Sea urchin *Arbacia punctulata* feeding preference for algal turf over kelp in a degraded kelp forest ecosystem

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Abstract. Climate change is driving a shift in the distribution of global kelp forests, with the contraction of kelp habitats occurring at warm range edges. Declining kelps often have been replaced by novel algal turf assemblages, which are reinforced by ecological feedback mechanisms and provide fewer ecosystem services. Trophic interactions among marine herbivores, algal turfs, and kelps on algal turf-dominated reefs remain poorly resolved but could have important implications for the stability of algal turf reefs and the potential for kelp forest recovery. Here, we examine herbivory by the Atlantic purple sea urchin, *Arbacia punctulata*, in a degraded kelp forest ecosystem dominated by algal turf in southern New England, USA. In a localized field survey, we observed lower algal turf cover on reef areas containing *A. punctulata* (mean ± SE: 62 ± 12% turf cover) as compared to areas with no sea urchins present (92 ± 4% turf cover). Reef areas with and without sea urchins had similarly low cover of the previously dominant kelp, *Saccharina latissima* (6–8% kelp cover). In laboratory and field experiments, individuals or groups of *A. punctulata* enclosed with a diet choice of algal turf versus kelp had higher grazing rates on the algal turf. *A. punctulata* in the laboratory also exhibited greater attraction to algal turf over kelp, physically moving towards this food source. In combination, the results provide evidence that *A. punctulata* has a feeding preference for algal turf over kelp in southern New England. Future research is warranted to further examine the grazing ecology of *A. punctulata*, particularly in the context of ongoing kelp forest restoration efforts in this region.

Keywords: Regime shift, herbivory, Northwest Atlantic, *Saccharina latissima*, restoration

1. INTRODUCTION

Kelp forests are expansive marine ecosystems that provide critical ecosystem services to humans, including habitat for marine species, nutrient filtration, carbon absorption and storage, and coastal protection (Gundersen et al. 2021, Starko et al. 2021, Feehan et al. 2021, Eger et al. 2023). While kelp forests contain various ecological feedback mechanisms that reinforce their stability, the fast pace of anthropogenic global change has led to a loss of ecological resilience and the decline of kelp forests in many regions (Krumhansl et al. 2016, Wernberg et al. 2019). In particular, ocean warming and marine heatwaves have triggered regime shifts from kelp forests to algal turf-dominated reefs or sea urchin barrens in various locations worldwide (Ling et al. 2009, Rogers-Bennett et al. 2019, Filbee-Dexter et al. 2020, Smale et al. 2020, McPherson et al. 2021). These undesirable changes are driving rapid research effort to develop kelp forest restoration strategies that recover healthy kelp forests, and this necessitates a clearer understanding of the ecological functioning of degraded kelp forest ecosystems (Morris et al. 2020, Eger et al. 2022).

Ecosystem regime shifts from kelp forests to algal turf-dominated reefs yield a loss of ecosystem services, as algal turfs lack the 3-dimensional habitat complexity of kelp forest canopies and provide a globally homogenized habitat (Ware et al. 2019, Pessarrodona et al. 2021). Algal turf communities are dominated by species that tend to be short (<15 cm), filamentous, articulated, or corticated opportunistic algae (Connell et al. 2014, Pessarrodona et al. 2021). The turf algae grow densely in low-lying mats that carpet the benthos, monopolizing the hard substratum (Moy and Christie 2012). Algal turfs are generally tolerant to climatic extremes, providing a competitive edge over cold-adapted kelps under warming conditions (Airoldi 1998). Moreover, where algal turfs are established, ecological feedback mechanisms prevent natural recovery of the kelp forest (Connell and Russell 2010). For example, kelps that recruit onto the algal turf exhibit slower growth rates and are more easily dislodged than on rocky substrate, resulting in lower fitness (Burek et al. 2018, Feehan et al. 2019). Moreover, turf assemblages trap more sediments than kelp forests, which can smother kelp recruits (Gorman and Connell 2009, Pessarrodona et al. 2021). Micrograzers such as gastropods, harbored within the algal turf habitat, also may exert grazing pressure on microscopic kelp gametophytes, limiting kelp recruitment (Veenhof et al. 2022).

Grazing by marine herbivores can be a primary determinant of marine seaweed community structure (Iken 2012), but the role of grazers in mediating competitive interactions among kelp and algal turf species on algal turf-dominated reefs remains understudied (Veenhof et al. 2022). Indeed, while the occurrence and drivers (e.g., ocean warming, marine heatwaves, eutrophication, and invasive species) of regime shifts from kelp forests to algal turf communities are well documented, the potential for recovery of kelp forests on degraded turf-dominated reefs is not well understood (Filbee-Dexter and Wernberg 2018, Christie et al. 2019). Given that algal turf communities may be an alternative stable state of the kelp forest ecosystem, reinforced by ecological feedback mechanisms (such as low kelp recruitment), natural recovery of kelp forests on algal turf-dominated reefs may be rare (Filbee-Dexter and Wernberg 2018). Active human interventions may therefore be needed to directly reforest degraded reefs or remove algal turfs to allow for natural kelp recovery, and such interventions could benefit from the identification of grazers that act as biocontrol of algal turf (Feehan et al. 2019, Fredriksen et al. 2020).

Here, we examine the grazing behavior of the Atlantic purple sea urchin, *Arbacia punctulata*, in a degraded kelp forest ecosystem in southern New England, USA. The study location is at the warm (south) range limit of kelp forests in the Northwest Atlantic, where ocean warming and marine heatwaves have severely diminished the kelp populations, *Saccharina latissima* and *Laminaria digitata*, over the past four decades (Feehan et al. 2019, Filbee-Dexter et al. 2020). *A. punctulata* is a thermophilic species that is at its cold (north) range limit in southern New England, while its warm (south) range limit is in Florida, USA (Gianguzza 2020). *A. punctulata* and other sea urchins in the *Arbacia* genus are documented as omnivorous (Gianguzza 2020). In Florida, *A. punctulata* consumes sessile invertebrates, available detritus, and macroalgae (e.g., *Gracilaria foliifera*, *Codium* sp., *Padina* sp., *Dictyota* sp., and *Sargassum filipendula*), but will adjust its diet to reflect the availability of various food sources (Hay et al. 1986, Cobb and

Lawrence 2005). For example, Cobb and Lawrence (2005) found that *A. punctulata* in Florida will consume macroalgae when it is in high abundance and animal prey is scarce. Other species in the *Arbacia* genus exhibit strong herbivory pressure on turf-forming macroalgae species (Bulleri et al. 1999, Bonaviri et al. 2011). For example, a closely related species, *Arbacia lixula*, is a common grazer of algal turf on Mediterranean reefs (Bulleri et al. 1999, Bonaviri et al. 2011).

At our study location in southern New England, divers have observed *A. punctulata* grazing within small gaps in the algal turf-dominated reef, while not appearing to actively consume the historically dominant but now rare kelp, *S. latissima* (Grace and Feehan 2020). These observations are in contrast to the typically reported role of temperate sea urchins as voracious grazers of kelp (Filbee-Dexter and Scheibling 2014). It is well documented that temperate sea urchins are major kelp grazers (e.g., *Centrostephanus rodgersii* in Tasmania, *Strongylocentrotus polyacanthus* in Alaska, *Strongylocentrotus purpuratus* on the US west coast, and *Strongylocentrotus droebachiensis* on both sides of the North Atlantic) and destructive grazing by sea urchins has driven regime shifts from kelp forests to less productive sea urchin barrens worldwide (Skadsheim et al. 1995, Scheibling et al. 1999, Ling et al. 2009, Konar et al. 2014, Rogers-Bennett et al. 2019). Here, we examine the grazing behavior of *A. punctulata* in the field and laboratory as a first step towards understanding its potential to remove algal turf in the degraded kelp forest ecosystem in southern New England. We analyze localized field survey data of kelp and algal turf abundance in reef areas with and without sea urchins present, and we conduct complementary laboratory and field experiments measuring grazing rates on kelp and algal turf and examining the attraction of *A. punctulata* to these diet items. Understanding the grazing ecology of *A. punctulata* in southern

New England is relevant in the context of ongoing efforts in this region to actively restore kelp forests (Connecticut Sea Grant 2021).

2. METHODS

2.1. Field Survey

The field survey occurred in Narragansett Bay, Rhode Island, USA at Fort Wetherill State Park, Jamestown (41.478ºN, 71.362ºW). The site consists of sloping bedrock and large boulders that grade to sand at ~7 m depth and was historically a dense kelp forest (*S. latissima* intermixed with sparser *L. digitata*) (Brady-Campbell et al. 1984). Reductions in populations of *S. latissima* and *L. digitata* in this region were due to regional ocean warming and recurrent marine heatwaves (Feehan et al. 2019, Filbee-Dexter et al. 2020) and the site is currently dominated by algal turfs (e.g., *Ceramium* sp., *Chondrus crispus*, *Coccotylus truncatus*, *Gracilaria* sp., *Palmaria palmata*, *Phyllophora pseudoceranoides*, *Polysiphonia* sp., and *Ulva* sp.) (Pessarrodona et al. 2021).

On 1 December 2017 and 9 February 2018, SCUBA divers observed groups of *A. punctulata* within small clearings (~0.5 m diameter) in the algal turf-dominated reef. To examine the association of sea urchin presence/absence with the abundance of algal turf, on each date a single 30 m transect line was haphazardly placed parallel to shore at 2–3 m depth (depth of historical maximum kelp density; Brady-Campbell et al. 1984) and videoed with a GoPro Hero 4 camera positioned ~0.5 m above the bottom. Aerial percent cover of kelp, algal turf, and open space (rock bottom) were measured within the transect by extracting photo quadrats (0.5 x 0.5 m L x W) at locations of recorded *A. punctulata* groups, and at locations without sea urchins 1 m away from the groups (December transect: n = 2 urchins present and 2 urchins absent photo quadrats; February transect: n = 6 urchins present and 6 urchins absent photo quadrats). The gradated transect line was used as a scale in the photo quadrats. A grid of 81 points was superimposed on each photo quadrat and percent cover of kelp, algal turf, and open space was estimated with the point-count method (Aronson et al. 1994). The image analysis was conducted with Image-Pro Plus.

To statistically examine the relationship between *A. punctulata* presence/absence and the percent cover of kelp, algal turf, and open space, we used beta regressions with factors Urchin (2 levels, fixed: present and absent) and Date (2 levels, random: December and February). Beta regressions are used when the response variable is restricted to an interval (0,1) and thus does not follow a Gaussian distribution (Ferrari et al. 2004). The analyses were conducted in the software R (R Core Team 2023) using the package *glmmTLMB* (Mollie et al. 2017) with code modified from Douma and Weedon (2019). A covariate dispersion parameter was incorporated in the models that allowed for different dispersions by treatment (Urchin and Date). Proportional data were rescaled to remove 0 and 1 using the following formula: $p^* = \frac{p(n-1)+\frac{1}{C}}{n}$; where p is the proportion of a category, n is the total number of observations in the dataset, and C is the number of categories ($C = 3$) (Smithson and Verkuilen 2006). The α for the analyses was corrected to account for the multiple hypotheses tested on data obtained from the same quadrat with the formula: $\alpha_{adj} = \frac{\alpha}{m}$; where m is the number of hypotheses tested ($m = 3$), so $\alpha = 0.017$ for the analyses.

2.2. Laboratory Feeding Choice Experiment

Field observations of groups of *A. punctulata* within clearings in the algal turf-dominated reef prompted us to conduct a laboratory feeding experiment to examine whether *A. punctulata* preferentially grazes algal turf over kelp.

The laboratory experiment was conducted in an ~115 L aquarium in a recirculating artificial seawater system (Instant Ocean®) in the Department of Biology at Montclair State University, New Jersey. The experimental design was a “choice” feeding experiment, wherein a diet choice between kelp and an algal turf species assemblage was provided to the sea urchins. On 10 August 2021 and 14 September 2021, sea urchins *A. punctulata*, kelp *S. latissima*, and three locally dominant algal turf species (*Coccotylus truncatus*, *Chaetomorpha linum*, and *Grateloupia turuturu*) were collected with SCUBA at <7 m depth at Fort Wetherill, placed in coolers with seawater from the field site, and transported to the seawater system within 5 hours of collection. Sea temperature at depth on each collection date was ~20°C. *A. punctulata* were acclimated to aquarium conditions overnight with a drip line and received constant aeration with an air stone. The sea urchins were fed *ad libitum* on dried kelp *Alaria esculenta* (Maine Coast Sea Vegetables), followed by a 2-day starvation period prior to the experimental trials to standardize feeding history. Kelp and algal turf species were rinsed in the laboratory to remove sediment and small invertebrates prior to transfer to a separate aquarium in the seawater system. Only healthy intact kelp and algal turf tissue without epibionts was used in the experiment. North and west facing windows provided natural light exposure to the laboratory.

Two experimental trials were conducted (Trial 1: 20–24 August 2021; and Trial 2: 18–20 September 2021), each with recently collected sea urchins, kelp, and algal turfs. For each trial, ~2.5 g of kelp and ~2.5 g of the combined algal turfs (wet weights) were added together to n = 6

~500 mL cylindrical (10 cm diameter) plastic containers with an individual *A. punctulata* enclosed. All containers had 5 x 4 cm (L x W) holes excised on two sides that were covered with 500 µm plastic mesh to allow water flow but prevent loss of algal material. The kelp and algal turfs sank to the bottom of the containers, providing similar access for the sea urchins. The algal turfs consisted of the three algal turf species (*C. truncatus*, *C. lineum*, and *G. turuturu*) massed separately and combined in equal parts to give the total ~2.5 g mass (~0.83 g per species). As a no-grazer control to detect autogenic changes in algal mass, ~2.5 g of kelp and ~2.5 g of the combined algal turfs were placed together in containers without a sea urchin present (n = 1 and n = 3 containers in Trial 1 and 2, respectively). A single no-grazer control was used in Trial 1, as autogenic changes that could obscure grazing effects were expected to be small over the short period of the experiment (days). Additional no-grazer controls (n = 3) were included in Trial 2 to confirm this assumption. Trials 1 and 2 were intended to last 2 days; however, tropical storm Henri led to substantial flooding near the University on 22 August 2021, preventing access to the laboratory. As a result, Trial 1 lasted 4 days, while Trial 2 lasted the planned 2 days.

Sea urchin test diameters were measured with calipers (nearest 0.1 mm) at the onset of each trial. Mean (± SD) sea urchin test diameter was 32.2 ± 4.2 mm in Trial 1 and 32.8 ± 4.8 mm in Trial 2. Water temperature in the aquarium was measured hourly with an Onset HOBO® Pendant temperature logger. Mean (± SD) aquarium temperature was 19.6 ± 0.3°C in Trial 1 and 19.5 ± 0.3°C in Trial 2. At the end of each trial, the remaining mass of kelp and algal turf were measured (wet weights) in each container to determine kelp mass loss (ΔK, g algae d^{-1}) and algal turf mass loss (ΔT, g algae d^{-1}), calculated as the difference in mass at the start (M_{start}) and end (M_{end}) of the experiment, divided by the total number of experimental days (d) (ΔK or $\Delta T = (M_{start} - M_{end}) / d$) (i.e., grazing rate or autogenic change).

To test for a diet preference, the data were statistically analyzed according to the methods of Peterson and Renauld (1989) for feeding preference experiments. Specifically, the kelp mass loss within each container (ΔK) was subtracted from the algal turf mass loss within each container (ΔT) to calculate the difference in kelp and turf mass loss per container (KT_{diff}, g algae d^{-1}) ($KT_{diff} = \Delta T - \Delta K$). If there were no diet preference by the sea urchin for algal turf over kelp, KT_{diff} should be statistically non-significant between the urchin present treatment and the no-grazer control (null hypothesis of no differential grazing rate on algal turf versus kelp) (Peterson and Renauld 1989). KT_{diff} between the treatment and control was analyzed with a one-sample one-tailed t-test in Trial 1 (due to a single control container in Trial 1) and with a two-sample one-tailed t-test in Trial 2 (due to multiple, n = 3, control containers in Trial 2). Homogeneity of variance was confirmed for Trial 2 with Levene's test ($p = 0.18$). The assumption of normality was met for the data in both trials (Kolmogorov-Smirnov test, $\alpha = 0.05$).

2.3. Laboratory Food Attraction Experiment

A second laboratory experiment was conducted in the flow-through seawater system at the Marine Biological Laboratory (MBL) in Woods Hole, Massachusetts, USA to confirm a preferential attraction of *A. punctulata* to algal turf versus kelp.

Sea urchins *A. punctulata*, kelp *S. latissima*, and local algal turf species (*Ulva* sp., *Ceramium* sp., and *Gracilaria tikvahiae*) were collected for the experiment nearby MBL in early to mid-May 2022. Sea urchins were dredged from ~10 m depth in Vineyard Sound, Falmouth, Massachusetts via the MBL research vessel *R/V Gemma* (Fig. 1A). Algal turf species were collected off the city dock at Eel Pond, Woods Hole, Massachusetts. Kelp was collected as drift at Scusset Beach State Reservation, Sagamore Beach, Massachusetts. Sea urchins and algae were maintained in laboratory seawater tables in ambient flow-through seawater prior to the experiment. Sediment and small invertebrates were removed from the kelp and algal turf species by rinsing with distilled water. Sea urchins were fed *ad libitum* on an assortment of locally collected macroalgae prior to the onset of a 2-day starvation period to standardize feeding history for the experiment. Only healthy intact kelp and algal turf tissue without epibionts was used in the experiment.

On 18 May 2022, groups of 5 sea urchins were placed in a line at the bottom center of each of n = 2 ~28 L seawater aquaria contained within a seawater table (130 x 75 x 12 cm; L x W x H). The aquaria were perforated with small ~5 mm holes on the two sides perpendicular to the direction of flow to allow seawater to pass through the aquaria and aerate the sea urchins. The sea urchins were placed within each replicate aquarium equidistant from two rectangular ~2 L pens composed of plastic egg crate and containing either 21 g of kelp or 21 g of the combined algal turfs (~7 g per turf species) (Fig. 1B). After 24 h, the location of each sea urchin was recorded as adjacent to the kelp (touching the kelp pen) or adjacent to the algal turf (touching the algal turf pen) (Fig. 1C). To ensure that the attractant was the algal food and not another stimulus in the room (e.g., light), the location of the kelp and algal turf pens was reversed between the replicates. To ensure that similar levels of chemical cues emanated from the kelp and algal turf, the flow was oriented perpendicular to the algal pens.

Sea urchin test diameters were measured with calipers (nearest 0.1 mm) at the onset of the experiment, and the overall mean (± SD) test diameter was 35.3 ± 2.7 mm. Seawater temperature sourced to the laboratory was measured with a digital thermometer once at the beginning and end of the experiment (mean temperature = 14.0°C). Artificial light was provided to the room on a 12/12 h light/dark cycle.

A Chi-squared test was used to determine whether the frequency of sea urchins adjacent to the kelp pen versus algal turf pen after 24 h, pooled across replicates, was significantly different from 1:1 (kelp:turf) (null hypothesis of no preferential food attraction). A single sea urchin with an ambiguous location (not in contact with either pen) was excluded from the statistical analysis.

2.4. Field Feeding Choice Experiment

To examine grazing rates on kelp and algal turf under ambient field conditions, a field experiment was conducted with a similar experimental design to the laboratory feeding choice experiment (section 2.2). The field experiment lasted 48 h and occurred at Fort Wetherill, the site of the initial field survey (section 2.1).

On 22 August 2022, sea urchins *A. punctulata*, kelp *S. latissima*, and the locally dominant algal turf species *Ceramium* sp. were collected at <7 m depth at Fort Wetherill via SCUBA and snorkeling. Onshore, ~25 g of kelp and ~25 g of algal turfs were immediately placed together in each of 6 cages composed of 43 x 29 x 15 cm (L x W x H) plastic containers with the tops and sides excised and covered with 1 cm opening mesh to allow for ample water flow while preventing algal loss (Fig. 2). To generate a grazer treatment, groups of 3 sea urchins were haphazardly placed into n = 3 cages containing the kelp and algal turf. The remaining n = 3 cages contained no sea urchins as a no-grazer control to detect autogenic changes in algal mass. Cage lids were secured with zip ties and the cages were transported by divers to the seafloor and weighted ~1 m apart with

31 x 20 x 5 cm (L x W x H) cement blocks (Fig. 2). The sea urchins were not starved prior to the field experiment to minimize handling that could yield stress in the animals.

Sea urchin test diameters were measured to the nearest 0.1 mm with calipers at the onset of the experiment (mean ± SD = 39.1 ± 3.1 mm). Three data loggers (Onset HOBO MX2202) were placed across the field array to record temperature and light during the experiment (5 min interval). Mean (± SD) seawater temperature was 22.5 ± 0.4°C. Mean (± SD) daytime light was 8094 ± 314 lux. After 48 h in the cages, the remaining algae was collected and weighed to determine kelp and algal turf mass loss (ΔK and ΔT, g algae d^{-1}) (i.e., grazing rate or autogenic change) calculated with the same method as in the laboratory feeding choice experiment (section 2.2).

Data were statistically analyzed according to the methods of Peterson and Renauld (1989), in an identical manner as in Trial 2 of the laboratory feeding choice experiment (section 2.2). Specifically, the difference in the mass loss of kelp versus algal turf (KT_{diff}) was analyzed between the urchin present treatment and no-grazer control with a two-sample one-tailed t-test (n = 3 cages per treatment and control). The data were square transformed to conform to the assumption of homogeneity of variance (Levene's test, p = 0.12). The assumption of normality was met for the square transformed data (Kolmogorov-Smirnov test, p = 0.47).

3. RESULTS

3.1. Field Survey

There was strong evidence for a difference in the percent cover of algal turf and open space, but not kelp, between the urchins present and urchins absent photo quadrats in the field (Table 1). There was lower mean cover of algal turf (62 ± 12% versus 92 ± 4%; ± SE) and higher mean cover of open space (31 ± 7% versus 2 ± 1%) in the urchins present versus urchins absent photo quadrats

(Fig. 3). Mean kelp cover was 8 ± 5% and 6 ± 4% in the urchins present and urchins absent photo quadrats, respectively (Fig. 3). The overall high cover of algal turf and low cover of kelp indicates a degraded algal turf-dominated ecosystem (Fig. 3).

3.2. Laboratory Feeding Choice Experiment

In Trial 1 of the laboratory feeding choice experiment, kelp loss (ΔK) was -0.03 g algae d^{-1} (i.e., kelp mass slightly increased) and algal turf loss (ΔT) was 0.10 g algae d^{-1} in the single no-grazer control (n = 1 container) (Fig. 4A). With a sea urchin present in Trial 1 (n = 6 containers), kelp loss (ΔK) was 0.16 ± 0.04 g algae d^{-1} (mean ± SE) and algal turf loss (ΔT) was 0.44 ± 0.07 g algae d^{-1} (Fig. 4A). There was moderate evidence for a difference in mass loss of kelp and algal turf (KT_{diff}) in Trial 1 between containers with a sea urchin present versus the no-grazer control (one-sample t-test: $t_{0.05,(1),5} = 2.6$, $p = 0.048$). There was a smaller difference in kelp and algal turf mass loss in the no-grazer control ($KT_{diff} = 0.13$ g algae d^{-1}) than in the sea urchin present treatment ($KT_{diff} = 0.27 \pm 0.06$ g algae d^{-1}) (Fig. 4B). Similar results occurred in Trial 2 (Fig. 4C,D). In Trial 2, kelp loss (ΔK) was 0.02 ± 0.01 g algae d^{-1} and algal turf loss (ΔT) was -0.004 ± 0.002 g algae d^{-1} (i.e., turf mass slightly increased) in the no-grazer control (n = 3 containers) (Fig. C). With a sea urchin present in Trial 2 (n = 6 containers), kelp loss (ΔK) was 0.08 ± 0.05 g algae d^{-1} and algal turf loss (ΔT) was 0.25 ± 0.03 g algae d^{-1} (Fig. 4C). There was strong evidence for a difference in mass loss of kelp and algal turf (KT_{diff}) in Trial 2 between the sea urchin present treatment versus the no-grazer control (two-sample t-test: $t_{0.05,(1),7} = 3.5$, $p = 0.010$). There was a smaller difference in kelp and algal turf loss in the no-grazer control ($KT_{diff} = -0.02 \pm 0.01$ g algae d^{-1}) than in the sea urchin present treatment ($KT_{diff} = 0.17 \pm 0.04$ g algae d^{-1}) (Fig. 4D).

Grazing rates were generally similar across the three algal turf species offered in Trial 1 and 2 (*Coccotylus truncatus*, *Chaetomorpha linum*, and *Grateloupia turuturu*) (Supplementary Information Table S1).

3.3. Laboratory Food Attraction Experiment

In the first replicate of the laboratory food attraction experiment, all 5 sea urchins moved adjacent to the algal turf pen. In the second replicate, 3 sea urchins moved adjacent to the algal turf pen, 1 sea urchin moved adjacent to the kelp pen, and the location of 1 sea urchin was ambiguous (in contact with neither pen). A Chi-squared test on the pooled frequency of sea urchins adjacent to kelp (1 urchin) versus algal turf (8 urchins) indicated a significant overall food attraction to algal turf ($\chi^2 = 5.44$, df = 1, p = 0.020).

3.4. Field Feeding Choice Experiment

In the field feeding choice experiment, kelp loss (ΔK) was 0.97 ± 0.19 g algae d^{-1} (mean ± SE) and algal turf loss (ΔT) was 4.40 ± 2.26 g algae d^{-1} in the no-grazer control (n = 3 cages) (Fig. 5A). With a group of sea urchins present (n = 3 cages), kelp loss was 0.79 ± 0.50 g algae d^{-1} and algal turf loss was 7.93 ± 0.66 g algae d^{-1} (Fig. 5A). There was only weak evidence for a difference in mass loss of kelp and algal turf (KT_{diff}) between cages with a group of sea urchins present versus the no-grazer control (two-sample t-test: $t_{0.05,(1),4} = 1.9$, p = 0.064), with a pattern of greater difference in kelp and algal turf loss in the sea urchins present treatment ($KT_{diff} = 7.13 \pm 0.21$ g algae d^{-1}) than in the no-grazer control ($KT_{diff} = 3.44 \pm 2.40$ g algae d^{-1}) (Fig. 5B).

4. DISCUSSION

Substantial declines in kelp forest cover and extent have occurred in southern New England, USA, linked to ocean warming and increasingly frequent and severe marine heatwaves (Feehan et al. 2019, Filbee-Dexter et al. 2020). The kelp forest ecosystem is currently dominated by warm-tolerant, opportunistic algal turf species that provide fewer ecosystem services than kelp (Pessarrodona et al. 2021). The potential for kelp forest recovery in this region, and other globally degraded kelp forest ecosystems, is not well understood (Filbee-Dexter and Wernberg 2018, Feehan et al. 2019). Here, we examined grazing of kelp and algal turf by the sea urchin *A. punctulata* as a first step towards understanding factors that may destabilize the algal turf-dominated ecosystem. Our combined field survey and laboratory and field experimental results indicate that at its cold (north) range limit in the Northwest Atlantic, *A. punctulata* preferentially consumes algal turfs over the formerly dominant kelp *S. latissima*. While the laboratory feeding choice experiment provided strong evidence for a preference for algal turf over kelp, there was a weaker contribution of evidence from the field experiment ($p = 0.06$). This result is likely explained by a combination of a smaller sample size and higher variability under field conditions and may be due in part to the fact that sea urchins were not starved prior to the field experiment (to minimize handling stress) and therefore individual feeding history was not standardized.

Laboratory grazing rates by *A. punctulata* on *S. latissima* observed in this study (mean: 0.08–0.16 g urchin^{-1} d^{-1}) are similar to the grazing rates observed for the sea urchin *S. droebachiensis* on the same kelp species in a laboratory study in Nova Scotia, Canada (mean: ~0.1–0.2 g urchin^{-1} d^{-1}) (Sumi and Scheibling 2005). However, unlike our findings, *S. droebachiensis* had lower grazing rates on an alternate diet item (the invasive macroalgae *Codium fragile* ssp. *tomentosoides*) in the laboratory; and in field cages, *S. droebachiensis* consumed turf-forming red algae only once all of the kelp had been consumed (Sumi and Scheibling 2005). Accordingly, in Nova Scotia, groups of *S. droebachiensis* have cooperatively and destructively grazed kelp forests yielding sea urchin barrens along 100s of km of coastline (Scheibling et al. 1999). By contrast, our field survey indicated a negative association between *A. punctulata* presence and the abundance of algal turf, but not kelp. Based on our laboratory and field experimental findings, it is likely that this natural field pattern is explained by a feeding preference by *A. punctulata* for algal turfs over kelp.

It is possible for dietary history to affect sea urchin feeding preference in experimental feeding trials (Lyons and Scheibling 2007). For example, Lyons and Scheibling (2007) found that diet conditioning led *S. droebachiensis* to prefer an unfamiliar diet item in the short term. Across our experiments, sea urchins were maintained on dried kelp *Alaria esculenta* (laboratory feeding choice experiment), an assortment of locally collected macroalgae (laboratory food attraction experiment), and a natural field diet where kelp was rare (field feeding choice experiment). Given that this range of dietary history includes both kelp and algal turf, it is unlikely that a preference for algal turf over kelp observed across our experiments was due to dietary history. Additionally, the effect of dietary history on sea urchin food preference in the laboratory was likely diminished by starving the sea urchins prior to the onset of each experiment, which is a standard approach in urchin feeding studies (Peterson and Renaud 1989).

In the tropics, sea urchin species that graze macroalgae have been used as a biocontrol agent of problematic seaweeds on degraded coral reefs to enhance coral recruitment and cover (Neilson et al. 2018, Williams 2022). Analogous efforts have not to our knowledge been undertaken to control algal turfs in kelp forest ecosystems. This is likely because many wellstudied temperate sea urchin species target kelp as a primary diet item (Filbee-Dexter et al. 2014). The apparent preference by *A. punctulata* for algal turf over kelp observed across our experiments begs the question of whether targeted introduction of *A. punctulata* to turf-dominated reefs in southern New England could clear space for kelp seeding (e.g., with “green gravel”; Fredriksen et al. 2020) or natural kelp recruitment. However, caution is advised, as it remains unknown whether the diet preference of *A. punctulata* will shift with shifting kelp and algal turf abundance on reefs. For example, previous studies in Florida found that *A. punctulata* targeted the proportionally most abundant food source (Hay et al. 1986, Cobb and Lawrence 2005). In addition, the feeding behavior of *Arbacia* spp. has been shown to shift under future ocean warming scenarios, compensating for energy deficits (Hill and Lawrence 2006, Minuti et al. 2021). The response of *A. punctulata* grazing behavior to shifting environmental factors, including kelp and turf availability and climate change, remains an area of active research.

As a thermophilic species, *A. punctulata* is expected to benefit from warming sea temperatures and increasingly frequent and severe marine heatwaves in southern New England (Bojorquez and Feehan 2021). Previous laboratory experiments have shown that early embryonic development of *A. punctulata* is accelerated during marine heatwaves (Bojorquez and Feehan 2021), which may reduce the time spent by larvae in the plankton, and therefore, their mortality during sensitive early life-history stages, facilitating population recruitment (Vaughn and Allen 2010). Yet, surveys of *A. punctulata* population abundance and distribution are lacking in southern New England. These data would be required to predict and track changes in population size and extent and assess the effects of natural grazing on algal turf and kelp populations. Additionally, controlled field studies are needed to examine the effects of *A. punctulata* on the benthos at varying urchin densities in combination with varying kelp and algal turf cover—ranging from algal turf to kelp dominance. The effects of *A. punctulata* grazing on the abundance of micrograzers (e.g., gastropods), through removal of their algal turf habitat, also should be examined due to the possible indirect effects on kelp recruitment through changes in micrograzing on kelp recruits (Veenhof et al. 2022). Hence, there is a need to fill many knowledge gaps in the ecology of *A. punctulata*—from population dynamics to foraging behavior—while also bearing in mind the impacts of ongoing climate change and the need for effective kelp forest restoration.

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Tables and Figures

Table 1. Field survey beta regression models to examine the relationship between Urchin (2 levels, fixed: present and absent) and Date (2 levels, random: December and January) and the percent cover of kelp, algal turf, and open space. Significant results at $\alpha = 0.017$ (corrected to account for multiple hypothesis tests) are **bolded**.

Source	df	Estimate	SE	Z value	P
Kelp					
Urchin	1	0.2626	0.5729	9.318	0.647
Residuals	9				
Turf					
Urchin	**1**	**-1.4931**	**0.1408**	**-10.601**	**<0.00001**
Residuals	9				
Open space					
Urchin	**1**	**2.0034**	**0.2150**	**9.318**	**<0.00001**
Residuals	9				

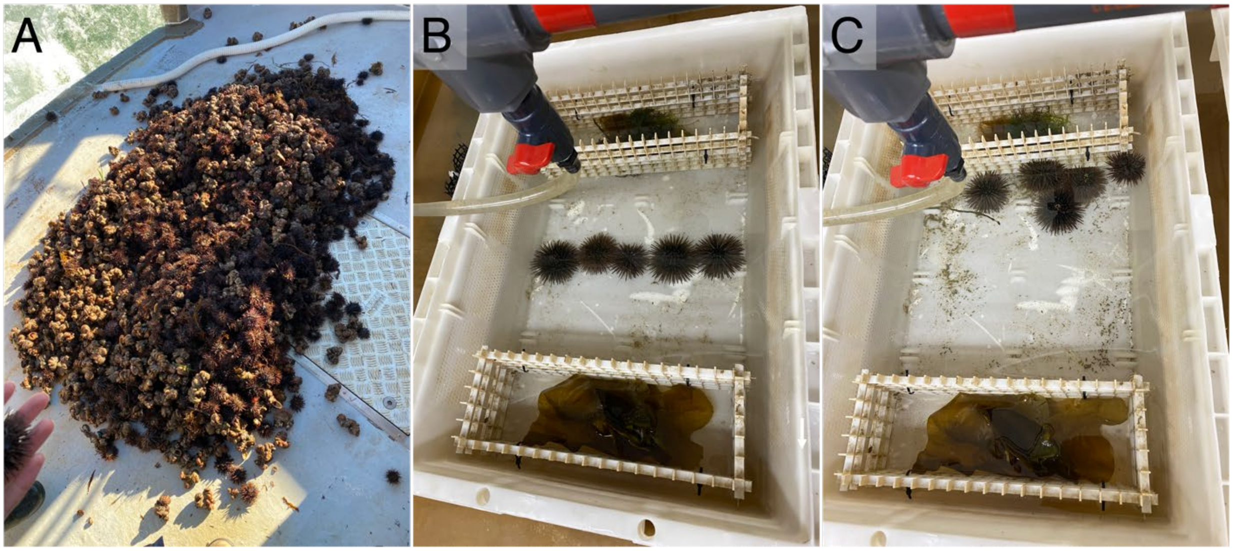

Fig. 1. Laboratory food attraction experiment. A. Sea urchins *Arbacia punctulata* dredged at 10 m depth in Vineyard Sound, Falmouth, Massachusetts, USA via the Marine Biological Laboratory (MBL) research vessel *R/V Gemma* (seen also are molluscs *Crepidula fornicata*). **B.** Five sea urchins were placed in a line equidistant to pens containing either kelp *Saccharina latissima* or algal turfs. **C.** After 24 h, the side selected by each sea urchin (kelp or algal turfs) was recorded (all turf in this example). For scale, sea urchins are ~35 mm test diameter on average in B and C. Photo credit: S. Kelly.

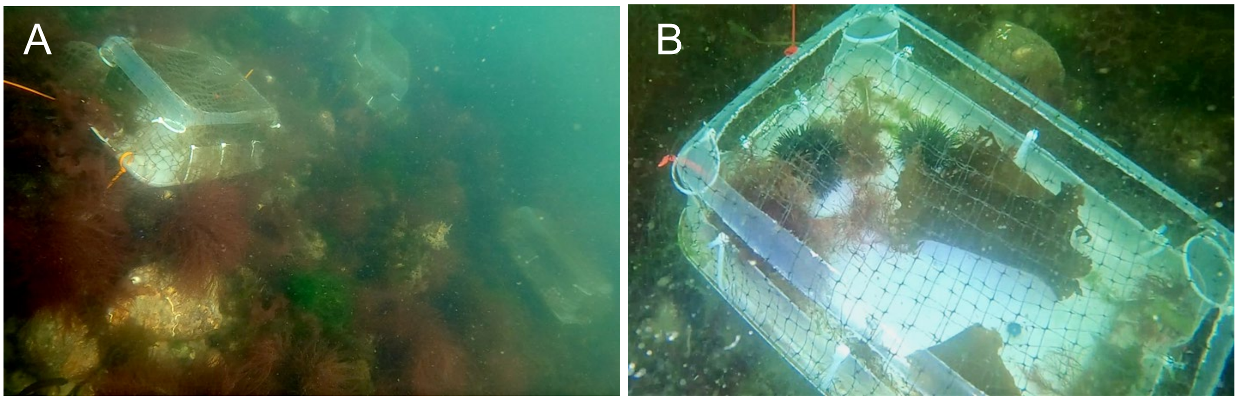

Fig. 2. Field feeding choice experiment. A. Field cages are visible on the seafloor surrounded by the natural algal turf-dominated reef. **B.** A field cage containing a group of three sea urchins *Arbacia punctulata* and food choices of kelp *Saccharina latissima* and algal turf *Ceramium* sp. Photo credit: S. Kelly.

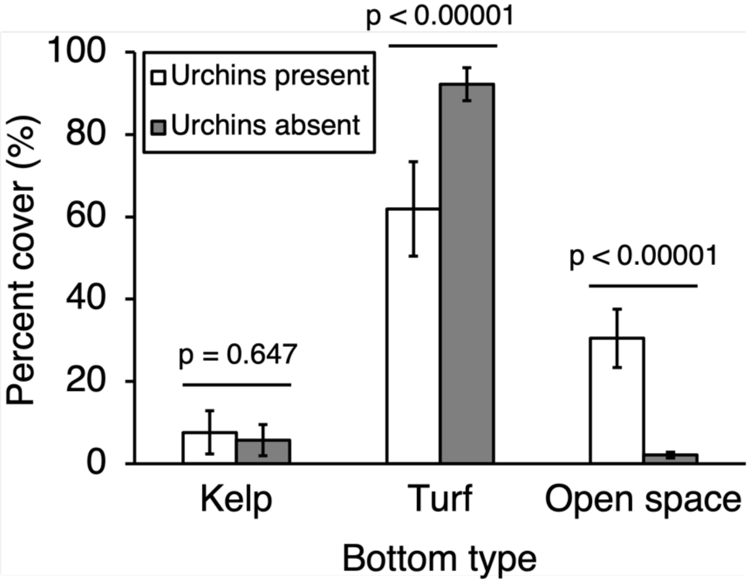

Fig. 3. Field survey. Percent cover (%) of kelp, algal turf, and open space (rock bottom) in photo quadrats with naturally occurring sea urchins *Arbacia punctulata* (urchins present) or no sea urchins (urchins absent) in the field. Errors are SE for n = 8 photo quadrats pooled across two sampling dates (December 2017 and February 2018). P-values are from beta regressions presented in Table 1.

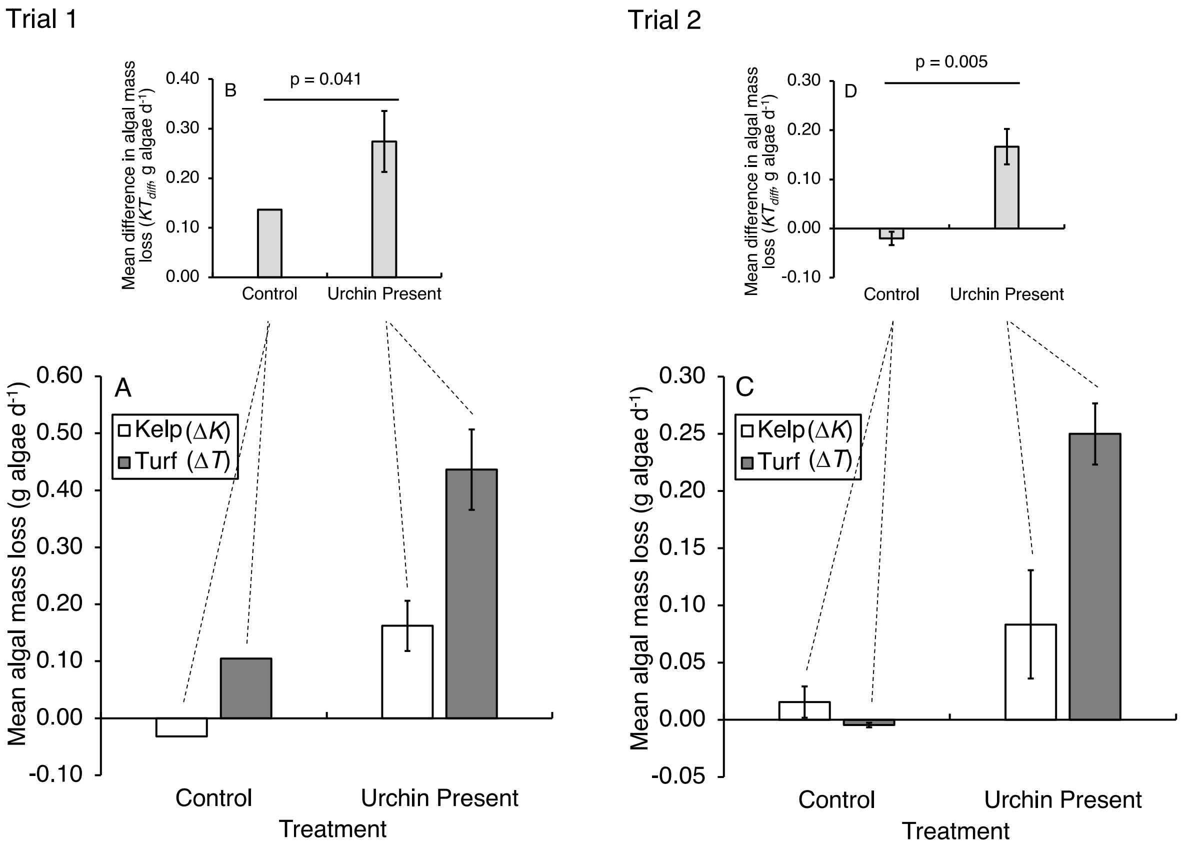

Fig. 4. Laboratory feeding choice experiment. A,C. Mean algal mass loss of kelp *Saccharina latissima* (ΔK) and algal turfs (ΔT) (g algae d^{-1}) in the absence (control) and presence (urchin present) of a single *Arbacia punctulata* over 4 and 2 d in Trial 1 and 2, respectively. **B,D.** Mean difference in algal mass loss of kelp versus turf (KT_{diff}, g algae d^{-1}) in the control and urchin present treatment. Errors are SE for n = 6 urchin present containers in both trials, and n = 1 and 3 control containers in Trial 1 and 2, respectively. P-values are from a one-sample (B) and two-sample (D) one-tailed t-test. Dashed lines indicate the source of data in B and D ($KT_{diff} = \Delta T - \Delta K$).

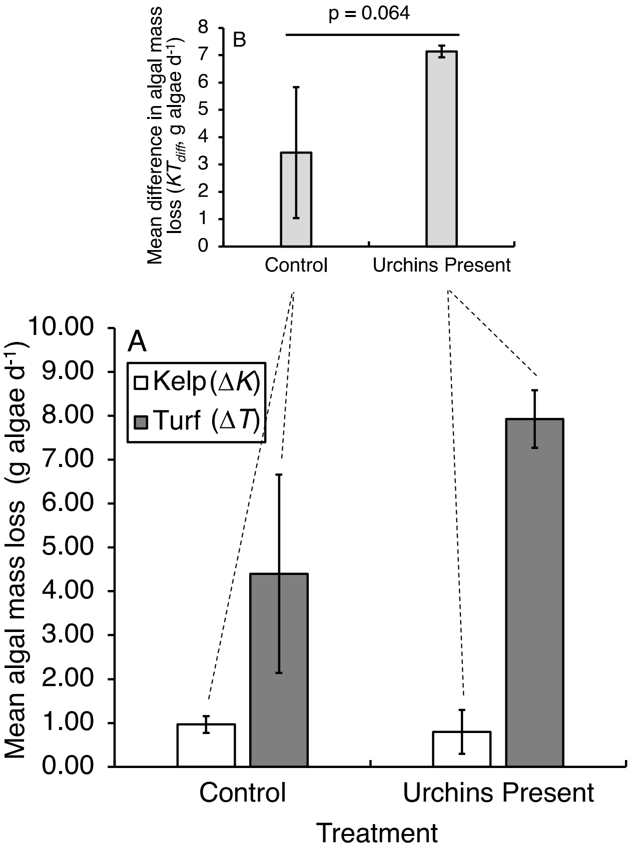

Fig. 5. Field feeding choice experiment. A. Mean algal mass loss of kelp *Saccharina latissima* (ΔK) and algal turf *Ceramium* sp. (ΔT) (g algae d^{-1}) in the absence (control) and presence (urchins present) of a group of 3 *Arbacia punctulata* over 2 d. **B.** Mean difference in algal mass loss of kelp versus turf (KT_{diff}, g algae d^{-1}) in the control and urchins present treatment. Errors are SE for n = 3 cages for the treatment and control. P-value is for a two-sample one-tailed t-test. Dashed lines indicate the source of the data in B ($KT_{diff} = \Delta T - \Delta K$).

Supplementary Information

Table S1. Algal mass loss (g algae d^{-1}) of kelp *Saccharina latissima* and each of three algal turf species (*Coccotylus truncatus*, *Chaetomorpha linum*, and *Grateloupia turuturu*) in the sea urchin present treatment and no-grazer control of Trial 1 and Trial 2 of the laboratory choice feeding experiment. Data are mean (± SE) aside from the unreplicated control in Trial 1.

		Algal species			
Trial	Treatment	*S. latissima*	*C. truncatus*	*C. linum*	*G. turuturu*
1	Urchin present	0.16 ± 0.04	0.20 ± 0.04	0.13 ± 0.06	0.11 ± 0.02
	Control	-0.03	0.07	0.00	0.04
2	Urchin present	0.08 ± 0.05	0.15 ± 0.04	0.09 ± 0.01	0.00 ± 0.01
	Control	0.02 ± 0.01	0.02 ± 0.00	-0.02 ± 0.01	0.00 ± 0.02