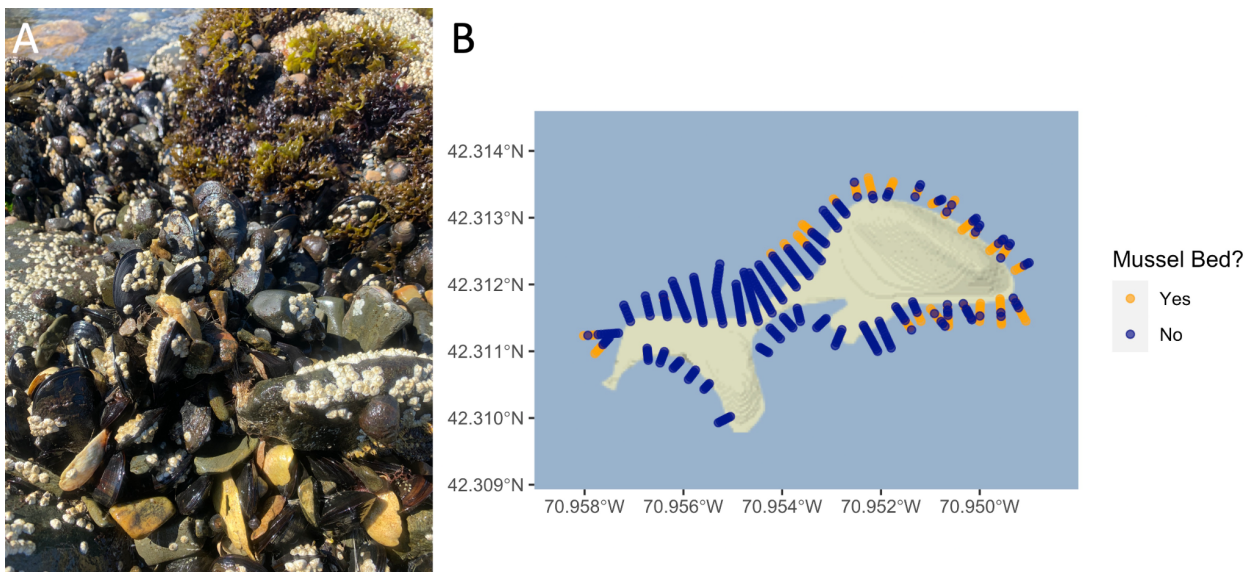




29 mitigation under changing climate conditions (e.g., sea level rise and increasing storm and wave  
30 intensity). The results of these larger scale *in situ* experiments are intended to provide transferable  
31 knowledge and serve as a model for Boston and other urban waterfronts throughout the world. Alongside  
32 whole-island surveys of substrates, the lab conducted detailed quadrat-based sampling of the intertidal  
33 and subtidal ROV surveys of mobile fauna on both Rainsford and three surrounding islands - Georges,  
34 Peddocks, and Gallops Island. These latter three were to serve as control sites in monitoring community  
35 change after large-scale installations of structures on the north and northeast shorelines of Rainsford  
36 Island. Together, these surveys showed that, despite region-wide declines in mussels, the rocky areas of  
37 these inner islands had large dense intertidal mussel beds.

38



39

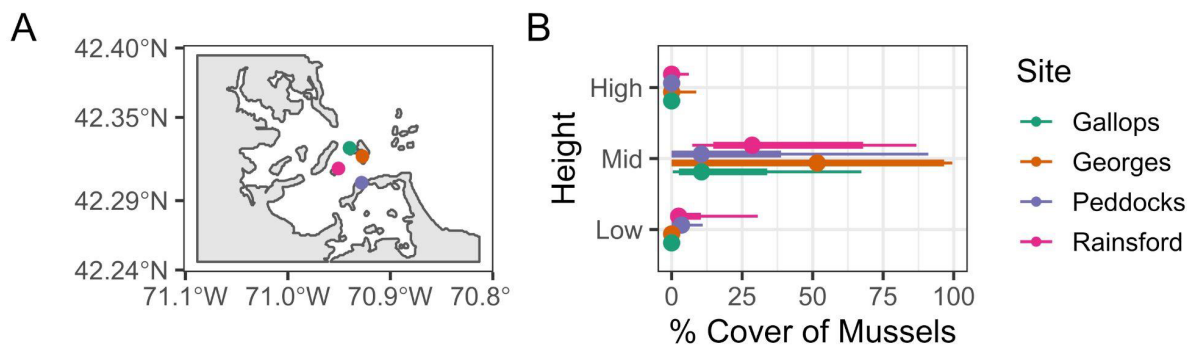
40

41 **Figure 1.** Mussel beds around Rainsford Island. A) A photograph taken along the edge of the northern  
42 bed in the mid-intertidal. B) Survey results from transects in the intertidal recording the presence of  
43 absence of mussel beds under survey points.

44

45 Briefly, to survey the extent of beds around Rainsford, in October of 2020, we walked 51 transects  
46 perpendicular to shore starting at the low tide mark, taking samples with a clam rake every 5m as far as

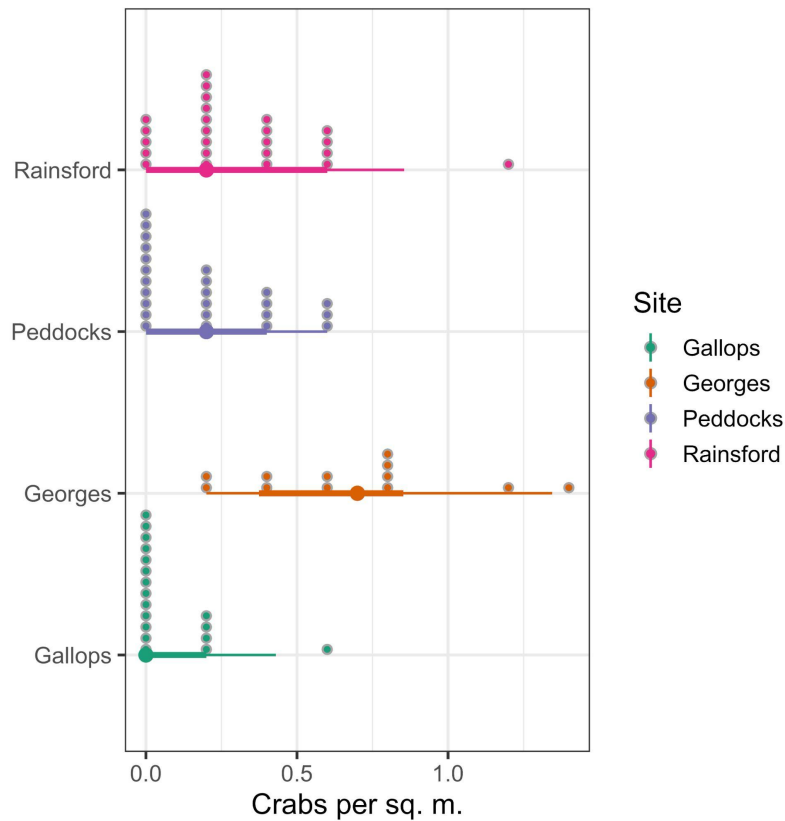
47 was safe in waders in order to determine substrate type and mussel presence. To determine mussel  
 48 density, we conducted intertidal surveys during spring tides in June 2021. We divided a 30m stretch of  
 49 intertidal on the northeast side of each island into high, mid, and low zones and recorded percent cover of  
 50 all sessile species in six 0.25m<sup>2</sup> quadrats per zone, with quadrats randomly placed within three 10m  
 51 horizontal blocks to ensure even sampling (i.e., each zone-block receiving 2 randomly placed quadrats).  
 52 To assess the abundance of predators that could move in with the tide, we conducted subtidal video  
 53 surveys using a Blue Robotics BlueROV2. The ROV ran along 120m of chain marked in 5m intervals  
 54 sunk at the 10m isobath offshore of intertidal sites. We recorded *Cancer* crab, green crab (*Carcinus*  
 55 *maenas*), sea star, lobster (*Homarus americanus*), fish, and moon snail abundance in each interval,  
 56 limiting field of view to 1m on either side of the transect, creating six 5x2m belt transects.



57  
 58 **Figure 2.** Map of the Boston Harbor islands highlighting A) sites surveyed and B) the percent cover of  
 59 mussels in each zone on each island. Points indicate medians with the thick and thin bars highlighting the  
 60 interval covering 66% and 95% of the data respectively

61  
 62 In our spatial survey, we found mussels around the entire east side of the island, wrapping from the north  
 63 shore, around the end of the island, and covering the south shore as well (Fig. 1). Further, we found more  
 64 beds on the rocky intertidal on the extreme east end. These were not areas of sparse mussels. Our quadrat  
 65 surveys on Rainsford found plots with a median cover of 30% and up to ~87% cover in the mid-intertidal

66 (Fig. 2). Other islands were similar. While not quantified, on the northern end of Lovells Island, just to  
 67 the east of surveyed islands but protected by the outer harbor islands, we walked the edge of a mussel bed  
 68 during low tide that covered roughly 30,000 m<sup>2</sup>. None of these sites were low in predator abundance (Fig.  
 69 3). Our subtidal surveys, which likely undercounted crabs given that we could not actively search  
 70 crevices, showed an average of between 0.2-0.7 crabs per m<sup>2</sup>. Curiously, in rocky intertidal surveys, the  
 71 abundance of the predatory dog whelk, *Nucella lapullis*, was low (8 found on all surveys). However, the  
 72 whelks we did find often measured 5-6cm in length - quite large relative to many populations studied  
 73 (Etter 1989). Initial site surveys outside of quadrats matched with our quadrat observations for these  
 74 important predators.



75  
 76 **Figure 3.** The abundance of crabs in the shallow subtidal from ROV data. Central points indicate medians  
 77 with the thick and thin bars highlighting the interval covering 66% and 95% of the data respectively.  
 78 Points above the bars are the raw data points themselves.

79

80 Given the decline of mussels throughout the Gulf of Maine, we were surprised to find such large  
81 seemingly healthy mussel beds. More surprising, these beds were all in areas relatively 1) sheltered from  
82 wave exposure and 2) had robust abundances of a major predator in the nearby subtidal - a predator that  
83 migrates in on high tide to consume mussels, although a diminished assemblage of intertidal whelk  
84 predators. Waves at these sites are reduced >70% in height relative to the outer harbor islands (calculated  
85 from the Massachusetts Coastal Flood Risk model from Bosma et al. 2015). The dominant paradigm in  
86 New England marine ecology is that these sites should be algal beds (Menge 1976, Lubchenco and  
87 Menge 1978, Bertness et al. 2002). While the high intertidal was often replete with *Fucus* and the lower  
88 often hosted a diverse mix of red algae, the presence of such large persistent mussel beds in these  
89 locations was surprising. How have these beds survived in the midst of massive decline? High flow rates  
90 are one potential answer. As any mariner will tell you, tidal currents between islands the inner Boston  
91 Harbor Islands are extremely strong. NOAA tides and currents show current speeds of up to 80-90 cm/s  
92 within certain constrictions within Boston Harbor during spring tides, while at the same time the nearby  
93 open coastline has velocities less than half in magnitude (“NOAA Tides and Currents” 2022).  
94 Additionally, highly detailed hydrodynamic modeling within Boston Harbor (Sustainable Solutions Lab,  
95 UMass-Boston, 2018), indicates current magnitudes on the order of 40-60 cm/s in the vicinity of  
96 Rainsford Island, compared to velocities at similar tidal cycles of 10-20 cm offshore of Boston Harbor.  
97 This would enhance both food and larval delivery (Palardy and Witman 2014), can be very beneficial for  
98 filter feeders such as mussels (Fréchette et al. 1989, Leichter and Witman 1997), and reduce efficacy of  
99 predators (Leonard et al. 1998). It does not, however, explain why these beds have persisted while those  
100 at the nearby monitored beds in Nahant have declined to 3-5% average cover (Sorte et al. 2016). Further,  
101 we were able to obtain intertidal photo quadrat data from the National Park Service’s Boston Harbor  
102 monitoring program (Long and Mitchell 2015) on the more wave exposed outer harbor islands - Calf,  
103 Green, and Outer Brewster. These areas fit the traditional profile of what should be a mussel dominated  
104 habitat given their exposure to open ocean swell. On these transects, beds rarely get above 5% cover, save  
105 for a brief pulse in 2016 with a maximum cover in one plot of 17%, far less than we observed. These

106 outer harbor island sites share a similar thermal and chemical environment to those we surveyed, at least  
107 allowing us to rule out those mechanisms, although they do possess higher wave exposure.

108

109 The ubiquity of the mussel beds we found throughout the harbor suggests some hope for the story of  
110 mussels in the Gulf of Maine. We need to better understand the role of hard substrate habitats in wave  
111 protected environments in high flow sites that sit in the middle of estuaries. While these are not the  
112 traditional sites ecologists have concentrated on, we suggest a greater need to understand their ecology for  
113 mussels. Further, the data of mussel bed locations often exists - albeit in the gray literature. Many states'  
114 marine resource management agencies have records of bed locations from environmental permitting (e.g.,  
115 permit reports from Woods Hole Group show beds in Nauset Estuary(Woods Hole Group 2021) that are,  
116 to our knowledge, unexamined by academic ecologists). These permitting reports represent an untapped  
117 font of knowledge to understand when and where mussel beds have been able to remain resilient in the  
118 face of whatever has caused their die-off throughout the Gulf. This understanding may well open up new  
119 vistas in both the fundamental understanding of intertidal ecology in the Gulf of Maine and ecological  
120 strategies to resist or adapt to global change.

121

## 122 **Acknowledgements**

123

124 All authors were supported by the Stone Foundation in this work. We thank Breckie McCollum, Liana  
125 Greenberg-Nielsen, Andrew Natter, and Hudson Filas for help collecting data in the field. We thank Russ  
126 Bowles for aid in accessing field sites. We thank Ron Etter for comments that greatly improved this  
127 manuscript. This is submission number 1 from the Stone Living Lab.

128

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