 S - 1997 S	1.088	1.00E+00	1995 S - 2000 L	3.897	2.69E-02	1996 L - 2021 B	-13.503	4.17E-39
1996 B - 1997 S	8.911	1.39E-16	1996 B - 2000 L	9.405	1.44E-18	1996 S - 2021 B	-11.367	1.69E-27
1996 L - 1997 S	-4.216	6.86E-03	1996 L - 2000 L	0.329	1.00E+00	1997 B - 2021 B	8.862	2.17E-16
1996 S - 1997 S	-1.744	1.00E+00	1996 S - 2000 L	2.092	1.00E+00	1997 L - 2021 B	-9.962	6.17E-21
1997 B - 1997 S	20.604	7.02E-92	1997 B - 2000 L	17.268	2.27E-64	1997 S - 2021 B	-8.859	2.22E-16
1997 L - 1997 S	-1.317	1.00E+00	1997 L - 2000 L	2.119	1.00E+00	1998 B - 2021 B	9.285	4.48E-18
1995 B - 1998 B	-7.492	1.88E-11	1997 S - 2000 L	3.115	5.08E-01	1998 L - 2021 B	-11.442	7.11E-28
1995 L - 1998 B	-17.430	1.34E-65	1998 B - 2000 L	17.481	5.50E-66	1998 S - 2021 B	-10.410	6.14E-23
1995 S - 1998 B	-19.145	2.93E-79	1998 L - 2000 L	1.205	1.00E+00	1999 B - 2021 B	9.990	4.65E-21
1996 B - 1998 B	-13.960	7.57E-42	1998 S - 2000 L	1.380	1.00E+00	1999 L - 2021 B	-9.751	5.03E-20
1996 L - 1998 B	-27.901	7.12E-169	1999 B - 2000 L	17.966	9.87E-70	1999 S - 2021 B	-9.213	8.77E-18
1996 S - 1998 B	-25.683	4.94E-143	1999 L - 2000 L	0.247	1.00E+00	2000 B - 2021 B	7.146	2.46E-10
1997 B - 1998 B	-0.957	1.00E+00	1999 S - 2000 L	0.045	1.00E+00	2000 L - 2021 B	-9.650	1.36E-19
1997 L - 1998 B	-21.576	8.35E-101	2000 B - 2000 L	15.745	2.05E-53	2000 S - 2021 B	-7.721	3.19E-12
1997 S - 1998 B	-20.554	1.97E-91	1995 B - 2000 S	9.542	3.88E-19	2019 B - 2021 B	-4.378	3.31E-03
1995 B - 1998 L	14.552	1.57E-45	1995 L - 2000 S	2.223	1.00E+00	2019 L - 2021 B	-3.817	3.73E-02

1995 L - 1998 L	3.564	1.01E-01	1995 S - 2000 S	2.238	1.00E+00	2019 S - 2021 B	-1.770	1.00E+00
1995 S - 1998 L	3.741	5.05E-02	1996 B - 2000 S	7.258	1.08E-10	1995 B - 2021 L	11.003	1.02E-25
1996 B - 1998 L	12.083	3.58E-31	1996 L - 2000 S	-1.186	1.00E+00	1995 L - 2021 L	1.040	1.00E+00
1996 L - 1998 L	-1.349	1.00E+00	1996 S - 2000 S	0.449	1.00E+00	1995 S - 2021 L	1.019	1.00E+00
1996 S - 1998 L	1.215	1.00E+00	1997 B - 2000 S	14.564	1.31E-45	1996 B - 2021 L	8.196	6.84E-14
1997 B - 1998 L	24.024	4.28E-125	1997 L - 2000 S	0.573	1.00E+00	1996 L - 2021 L	-3.900	2.65E-02
1997 L - 1998 L	1.284	1.00E+00	1997 S - 2000 S	1.496	1.00E+00	1996 S - 2021 L	-1.609	1.00E+00
1997 S - 1998 L	2.663	1.00E+00	1998 B - 2000 S	14.830	2.60E-47	1997 B - 2021 L	18.893	3.59E-77
1998 B - 1998 L	23.817	6.09E-123	1998 L - 2000 S	-0.309	1.00E+00	1997 L - 2021 L	-1.236	1.00E+00
1995 B - 1998 S	13.179	3.20E-37	1998 S - 2000 S	-0.086	1.00E+00	1997 S - 2021 L	-0.001	1.00E+00
1995 L - 1998 S	3.059	6.12E-01	1999 B - 2000 S	15.314	1.71E-50	1998 B - 2021 L	18.968	8.65E-78
1995 S - 1998 S	3.173	4.16E-01	1999 L - 2000 S	-1.001	1.00E+00	1998 L - 2021 L	-2.490	1.00E+00
1996 B - 1998 S	10.626	6.25E-24	1999 S - 2000 S	-1.129	1.00E+00	1998 S - 2021 L	-2.046	1.00E+00
1996 L - 1998 S	-1.554	1.00E+00	2000 B - 2000 S	13.277	8.74E-38	1999 B - 2021 L	19.520	2.06E-82
1996 S - 1998 S	0.778	1.00E+00	2000 L - 2000 S	-1.205	1.00E+00	1999 L - 2021 L	-2.835	1.00E+00
1997 B - 1998 S	21.370	6.95E-99	1995 B - 2019 B	7.269	1.00E-10	1999 S - 2021 L	-2.834	1.00E+00
1997 L - 1998 S	0.899	1.00E+00	1995 L - 2019 B	-3.974	1.95E-02	2000 B - 2021 L	16.467	1.74E-58
1997 S - 1998 S	2.168	1.00E+00	1995 S - 2019 B	-4.440	2.48E-03	2000 L - 2021 L	-3.005	7.32E-01
1998 B - 1998 S	21.359	8.83E-99	1996 B - 2019 B	3.468	1.45E-01	2000 S - 2021 L	-1.449	1.00E+00
1998 L - 1998 S	-0.301	1.00E+00	1996 L - 2019 B	-11.137	2.29E-26	2019 B - 2021 L	5.259	3.99E-05
1995 B - 1999 B	-8.273	3.59E-14	1996 S - 2019 B	-8.518	4.48E-15	2019 L - 2021 L	1.963	1.00E+00
1995 L - 1999 B	-18.001	5.27E-70	1997 B - 2019 B	16.765	1.21E-60	2019 S - 2021 L	4.246	6.00E-03
1995 S - 1999 B	-19.710	4.92E-84	1997 L - 2019 B	-7.021	6.10E-10	2021 B - 2021 L	8.357	1.77E-14
1996 B - 1999 B	-14.682	2.31E-46	1997 S - 2019 B	-5.692	3.46E-06	1995 B - 2021 S	9.283	4.56E-18
1996 L - 1999 B	-28.284	1.48E-173	1998 B - 2019 B	16.778	9.82E-61	1995 L - 2021 S	0.529	1.00E+00
1996 S - 1999 B	-26.113	7.10E-148	1998 L - 2019 B	-8.716	7.92E-16	1995 S - 2021 S	0.477	1.00E+00
1997 B - 1999 B	-2.035	1.00E+00	1998 S - 2019 B	-7.624	6.78E-12	1996 B - 2021 S	6.579	1.31E-08
1997 L - 1999 B	-22.095	9.77E-106	1999 B - 2019 B	17.420	1.61E-65	1996 L - 2021 S	-3.831	3.53E-02
1997 S - 1999 B	-21.094	2.49E-96	1999 L - 2019 B	-7.255	1.11E-10	1996 S - 2021 S	-1.846	1.00E+00
1998 B - 1999 B	-1.048	1.00E+00	1999 S - 2019 B	-6.828	2.37E-09	1997 B - 2021 S	15.693	4.69E-53
1998 L - 1999 B	-24.298	5.69E-128	2000 B - 2019 B	13.699	2.84E-40	1997 L - 2021 S	-1.515	1.00E+00
1998 S - 1999 B	-21.873	1.29E-103	2000 L - 2019 B	-7.222	1.41E-10	1997 S - 2021 S	-0.426	1.00E+00
1995 B - 1999 L	11.881	4.08E-30	2000 S - 2019 B	-5.254	4.11E-05	1998 B - 2021 S	15.919	1.29E-54
1995 L - 1999 L	3.674	6.60E-02	1995 B - 2019 L	5.363	2.25E-05	1998 L - 2021 S	-2.622	1.00E+00
1995 S - 1999 L	3.764	4.61E-02	1995 L - 2019 L	-1.226	1.00E+00	1998 S - 2021 S	-2.235	1.00E+00
1996 B - 1999 L	9.553	3.47E-19	1995 S - 2019 L	-1.324	1.00E+00	1999 B - 2021 S	16.468	1.71E-58
1996 L - 1999 L	0.025	1.00E+00	1996 B - 2019 L	3.045	6.42E-01	1999 L - 2021 S	-2.966	8.34E-01
1996 S - 1999 L	1.873	1.00E+00	1996 L - 2019 L	-4.588	1.23E-03	1999 S - 2021 S	-2.970	8.22E-01
1997 B - 1999 L	17.827	1.19E-68	1996 S - 2019 L	-3.123	4.94E-01	2000 B - 2021 S	13.910	1.53E-41
1997 L - 1999 L	1.909	1.00E+00	1997 B - 2019 L	9.644	1.43E-19	2000 L - 2021 S	-3.127	4.88E-01
1997 S - 1999 L	2.948	8.83E-01	1997 L - 2019 L	-2.839	1.00E+00	2000 S - 2021 S	-1.676	1.00E+00
1998 B - 1999 L	18.022	3.61E-70	1997 S - 2019 L	-2.017	1.00E+00	2019 B - 2021 S	4.095	1.17E-02
1998 L - 1999 L	0.953	1.00E+00	1998 B - 2019 L	9.975	5.44E-21	2019 L - 2021 S	1.556	1.00E+00
1998 S - 1999 L	1.143	1.00E+00	1998 L - 2019 L	-3.688	6.25E-02	2019 S - 2021 S	3.684	6.34E-02
1999 B - 1999 L	18.517	4.13E-74	1998 S - 2019 L	-3.380	2.00E-01	2021 B - 2021 S	7.057	4.69E-10
1995 B - 1999 S	11.120	2.77E-26	1999 B - 2019 L	10.457	3.77E-23	2021 L - 2021 S	-0.407	1.00E+00

Table S2: Variance to Mean Ratio (VMR > 1 indicates an aggregated population, VMR < 1 indicates an evenly dispersed population, VMR ~ 1 indicate a randomly distributed population) and results of t-test (If t_{obv} > t_{crit} at 0.05 level, then the distribution significantly different from a random distribution).

Year	VMR	Observed t-value	Critical t-value
1995	1.465252	14.53866	1.961179
1996	1.521572	22.97583	1.960575
1997	1.525058	19.38807	1.960834
1998	1.543027	18.60611	1.960975
1999	1.297589	8.160677	1.961543
2000	1.315361	8.153764	1.96174
2019	0.963285	-0.97382	1.961651
2021	0.992158	-0.20851	1.961643

Table S3: Z-score and p-values of multiple pairwise comparison of lobster shelter use (0=No Shelter, 1=Rocky, 2=Sediment, 3=Algae) by year using Dunn's test with Bonferroni correction ($p < 0.05$ sig. level)

Comparisons	Z	P	Comparisons	Z	P	Comparisons	Z	P
1996 0 - 1996 1	-5.078	6.70E-05	1999 1 - 2000 0	6.079	2.13E-07	1996 3 - 2019 3	-1.929	1.00E+00
1996 0 - 1996 2	0.151	1.00E+00	1999 2 - 2000 0	-1.118	1.00E+00	1997 0 - 2019 3	-3.351	1.41E-01
1996 1 - 1996 2	4.010	1.06E-02	1999 3 - 2000 0	0.531	1.00E+00	1997 1 - 2019 3	3.242	2.08E-01
1996 0 - 1996 3	-0.652	1.00E+00	1996 0 - 2000 1	-5.504	6.50E-06	1997 3 - 2019 3	-1.523	1.00E+00
1996 1 - 1996 3	4.369	2.19E-03	1996 1 - 2000 1	-0.124	1.00E+00	1998 0 - 2019 3	-2.994	4.84E-01
1996 2 - 1996 3	-0.663	1.00E+00	1996 2 - 2000 1	-4.230	4.10E-03	1998 1 - 2019 3	2.569	1.00E+00
1996 0 - 1997 0	0.448	1.00E+00	1996 3 - 2000 1	-4.751	3.55E-04	1998 2 - 2019 3	-2.830	8.17E-01
1996 1 - 1997 0	5.994	3.59E-07	1997 0 - 2000 1	-6.560	9.43E-09	1998 3 - 2019 3	-1.018	1.00E+00
1996 2 - 1997 0	0.185	1.00E+00	1997 1 - 2000 1	0.069	1.00E+00	1999 0 - 2019 3	-3.076	3.68E-01
1996 3 - 1997 0	1.146	1.00E+00	1997 3 - 2000 1	-4.806	2.70E-04	1999 1 - 2019 3	3.214	2.30E-01
1996 0 - 1997 1	-5.771	1.39E-06	1998 0 - 2000 1	-6.401	2.72E-08	1999 2 - 2019 3	-2.658	1.00E+00
1996 1 - 1997 1	-0.193	1.00E+00	1998 1 - 2000 1	-0.612	1.00E+00	1999 3 - 2019 3	-1.877	1.00E+00
1996 2 - 1997 1	-4.356	2.32E-03	1998 2 - 2000 1	-4.923	1.50E-04	2000 0 - 2019 3	-2.515	1.00E+00
1996 3 - 1997 1	-4.989	1.07E-04	1998 3 - 2000 1	-4.317	2.78E-03	2000 1 - 2019 3	3.031	4.28E-01
1997 0 - 1997 1	-6.927	7.57E-10	1999 0 - 2000 1	-6.769	2.28E-09	2000 2 - 2019 3	-2.558	1.00E+00
1996 0 - 1997 3	-1.345	1.00E+00	1999 1 - 2000 1	0.012	1.00E+00	2000 3 - 2019 3	-1.663	1.00E+00
1996 1 - 1997 3	4.315	2.81E-03	1999 2 - 2000 1	-4.499	1.20E-03	2019 0 - 2019 3	-0.672	1.00E+00
1996 2 - 1997 3	-1.169	1.00E+00	1999 3 - 2000 1	-4.892	1.75E-04	2019 1 - 2019 3	1.240	1.00E+00
1996 3 - 1997 3	-0.615	1.00E+00	2000 0 - 2000 1	-5.741	1.65E-06	2019 2 - 2019 3	-2.061	1.00E+00
1997 0 - 1997 3	-1.974	1.00E+00	1996 0 - 2000 2	0.741	1.00E+00	1996 0 - 2021 0	-2.096	1.00E+00
1997 1 - 1997 3	5.128	5.14E-05	1996 1 - 2000 2	4.209	4.50E-03	1996 1 - 2021 0	3.558	6.55E-02
1996 0 - 1998 0	-0.023	1.00E+00	1996 2 - 2000 2	0.528	1.00E+00	1996 2 - 2021 0	-1.725	1.00E+00
1996 1 - 1998 0	5.786	1.27E-06	1996 3 - 2000 2	1.203	1.00E+00	1996 3 - 2021 0	-1.358	1.00E+00
1996 2 - 1998 0	-0.179	1.00E+00	1997 0 - 2000 2	0.459	1.00E+00	1997 0 - 2021 0	-2.804	8.85E-01
1996 3 - 1998 0	0.707	1.00E+00	1997 1 - 2000 2	4.501	1.19E-03	1997 1 - 2021 0	4.287	3.18E-03
1997 0 - 1998 0	-0.535	1.00E+00	1997 3 - 2000 2	1.678	1.00E+00	1997 3 - 2021 0	-0.852	1.00E+00
1997 1 - 1998 0	6.808	1.74E-09	1998 0 - 2000 2	0.796	1.00E+00	1998 0 - 2021 0	-2.403	1.00E+00
1997 3 - 1998 0	1.527	1.00E+00	1998 1 - 2000 2	4.123	6.56E-03	1998 1 - 2021 0	3.548	6.81E-02
1996 0 - 1998 1	-5.147	4.64E-05	1998 2 - 2000 2	0.026	1.00E+00	1998 2 - 2021 0	-2.410	1.00E+00
1996 1 - 1998 1	0.429	1.00E+00	1998 3 - 2000 2	2.000	1.00E+00	1998 3 - 2021 0	-0.309	1.00E+00
1996 2 - 1998 1	-3.926	1.52E-02	1999 0 - 2000 2	0.876	1.00E+00	1999 0 - 2021 0	-2.460	1.00E+00
1996 3 - 1998 1	-4.375	2.13E-03	1999 1 - 2000 2	4.483	1.29E-03	1999 1 - 2021 0	4.268	3.46E-03
1997 0 - 1998 1	-6.213	9.12E-08	1999 2 - 2000 2	-0.079	1.00E+00	1999 2 - 2021 0	-2.276	1.00E+00
1997 1 - 1998 1	0.723	1.00E+00	1999 3 - 2000 2	1.334	1.00E+00	1999 3 - 2021 0	-1.272	1.00E+00
1997 3 - 1998 1	-4.389	2.00E-03	2000 0 - 2000 2	1.017	1.00E+00	2000 0 - 2021 0	-1.917	1.00E+00
1998 0 - 1998 1	-6.038	2.74E-07	2000 1 - 2000 2	4.396	1.94E-03	2000 1 - 2021 0	3.999	1.12E-02
1996 0 - 1998 2	0.789	1.00E+00	1996 0 - 2000 3	-0.897	1.00E+00	2000 2 - 2021 0	-2.173	1.00E+00
1996 1 - 1998 2	4.680	5.03E-04	1996 1 - 2000 3	4.103	7.16E-03	2000 3 - 2021 0	-1.081	1.00E+00
1996 2 - 1998 2	0.542	1.00E+00	1996 2 - 2000 3	-0.855	1.00E+00	2019 0 - 2021 0	0.056	1.00E+00
1996 3 - 1998 2	1.301	1.00E+00	1996 3 - 2000 3	-0.245	1.00E+00	2019 1 - 2021 0	2.101	1.00E+00
1997 0 - 1998 2	0.479	1.00E+00	1997 0 - 2000 3	-1.407	1.00E+00	2019 2 - 2021 0	-1.623	1.00E+00
1997 1 - 1998 2	5.063	7.24E-05	1997 1 - 2000 3	4.695	4.67E-04	2019 3 - 2021 0	0.725	1.00E+00
1997 3 - 1998 2	1.850	1.00E+00	1997 3 - 2000 3	0.342	1.00E+00	1996 0 - 2021 1	-3.636	4.87E-02
1998 0 - 1998 2	0.859	1.00E+00	1998 0 - 2000 3	-0.980	1.00E+00	1996 1 - 2021 1	1.972	1.00E+00
1998 1 - 1998 2	4.628	6.49E-04	1998 1 - 2000 3	4.086	7.71E-03	1996 2 - 2021 1	-2.850	7.68E-01
1996 0 - 1998 3	-1.833	1.00E+00	1998 2 - 2000 3	-1.492	1.00E+00	1996 3 - 2021 1	-2.882	6.93E-01
1996 1 - 1998 3	3.851	2.06E-02	1998 3 - 2000 3	0.819	1.00E+00	1997 0 - 2021 1	-4.513	1.12E-03
1996 2 - 1998 3	-1.529	1.00E+00	1999 0 - 2000 3	-0.934	1.00E+00	1997 1 - 2021 1	2.493	1.00E+00
1996 3 - 1998 3	-1.095	1.00E+00	1999 1 - 2000 3	4.677	5.11E-04	1997 3 - 2021 1	-2.624	1.00E+00

1997 0 - 1998 3	-2.518	1.00E+00	1999 2 - 2000 3	-1.472	1.00E+00	1998 0 - 2021 1	-4.218	4.32E-03
1997 1 - 1998 3	4.623	6.64E-04	1999 3 - 2000 3	-0.106	1.00E+00	1998 1 - 2021 1	1.763	1.00E+00
1997 3 - 1998 3	-0.548	1.00E+00	2000 0 - 2000 3	-0.612	1.00E+00	1998 2 - 2021 1	-3.543	6.95E-02
1998 0 - 1998 3	-2.099	1.00E+00	2000 1 - 2000 3	4.469	1.38E-03	1998 3 - 2021 1	-2.096	1.00E+00
1998 1 - 1998 3	3.877	1.85E-02	2000 2 - 2000 3	-1.375	1.00E+00	1999 0 - 2021 1	-4.420	1.73E-03
1998 2 - 1998 3	-2.215	1.00E+00	1996 0 - 2019 0	-2.143	1.00E+00	1999 1 - 2021 1	2.459	1.00E+00
1996 0 - 1999 0	-0.120	1.00E+00	1996 1 - 2019 0	3.505	8.00E-02	1999 2 - 2021 1	-3.276	1.85E-01
1996 1 - 1999 0	6.046	2.61E-07	1996 2 - 2019 0	-1.760	1.00E+00	1999 3 - 2021 1	-2.898	6.58E-01
1996 2 - 1999 0	-0.254	1.00E+00	1996 3 - 2019 0	-1.405	1.00E+00	2000 0 - 2021 1	-3.645	4.69E-02
1996 3 - 1999 0	0.646	1.00E+00	1997 0 - 2019 0	-2.856	7.53E-01	2000 1 - 2021 1	2.289	1.00E+00
1997 0 - 1999 0	-0.673	1.00E+00	1997 1 - 2019 0	4.226	4.17E-03	2000 2 - 2021 1	-3.173	2.65E-01
1997 1 - 1999 0	7.264	6.61E-11	1997 3 - 2019 0	-0.907	1.00E+00	2000 3 - 2021 1	-2.600	1.00E+00
1997 3 - 1999 0	1.519	1.00E+00	1998 0 - 2019 0	-2.458	1.00E+00	2019 0 - 2021 1	-1.721	1.00E+00
1998 0 - 1999 0	-0.113	1.00E+00	1998 1 - 2019 0	3.488	8.53E-02	2019 1 - 2021 1	0.333	1.00E+00
1998 1 - 1999 0	6.409	2.56E-08	1998 2 - 2019 0	-2.445	1.00E+00	2019 2 - 2021 1	-2.747	1.00E+00
1998 2 - 1999 0	-0.953	1.00E+00	1998 3 - 2019 0	-0.365	1.00E+00	2019 3 - 2021 1	-0.935	1.00E+00
1998 3 - 1999 0	2.134	1.00E+00	1999 0 - 2019 0	-2.519	1.00E+00	2021 0 - 2021 1	-1.778	1.00E+00
1996 0 - 1999 1	-5.759	1.49E-06	1999 1 - 2019 0	4.207	4.54E-03	1996 0 - 2021 2	0.114	1.00E+00
1996 1 - 1999 1	-0.142	1.00E+00	1999 2 - 2019 0	-2.307	1.00E+00	1996 1 - 2021 2	4.583	8.03E-04
1996 2 - 1999 1	-4.336	2.54E-03	1999 3 - 2019 0	-1.323	1.00E+00	1996 2 - 2021 2	-0.048	1.00E+00
1996 3 - 1999 1	-4.972	1.16E-04	2000 0 - 2019 0	-1.970	1.00E+00	1996 3 - 2021 2	0.698	1.00E+00
1997 0 - 1999 1	-6.925	7.63E-10	2000 1 - 2019 0	3.941	1.42E-02	1997 0 - 2021 2	-0.275	1.00E+00
1997 1 - 1999 1	0.062	1.00E+00	2000 2 - 2019 0	-2.205	1.00E+00	1997 1 - 2021 2	5.081	6.60E-05
1997 3 - 1999 1	-5.116	5.48E-05	2000 3 - 2019 0	-1.129	1.00E+00	1997 3 - 2021 2	1.298	1.00E+00
1998 0 - 1999 1	-6.809	1.72E-09	1996 0 - 2019 1	-3.907	1.64E-02	1998 0 - 2021 2	0.144	1.00E+00
1998 1 - 1999 1	-0.670	1.00E+00	1996 1 - 2019 1	1.667	1.00E+00	1998 1 - 2021 2	4.560	8.99E-04
1998 2 - 1999 1	-5.045	7.94E-05	1996 2 - 2019 1	-3.050	4.01E-01	1998 2 - 2021 2	-0.641	1.00E+00
1998 3 - 1999 1	-4.607	7.17E-04	1996 3 - 2019 1	-3.154	2.83E-01	1998 3 - 2021 2	1.721	1.00E+00
1999 0 - 1999 1	-7.275	6.06E-11	1997 0 - 2019 1	-4.811	2.64E-04	1999 0 - 2021 2	0.233	1.00E+00
1996 0 - 1999 2	0.838	1.00E+00	1997 1 - 2019 1	2.141	1.00E+00	1999 1 - 2021 2	5.063	7.24E-05
1996 1 - 1999 2	4.310	2.87E-03	1997 3 - 2019 1	-2.941	5.74E-01	1999 2 - 2021 2	-0.705	1.00E+00
1996 2 - 1999 2	0.612	1.00E+00	1998 0 - 2019 1	-4.535	1.01E-03	1999 3 - 2021 2	0.857	1.00E+00
1996 3 - 1999 2	1.299	1.00E+00	1998 1 - 2019 1	1.418	1.00E+00	2000 0 - 2021 2	0.441	1.00E+00
1997 0 - 1999 2	0.559	1.00E+00	1998 2 - 2019 1	-3.743	3.19E-02	2000 1 - 2021 2	4.895	1.73E-04
1997 1 - 1999 2	4.606	7.21E-04	1998 3 - 2019 1	-2.419	1.00E+00	2000 2 - 2021 2	-0.614	1.00E+00
1997 3 - 1999 2	1.779	1.00E+00	1999 0 - 2019 1	-4.762	3.37E-04	2000 3 - 2021 2	0.916	1.00E+00
1998 0 - 1999 2	0.898	1.00E+00	1999 1 - 2019 1	2.103	1.00E+00	2019 0 - 2021 2	1.991	1.00E+00
1998 1 - 1999 2	4.227	4.15E-03	1999 2 - 2019 1	-3.453	9.72E-02	2019 1 - 2021 2	3.511	7.82E-02
1998 2 - 1999 2	0.111	1.00E+00	1999 3 - 2019 1	-3.188	2.51E-01	2019 2 - 2021 2	0.040	1.00E+00
1998 3 - 1999 2	2.102	1.00E+00	2000 0 - 2019 1	-3.950	1.37E-02	2019 3 - 2021 2	2.440	1.00E+00
1999 0 - 1999 2	0.980	1.00E+00	2000 1 - 2019 1	1.956	1.00E+00	2021 0 - 2021 2	1.950	1.00E+00
1999 1 - 1999 2	4.588	7.87E-04	2000 2 - 2019 1	-3.350	1.42E-01	2021 1 - 2021 2	3.276	1.85E-01
1996 0 - 1999 3	-0.834	1.00E+00	2000 3 - 2019 1	-2.872	7.17E-01	1996 0 - 2021 3	-2.447	1.00E+00
1996 1 - 1999 3	4.460	1.44E-03	2019 0 - 2019 1	-2.043	1.00E+00	1996 1 - 2021 3	3.238	2.11E-01
1996 2 - 1999 3	-0.798	1.00E+00	1996 0 - 2019 2	0.057	1.00E+00	1996 2 - 2021 3	-1.979	1.00E+00
1996 3 - 1999 3	-0.150	1.00E+00	1996 1 - 2019 2	3.911	1.61E-02	1996 3 - 2021 3	-1.702	1.00E+00
1997 0 - 1999 3	-1.372	1.00E+00	1996 2 - 2019 2	-0.080	1.00E+00	1997 0 - 2021 3	-3.200	2.41E-01
1997 1 - 1999 3	5.166	4.19E-05	1996 3 - 2019 2	0.569	1.00E+00	1997 1 - 2021 3	3.939	1.43E-02
1997 3 - 1999 3	0.484	1.00E+00	1997 0 - 2019 2	-0.283	1.00E+00	1997 3 - 2021 3	-1.247	1.00E+00
1998 0 - 1999 3	-0.921	1.00E+00	1997 1 - 2019 2	4.251	3.73E-03	1998 0 - 2021 3	-2.821	8.40E-01
1998 1 - 1999 3	4.502	1.18E-03	1997 3 - 2019 2	1.068	1.00E+00	1998 1 - 2021 3	3.193	2.47E-01
1998 2 - 1999 3	-1.454	1.00E+00	1998 0 - 2019 2	0.078	1.00E+00	1998 2 - 2021 3	-2.668	1.00E+00
1998 3 - 1999 3	0.993	1.00E+00	1998 1 - 2019 2	3.822	2.33E-02	1998 3 - 2021 3	-0.703	1.00E+00

1999 0 - 1999 3	-0.871	1.00E+00	1998 2 - 2019 2	-0.622	1.00E+00	1999 0 - 2021 3	-2.913	6.29E-01
1999 1 - 1999 3	5.152	4.53E-05	1998 3 - 2019 2	1.428	1.00E+00	1999 1 - 2021 3	3.918	1.57E-02
1999 2 - 1999 3	-1.433	1.00E+00	1999 0 - 2019 2	0.150	1.00E+00	1999 2 - 2021 3	-2.503	1.00E+00
1996 0 - 2000 0	-0.363	1.00E+00	1999 1 - 2019 2	4.231	4.08E-03	1999 3 - 2021 3	-1.638	1.00E+00
1996 1 - 2000 0	5.212	3.27E-05	1999 2 - 2019 2	-0.686	1.00E+00	2000 0 - 2021 3	-2.311	1.00E+00
1996 2 - 2000 0	-0.435	1.00E+00	1999 3 - 2019 2	0.701	1.00E+00	2000 1 - 2021 3	3.661	4.40E-02
1996 3 - 2000 0	0.346	1.00E+00	2000 0 - 2019 2	0.335	1.00E+00	2000 2 - 2021 3	-2.400	1.00E+00
1997 0 - 2000 0	-0.887	1.00E+00	2000 1 - 2019 2	4.127	6.45E-03	2000 3 - 2021 3	-1.422	1.00E+00
1997 1 - 2000 0	6.085	2.05E-07	2000 2 - 2019 2	-0.602	1.00E+00	2019 0 - 2021 3	-0.333	1.00E+00
1997 3 - 2000 0	1.081	1.00E+00	2000 3 - 2019 2	0.760	1.00E+00	2019 1 - 2021 3	1.733	1.00E+00
1998 0 - 2000 0	-0.390	1.00E+00	2019 0 - 2019 2	1.659	1.00E+00	2019 2 - 2021 3	-1.877	1.00E+00
1998 1 - 2000 0	5.364	1.42E-05	2019 1 - 2019 2	2.948	5.62E-01	2019 3 - 2021 3	0.367	1.00E+00
1998 2 - 2000 0	-1.104	1.00E+00	1996 0 - 2019 3	-2.638	1.00E+00	2021 0 - 2021 3	-0.389	1.00E+00
1998 3 - 2000 0	1.624	1.00E+00	1996 1 - 2019 3	2.697	1.00E+00	2021 1 - 2021 3	1.405	1.00E+00
1999 0 - 2000 0	-0.307	1.00E+00	1996 2 - 2019 3	-2.160	1.00E+00	2021 2 - 2021 3	-2.251	1.00E+00

Table S4: P-values of multiple pairwise comparison of lobster size frequency distributions across years using Kolmogorov-Smirnov test ($p < 0.05$ sig. level).

Comparison	Statistic	P-value
1996 - 1997	0.111	0.111
1996 - 1998	0.093	0.001
1996 - 1999	0.112	0.000
1996 - 2000	0.085	0.010
1996 - 2019	0.315	0.000
1996 - 2021	0.218	0.000
1997 - 1998	0.051	0.081
1997 - 1999	0.034	0.541
1997 - 2000	0.088	0.001
1997 - 2019	0.422	0.000
1997 - 2021	0.322	0.000
1998 - 1999	0.043	0.330
1998 - 2000	0.046	0.328
1998 - 2019	0.392	0.000
1998 - 2021	0.298	0.000
1999 - 2000	0.068	0.043
1999 - 2019	0.421	0.000
1999 - 2021	0.325	0.000
2000 - 2019	0.382	0.000
2000 - 2021	0.275	0.000
2019 - 2021	0.187	0.000

Table S5: Results from multiple pairwise comparison of lobster claw number across time period and substrate type (B=Boulder, L=Ledge, S= Sediment) using Dunn's test with Bonferroni correction ($p < 0.05$ sig. level)).

Comparison	Z	P.unadj	P.adj
1995to2000 B - 1995to2000 L	1.194	0.232	1.000
1995to2000 B - 1995to2000 S	6.298	0.000	0.000
1995to2000 L - 1995to2000 S	3.191	0.001	0.021
1995to2000 B - 2019to2021 B	-1.186	0.236	1.000
1995to2000 L - 2019to2021 B	-1.730	0.084	1.000
1995to2000 S - 2019to2021 B	-5.793	0.000	0.000
1995to2000 B - 2019to2021 L	-0.327	0.744	1.000
1995to2000 L - 2019to2021 L	-0.960	0.337	1.000
1995to2000 S - 2019to2021 L	-3.432	0.001	0.009
2019to2021 B - 2019to2021 L	0.237	0.813	1.000
1995to2000 B - 2019to2021 S	2.153	0.031	0.470
1995to2000 L - 2019to2021 S	1.125	0.261	1.000
1995to2000 S - 2019to2021 S	-1.233	0.217	1.000
2019to2021 B - 2019to2021 S	2.510	0.012	0.181
2019to2021 L - 2019to2021 S	1.775	0.076	1.000

Table S6: P-values of multiple pairwise comparison of lobster claw number across time period and shelter type (0=No Shelter, 1=Rocky, 2=Sediment, 3=Algae) using Dunn's test with Bonferroni correction ($p < 0.05$ sig. level).

Comparison	Z	P.unadj	P.adj
1995to2000 0 - 1995to2000 1	-4.645	0.000	0.000
1995to2000 0 - 1995to2000 2	6.186	0.000	0.000
1995to2000 1 - 1995to2000 2	9.070	0.000	0.000
1995to2000 0 - 1995to2000 3	-2.183	0.029	0.813
1995to2000 1 - 1995to2000 3	3.163	0.002	0.044
1995to2000 2 - 1995to2000 3	-7.733	0.000	0.000
1995to2000 0 - 2019to2021 0	-0.057	0.954	1.000
1995to2000 1 - 2019to2021 0	3.459	0.001	0.015
1995to2000 2 - 2019to2021 0	-5.818	0.000	0.000
1995to2000 3 - 2019to2021 0	1.685	0.092	1.000
1995to2000 0 - 2019to2021 1	-5.169	0.000	0.000
1995to2000 1 - 2019to2021 1	-2.190	0.029	0.799
1995to2000 2 - 2019to2021 1	-9.348	0.000	0.000
1995to2000 3 - 2019to2021 1	-3.921	0.000	0.002
2019to2021 0 - 2019to2021 1	-4.217	0.000	0.001
1995to2000 0 - 2019to2021 2	1.979	0.048	1.000
1995to2000 1 - 2019to2021 2	3.130	0.002	0.049
1995to2000 2 - 2019to2021 2	-1.143	0.253	1.000
1995to2000 3 - 2019to2021 2	2.598	0.009	0.262
2019to2021 0 - 2019to2021 2	1.962	0.050	1.000
2019to2021 1 - 2019to2021 2	3.518	0.000	0.012
1995to2000 0 - 2019to2021 3	-2.842	0.004	0.125
1995to2000 1 - 2019to2021 3	0.231	0.817	1.000
1995to2000 2 - 2019to2021 3	-7.758	0.000	0.000
1995to2000 3 - 2019to2021 3	-1.380	0.168	1.000
2019to2021 0 - 2019to2021 3	-2.430	0.015	0.423
2019to2021 1 - 2019to2021 3	1.494	0.135	1.000
2019to2021 2 - 2019to2021 3	-2.952	0.003	0.088