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Feeding Preference of the Sea Urchin *Arbacia punctulata* for Algal Turf Over Kelp in a Degraded Kelp Forest Ecosystem

Kenneth J. Hamel

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ABSTRACT

Increasingly severe ocean warming and marine heatwave events are driving declines in habitat-forming kelps worldwide. Direct mortality from extreme temperatures, coupled with destabilization of kelp forest communities, commonly trigger ecological community shifts from dominant kelp forests to an algal turf dominated state. Opportunistic algal turf species are more resilient to warming and lack the fundamental structure of kelp forests, and thus reduce ecosystem services and biodiversity. Once in place, algal turf communities contain ecological feedback mechanisms, diminishing kelp recruitment, and potential recovery. The various feedback mechanisms and ecological thresholds that maintain or drive community shifts between kelp forest and algal turf are not well understood. Likewise, the effects of sea urchin herbivory within these degraded algal turf communities remain poorly described, but likely have profound effects on the maintenance or drivers between these ecosystem states. Here, I present research into the grazing preferences of the thermophilic sea urchin *Arbacia punctulata* within a degraded *Saccharina latissima* kelp forest ecosystem dominated by algal turf in coastal Narragansett Bay, Rhode Island, USA. I find that *A. punctulata* grazes more heavily on algal turf assemblages than *S. latissima* with and without diet choice. My results corroborate field observations that *A. punctulata* graze on algal turf in the field and indicate the value of investigating *A. punctulata* grazing behavior further to understand their potential effects or utilization in kelp forest restoration strategies.

MONTCLAIR STATE UNIVERSITY

Feeding Preference of the sea urchin *Arbacia punctulata* for Algal Turf over Kelp in a Degraded Kelp Forest Ecosystem

By

Kenneth J. Hamel

A Master's Thesis Submitted to the Faculty of

Montclair State University

In Partial Fulfillment of the Requirements

For the Degree of

Master of Science

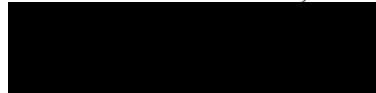
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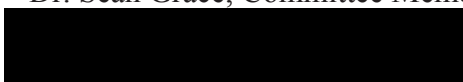
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Dr. Matt Schuler, Committee Member



Dr. Sean Grace, Committee Member



**FEEDING PREFERENCES OF THE SEA URCHIN *ARBACIA PUNCTULATA* FOR
ALGAL TURF OVER KELP IN A DEGRADED KELP FOREST ECOSYSTEM**

A THESIS

Submitted in partial fulfillment of the requirements
for the degree of Master of Science

by

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INTRODUCTION

Kelp forests are valuable ecosystems common in temperate and sub-polar latitudes, comprising approximately twenty-eight percent of global coastal habitat (Starko et al. 2021). Kelps (order *Laminariales*) are relatively large fleshy macroalgae, which tend to grow in dense, low-lying beds or high reaching canopies. These extensive canopies increase the structural complexity within marine habitats (Ware et al. 2019; Smale et al. 2013), which facilitates numerous ecosystem services and is the foundation of complex marine communities (Steneck et al. 2002; Feehan et al. 2021). The high primary productivity of kelp forests represent both additional habitat space and food resources, supporting highly biodiverse and resilient communities, which includes economically important target species (Paul & Steneck 1993; Wing et al. 2022). In addition to local productivity, kelp forest detritus increases nutrient inputs to adjacent, less productive benthic communities, which increases biodiversity and secondary production at regional scales (Krumhansl & Schibling 2012; Smale et al. 2021). Globally, kelp forests also contribute to carbon sequestration, through their high uptake of dissolved carbon dioxide during photosynthesis, as well as carbon export through kelp detritus transport to deep sediments (Krause-Jensen & Duarte 2016; Pedersen et al. 2020; Bayley et al. 2021). Kelp forests act as a buffer to coastal eutrophication through uptake of excess nutrients in densely populated areas, or coasts with increased terrestrial runoff (Neveus et al. 2018; Eger et al 2021). In recent years, aquaculture projects have sought to use kelp to help mitigate impacts of climate change (Chung et al. 2013; Kim et al. 2015; Yarish et al. 2017).

Under stable climatic conditions, kelp forests are resilient ecosystems due to various ecological feedback mechanisms supporting their dominance, which is facilitated by high biodiversity and substrate complexity (Layton et al. 2019; Randell et al. 2022). Despite their resilience, human activities are driving the decline of kelp forests worldwide, but they are threatened most by ocean warming and intensifying marine heatwave events (Krumhansl & Scheibling 2016; Oliver et al. 2018; Smale 2020). Kelps are cold-water adapted species and are reliant on thermal stability. At regional scales, gradual ocean warming caused by climate change increases thermal stress on kelp populations until hitting an upper threshold, where kelp primary productivity and seasonal growth rates can deteriorate (Simonson et al. 2015; Nepper-Davidsen et al. 2019). Exposure to marine heatwave events, which involve sudden and drastic shifts to

abnormally high temperatures, can quickly degrade kelp forests through increasing mortality (Hobday et al. 2016; Arafeh-Dalmau et al. 2020). This is especially true for more equatorial populations, which can be already pushed close to their thermal limits (Diehl et al. 2021).

Ocean warming and marine heatwave events diminish the strength of the ecological feedback mechanisms that typically stabilize kelp forest communities, which can tip stable kelp forest ecosystems into decline (Filbee-Dexter et al. 2020). On a global scale, kelp forest collapse triggered by thermal extremes commonly results in community phase shifts from kelp forest to algal turf dominated communities (Filbee-Dexter et al. 2016; Filbee-Dexter & Wernberg 2018). Algal turf species tend to be shorter (<15cm), opportunistic algae comprised of various assortments of filamentous, foliose, articulated, or corticated species (Connell et al. 2014). Algal turfs are generally tolerant of climactic extremes, giving them a competitive edge over kelps under warming conditions (Airoldi 1998; Anton et al. 2020). When established in a kelp forest community, they begin growing in densely growing low-lying mats which carpet the benthos, and quickly monopolize any hard substratum yielded by kelps (Moy & Christie 2012), preventing natural kelp forest recovery (Kennelly 1987; Connell & Russell 2010). In addition, kelps which manage to recruit on algal turf when no substrate is available are more easily dislodged and have greater mortality and slower growth rates than when on bare substrate (Burek et al. 2018; Feehan et al. 2019). These ecological feedback mechanisms increase the stability of algal turf ecosystems. This can result in a loss of ecosystem services, as algal turf species lack the distinctive habitat complexity provided by kelp forest canopies, and create a more homogenized habitat which supports less biodiversity (Ware et al 2019; Pessarrodona et al. 2021). In addition, turf species tend to trap more sediments where they encroach kelp forests and coral reefs, which can smother kelps, corals, and other benthic organisms (Gordon et al. 2016; Tebbett et al. 2020). In most aspects, algal turf communities represent a degraded, but generally stable ecosystem state with diminished ecosystem services compared to kelp forests.

In addition to thermal extremes, ecological collapse of kelp forests can be triggered by increased herbivory pressure from sea urchins (Filbee-Dexter & Scheibling 2014). Normally, kelp-associated predators moderate herbivory rates through top-down mechanisms. However, once kelp forests become destabilized from increasing temperatures or overfishing, predation pressure on urchins can slacken as biodiversity diminishes, resulting in increased herbivory (Steneck et al.

2004; Byrnes et al. 2006; Smith et al. 2021). In addition, thermal or biological drivers can induce local population spikes of sea urchins (Hart & Scheilbling 1988; Rogers-Bennett & Catton 2019), which then overgraze kelps and any remaining understory macroalgae resulting in a less productive urchin barren (Feehan et al. 2012; Filbee-Dexter & Scheilbling 2014). While the drivers of ecosystem shifts among kelp forest to algal turf reef or urchin barrens are well documented (ocean warming and marine heat waves, sea urchin recruitment pulses, trophic cascades), the dynamics driving kelp forest recovery from degraded ecosystem states remain less understood. Instances of kelp forest recovery from urchin barrens have occurred and are mainly due to sea urchin population crashes caused by disease outbreaks (Feehan & Scheibling 2014; Gizzi et al. 2021), the recovery of a sea urchin predator (Dayton et al. 1992; Smith et al. 2021) or shifts in local urchin larval recruitment (Norderhaug & Christie 2013). There are even fewer documented instances of kelp forest recovery from an algal turf ecosystem state, and the dynamics that regulate kelp forest recovery from algal turf remains unclear (Christie et al. 2019).

In this study, I examine the grazing behavior of the northwest Atlantic sea urchin *Arbacia punctulata* in Narragansett Bay, located along the coast of New England, USA, within a turf-dominated ecosystem. The field site at Fort Wetherill, RI is located at the southernmost extent of the New England *Saccharina latissima* and *Laminaria digitata* kelp forest. Over several decades, increasingly severe marine heatwaves have nearly extirpated kelps from their historic dominance within Narragansett Bay (Brady-Campbell et al. 1984), resulting in the dominance of algal turf at Fort Wetherill (Feehan et al. 2019; Filbee-Dexter et al. 2020). In this degraded ecosystem, the thermophilic sea urchin *A. punctulata* is common at this edge of its northernmost range (Guinguza 2020). Nonetheless, details about its diet and ecological interactions within *S. latissima* and algal turf communities remains unknown. Sea urchins in the *Arbacia* genus are generally omnivorous but tend towards carnivory and feed on sessile invertebrates and available detritus. However, *A. punctulata* has been shown to exhibit diet plasticity, switching between carnivory and feeding on macroalgae depending on the availability of food (Cobb & Lawrence 2005; Guinguza et al. 2020). Observational data of their feeding behavior at Fort Wetherill suggest that *A. punctulata* graze enthusiastically on algal turf, grazing gaps in the turf dominated reef (Feehan et al. 2019; Grace and Feehan 2020). To further investigate this observation, I test the hypothesis that *A. punctulata* preferentially consumes algal turf assemblages found at Fort Wetherill over *S. latissima* through two laboratory feeding assays. Isolated *A. punctulata* were given a choice between *S.*

latissima and algal turf species (choice feeding assay) or no choice in diet (no choice feeding assay) to measure grazing rates and infer diet preference.

METHODS

Animal and Macroalgae Collection and Maintenance: Urchins *A. punctulata*, *S. latissima* (referred hence as kelp), and three most dominant algal turf species (*Coccotylus truncatus*, *Chaetomorpha linum*, *Grateloupia turuturu*) were collected with SCUBA at < 7 m depth at Fort Wetherill, RI (West Cove in Narragansett Bay) on 10 August 2021 and 14 September 2021. Sea temperature at depth on 10 August 2021 and 14 September 2021 were ~22°C. and 24°C, respectively. The organisms were placed in coolers of seawater from the field site with ice packs to maintain the ambient field temperature of ~20°C-22°C and transported to Montclair State University, NJ within 4–five hours of collection. In the laboratory, three ~115L cycled aquaria with recirculating artificial seawater (Instant Ocean) set to ~20°C with Max Chill Aqua Euro Chillers, acted as holding tanks for *A. punctulata*, kelp, and algal turf. Kelp and algal turf species were rinsed with distilled water to remove sediment and small invertebrates prior to transfer into the seawater aquaria. Only fresh kelp tissue without epibionts (bryozoans) were used in the experiments. *A. punctulata* were acclimated to aquarium conditions overnight with a drip line, had constant aeration with an air stone, and were fed ad libitum on dried kelp (*Alaria esculanta*; Maine Coast Sea Vegetables) prior to the experiments. Water temperature, salinity, pH, ammonia, nitrites, and nitrates were monitored daily, and partial water changes occurred at least every 2 days. North and west facing windows provided natural light exposure.

Laboratory Feeding Assays

Field observations of *A. punctulata* grazing behavior by Feehan et al. (2019) prompted laboratory feeding experiments to confirm field observations of the urchin's preferential grazing on algal turf species over kelp. Two laboratory feeding assays were conducted to measure *A. punctulata* grazing rates on kelp and algal turf: (1) both diet items provided together to individual urchins (choice feeding assay), and (2) each diet item provided separately to individual urchins (no-choice feeding assay). Choice and no-choice feeding assays were conducted in a single ~115

L aquarium at Montclair State University as described above. For the experiments, individual *A. punctulata* were enclosed with a known mass of kelp and/or turf species in replicate ~500 mL plastic containers with lids. The containers had 5 x 4 cm (L x W) holes excised in two sides that were covered with 500 μ m plastic mesh to allow ample water flow. Stainless-steel washers were glued with aquarium-safe silicone to the lid of each container to prevent them from floating to the surface during the feeding trials. The three dominant algal turf species (*C. truncatus*, *C. linum*, *G. turuturu*) were massed separately, then combined in equal parts and summed to give a total algal turf mass in the containers for all algal turf treatments (see below) to better replicate field conditions. *A. punctulata* test diameters were measured with calipers (nearest 0.1 mm), and sea urchin mass measured (nearest 0.01g) before transfer to the container (Fig 1 for Trial 1, Fig. 2 for Trial 2). Water temperature in the aquarium was measured hourly during each experiment with an Onset HOBO® Pendant temperature logger.

For the choice individual feeding assay, two trials were conducted (Trial 1: 20–24 August 2021; and Trial 2: 18–20 September 2021), each with freshly collected *A. punctulata*, kelp, and algal turf. In Trials 1 and 2, ~2.5 g of kelp and ~2.5 g algal turf (pat-dry weights) were added together to containers with an individual *A. punctulata* enclosed ($n = 6$ containers). A no-grazer control containing ~2.5 g of kelp and ~2.5 g of algal turf (pat-dry weights) were also placed together in containers without an urchin ($n = 1$ and $n = 3$ containers for Trial 1 and 2, respectively). A single no-grazer control was used in Trial 1, as autogenic changes in algae were expected to be small over the short period of the experiment and cooler water temperature (~20°C). Additional controls were included in Trial 2 to confirm this assumption. Recorded mean (\pm SD) aquarium temperature was $19.6 \pm 0.3^\circ\text{C}$ in Trial 1 and $19.5 \pm 0.3^\circ\text{C}$ in Trial 2. Trials 1 and 2 were intended to last 2 days to minimize autogenic changes in the algae that could obscure grazing effects. However tropical storm Henri led to substantial flooding at and around the University from 21–23 August 2021, which prevented access to the laboratory. Therefore, Trial 1 occurred over 4 days while Trial 2 occurred over 2 days. Nonetheless, these were short periods over which autogenic algal changes (growth or degradation) were expected to be small (~20°C). After 4 or 2 days (Trial 1 and 2, respectively), the remaining kelp and algal turf were massed (pat-dry weights) to determine algal loss over time (g algae d^{-1}).

For the no-choice individual feeding assay, a single trial was conducted from 18–20 September 2021. To assess grazing rates of *A. punctulata* on kelp and algal turf without choice of

diet, either ~5 g of kelp or ~5 g of algal turf (pat-dry weights) was added to containers with an individual urchin enclosed (n = 6 containers for kelp, n = 6 containers for algal turf). No-grazer control containers held either ~5 g kelp (n = 3 containers) or ~5 g algal turf (n = 3 containers) (pat-dry weights) without an urchin to detect autogenic mass changes. Mean temperature in the aquarium was $19.6 \pm 0.3^{\circ}\text{C}$. The no-choice feeding assay occurred simultaneously with Trial 2 of the choice feeding assay (described above). After 2 days, the remaining kelp and algal turf masses (pat-dry weights) were determined to calculate algal loss over time (g-algae d^{-1}).

Statistical Analysis

Kelp mass loss per day was subtracted from algal turf mass loss per day within each container like the methods of Peterson and Renauld (1989). Assuming *A. punctulata* has no diet preference, algal loss attributed to grazing by urchins should be similar between diet treatments. Thus, the difference of kelp and algal turf mass loss with the urchin present and in the no-grazer control replicates should be non-significantly different when statistically compared with a t-test (Peterson and Renauld 1989). Data for Trial 1 were analyzed with a single sample t-test (due to the single autogenic control), while data for Trial 2 were analyzed with a two-sample t-test due to multiple autogenic controls (n=3).

Following the methods of Peterson and Renauld (1989), a 2-way ANOVA was used to test the effect of Diet (2 levels, fixed: kelp and algal turf) and Grazer (2 levels, fixed: grazer present and grazer absent) on algal loss between diet groups. Assuming *A. punctulata* has no diet preference, the interaction term of the 2-way ANOVA (Diet x Grazer) should be statistically non-significant (Peterson and Renauld 1989). The assumption of homogeneity of variance for ANOVA was met for the data ($\alpha = 0.05$, Cochran's C test). Statistical tests were conducted in Statistica and Microsoft Excel.

RESULTS

Choice Individual Feeding Assay: In Trial 1 of the choice feeding assay, the difference in algal mass loss between kelp and algal turf was greater in containers with *A. punctulata* present than in the no-grazer control container (single sample t-test: $t_5 = 2.6$, $p = 0.048$). While there was little difference in kelp and algal turf loss in the no-grazer control (difference = $0.14 \text{ g-algae d}^{-1}$),

there was a difference in kelp and algal turf loss when *A. punctulata* was present (difference = 0.27 ± 0.06 g-algae d⁻¹, mean \pm SE). Specifically in the no-grazer control, kelp loss was -0.03 g-algae d⁻¹ and algal turf loss was 0.01 g-algae d⁻¹. With *A. punctulata* present, mean kelp loss was 0.16 ± 0.04 g-algae d⁻¹ and mean algal turf loss was 0.44 ± 0.07 g-algae d⁻¹, indicating a preference for algal turf over kelp when given a choice of diet (Fig. 3). Similarly, in Trial 2, while there was little difference in kelp and algal turf loss in the no-grazer controls (difference = -0.02 ± 0.01 g-algae d⁻¹), there was a large difference in kelp and algal turf loss when *A. punctulata* was present (difference = 0.17 ± 0.04 g-algae d⁻¹) (two-sample t-test: $t_7 = 3.5$, $p = 0.010$). Specifically in the no-grazer controls, mean kelp loss was -0.02 ± 0.01 g-algae d⁻¹ and mean algal turf loss was -0.02 ± 0.05 g-algae d⁻¹. With *A. punctulata* present, mean kelp loss was 0.09 ± 0.05 g-algae d⁻¹ and mean algal turf loss was 0.39 ± 0.06 g algae d⁻¹, again indicating higher grazing rates on algal turf than kelp when given choice of diet (Fig. 3).

No-choice Individual Feeding Assay: In the no-choice feeding assay, the 2-way ANOVA indicated a statistically significant interaction between the factors diet (kelp versus algal turf) and grazer (present versus absent) ($p = 0.022$) (Table 2). The interaction was due to lower mass loss of kelp versus algal turf, but only when a grazer was present (mean kelp loss = 0.09 ± 0.05 g-algae d⁻¹; mean algal turf loss = 0.39 ± 0.06 g-algae d⁻¹) as compared to when a grazer was absent (mean kelp loss = -0.02 ± 0.01 g-algae d⁻¹; mean algal turf loss = -0.02 ± 0.05 g-algae d⁻¹), indicating higher grazing rates on algal turf than kelp even when no diet choice is provided (Fig. 4).

DISCUSSION

Both choice (Trials 1 and 2) and no choice feeding assay (single trial) measured higher grazing rates on algal turf comprised of three species (*C. truncatus*, *C. linum*, *G. turuturu*) than on *S. latissima* when compared to autogenic controls. These results corroborate field observations of *A. punctulata* grazing small gaps in the turf dominated reef at Fort Wetherill, RI (Feehan et al. 2019). In addition, *A. punctulata* exhibit faster grazing rates on algal turf species than on kelp in both the choice and no choice laboratory feeding assays. Although algal turf is dominant at the collection site, *A. punctulata* in the field have access to both kelp and algal turf species, similar to the choice feeding assay. If field observations that *A. punctulata* were grazing turf algae was

simply due to infrequent encounters with *S. latissima*, then it may be expected for *A. punctulata* given only kelp in the no choice feeding assay to feed at similar, if not faster, rates than urchins given only algal turf. However, there was an interaction between factors diet and grazer, indicating urchins still exhibited higher grazing rates on algal turf species than kelp.

Contrary to other northwestern Atlantic sea urchin species in kelp forests, but absent in Narragansett Bay, which are notoriously voracious kelp grazers (Watanabe & Harrold 1991; Carlsson & Christie 2019), *A. punctulata* does not seem to prefer grazing on kelp. In particular, *S. droebachiensis* grazing dynamics are extremely well documented in the northwestern Atlantic and have driven recurrent ecosystem phase shifts from kelp forests to urchin barrens (Feehan et al. 2012; Scheibling et al. 2020). On the Pacific coast of North America, another urchin *Strongylocentrotus purpuratus* grazes on giant kelp *Macrocystis pyrifera*, whose abundance is closely regulated by intense herbivory and urchin predation (Kenner 1992; Williams et al. 2021). But unlike these species, *A. punctulata* decreased grazing rate on kelp, but increased grazing rate on algal turf, could be a product of their diet preferences in its more southern ranges. Cobb & Lawrence (2005) noted *A. punctulata* consumes macroalgae, despite its carnivorous tendencies, when either animal prey is scarce, or macroalgae is in higher abundance along the coast of Florida and within its range in more equatorial latitudes. Macroalgal species commonly grazed were morphologically similar to algal turf assemblages than fleshy brown kelp species (*Cladophora* spp., *Dictyota* spp., *Ceramium* spp., *Laurencia* spp.) (Cobb & Lawrence 2005). In Narragansett Bay, it is possible that the tougher, less abundant kelp represent a less desirable food source to *A. punctulata* as compared to more familiar algal turf algae species, as *A. punctulata* only co-occur with kelp in a relatively small northern portion of their geographical range.

Although *A. punctulata* grazed more algal turf than kelp in each feeding assay, grazing rates may not necessarily indicate a diet preference, as the differing morphologies between kelp and algal turf species (fleshy vs filamentous, foliose, articulated) influence how efficiently urchins can handle, position, and consume each species. Therefore, a measured difference in grazing rates in a single-diet choice experiment may not indicate a diet preference, but rather a difference in the urchin's ability to consume different algae species (Underwood et al. 2004; Lyons, Devin, Scheibling 2007). Other diet preference studies with urchins frequently standardize diets through creating agar blocks (sometimes in addition to live macroalgae) which helps control for effects of food handling on urchin grazing rates. As this study seeks to understand the role of *A. punctulata*

as herbivores within a turf dominated system, using pieces of live macroalgae, rather than a standardized method, better replicates the conditions within the field. Longer feeding trials, or standardizing diets using powdered algae in agar, must be conducted to determine true diet preference. Whether caused by increased handling efficiency or diet preference, the results from this study suggest *A. punctulata* consumes algal turf at a greater rate than *S. latissima*, which indicates in the field, there is likely greater herbivory pressure on the dominant algal turf in this degraded ecosystem. This implies that *A. punctulata* feeding behavior could represent a positive feedback mechanism, whereby consuming proportionally more algal turf and exposing patches of hard substrate, *A. punctulata* may facilitate increased kelp recruitment in those areas. However, it is likely that natural kelp forest recovery is more strongly determined by staying within certain thermal thresholds, rather than herbivory or direct competition with algal turf species alone (Christie et al. 2019).

Future research should be directed towards clarifying the ecological role of *A. punctulata* in this kelp forest ecosystem in the Northwest Atlantic, as well as investigating how climate change (e.g., increasing marine heatwaves) in this region is influencing algal turf-kelp-grazer interactions. Being a thermophilic species, *A. punctulata* is expected to benefit from rising temperatures and heatwaves in this region (Bojorquez and Feehan 2021), while cold-adapted kelps, such as *S. latissima*, will continue to decline without active intervention such as kelp forest restoration (Coleman et al. 2020). Being a thermophilic Research shows *A. punctulata* fertilization success benefits from increased temperatures during marine heatwaves at their northern range edge (Bojorquez & Feehan 2021), which suggests their populations may expand and increase in their regional importance as grazers. *A. punctulata* may also compensate potential energy deficits following marine heatwave conditions with increased food consumption, as seen in other *Arbacia* species (Hill & Lawrence 2006; Minuti et al. 2021), potentially exacerbating or altering their grazing behavior and ecological influence within both turf and *S. latissima* ecosystems. New research also suggests that increasing ocean acidification may stabilize the dominance of algal turf communities through increased carbon dioxide enrichment, which can lock the community in a low-diversity state from early successional stages (Harvey et al. 2021)

Understanding how *A. punctulata* feeding behavior influences the persistence of algal turf communities is important to predict these ecosystem phase shifts and the future of *S. latissima* at its southern range in the northwest Atlantic. The ability of *A. punctulata* to expose bare substrate

through consuming algal turf can be applied in various kelp restoration methods, such as direct introduction into target areas. Preliminary research for this method has proven successful for a variety of degrading coral reefs, where urchin species were naturally or artificially introduced to remove invasive algal turf, which similarly outcompete corals (Idjadi et al. 2010; Westbrook et al. 2015; Neilson et al. 2018; Humphries et al. 2020). Additionally, a recent kelp restoration technique, Green Gravel, proposes a cheap and efficient method of seeding degraded kelp forests with lab-grown sporophytes (Fredricksen et al. 2020), and these efforts are currently underway in southern New England (CT Sea Grant, 2021). Rearing kelp sporophytes in the lab would also introduce the capacity for selective breeding or genetic modification of more tolerant strains, which might increase kelp survival and recruitment in a warming ocean (Coleman et. al 2020). Therefore, knowledge of how *A. punctulata* herbivory may impede or augment restoration efforts in southern New England is valuable for the best chance of kelp forest restoration success.

TABLES AND FIGURES

Table 1: Laboratory no-choice feeding assay. 2-way ANOVA results for effect of Diet (2 levels, fixed: kelp and algal turf) and Grazer (2 levels, fixed: present and absent) on algal loss (g algae d⁻¹). Significant results at $\alpha = 0.05$ are bolded.

Source	df	MS	<i>F</i>	<i>P</i>
Diet	1	0.094	6.858	0.020
Grazer	1	0.268	19.622	0.001
Diet x Grazer	1	0.091	6.661	0.022
Error	14	0.014		

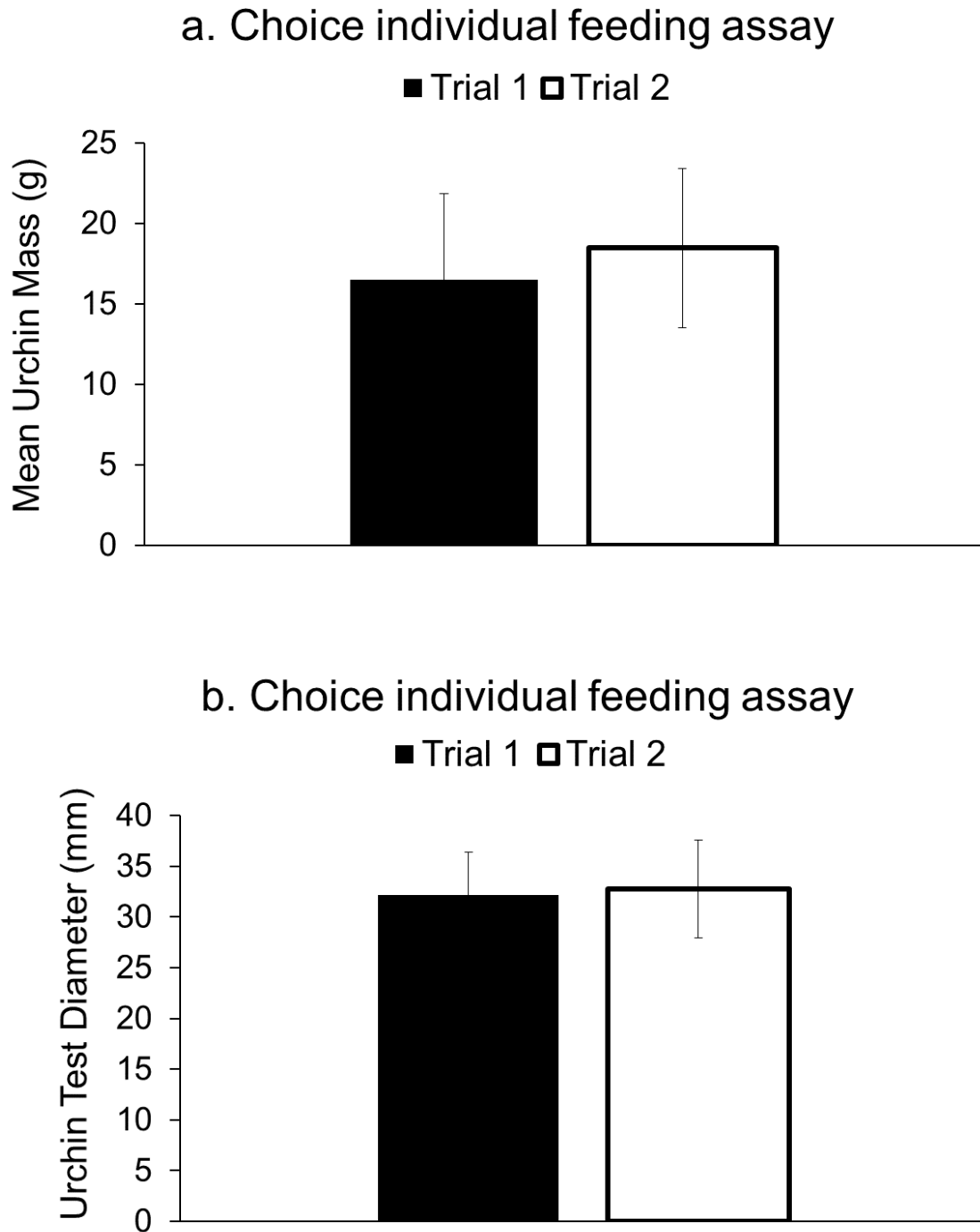
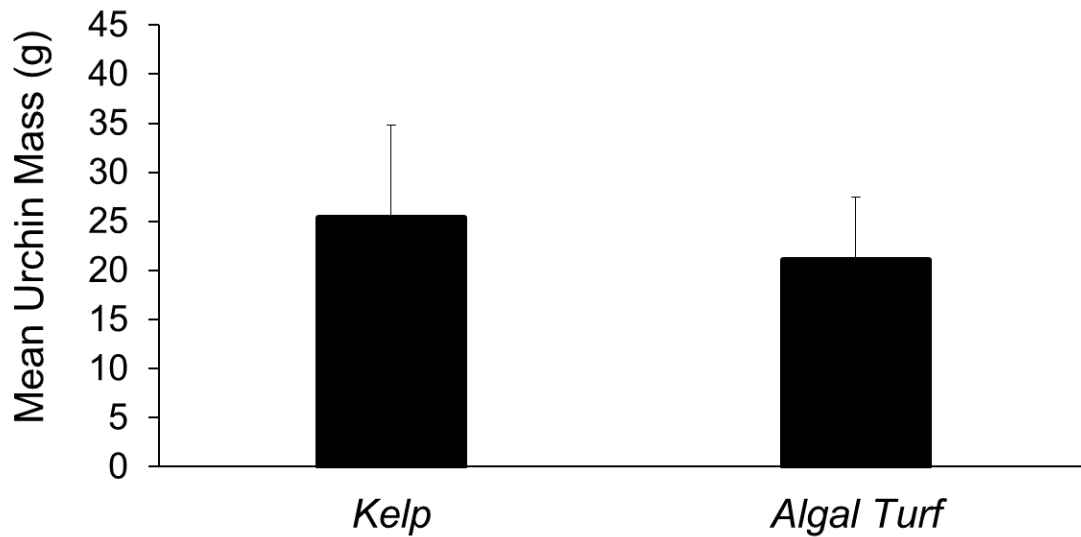


Figure 1. Laboratory choice feeding assay. (a.) *A. punctulata* mean mass to nearest 0.01g (b.) Average test diameter to nearest 0.01mm for Trials 1 and 2. Errors are SE for n=6 containers.

a. No Choice individual feeding assay



b. No Choice individual feeding assay

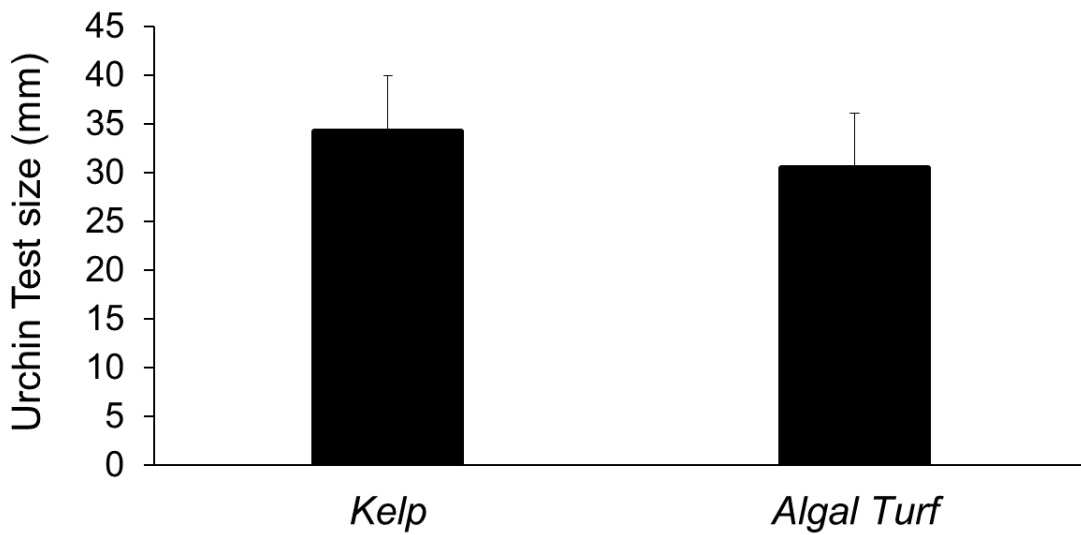


Figure 2. Laboratory no choice feeding assay. (a.) *A. punctulata* mean mass to nearest 0.01g (b.) Average test diameter to nearest 0.01mm for Trials 1 and 2. Errors are SE for n=6 containers.

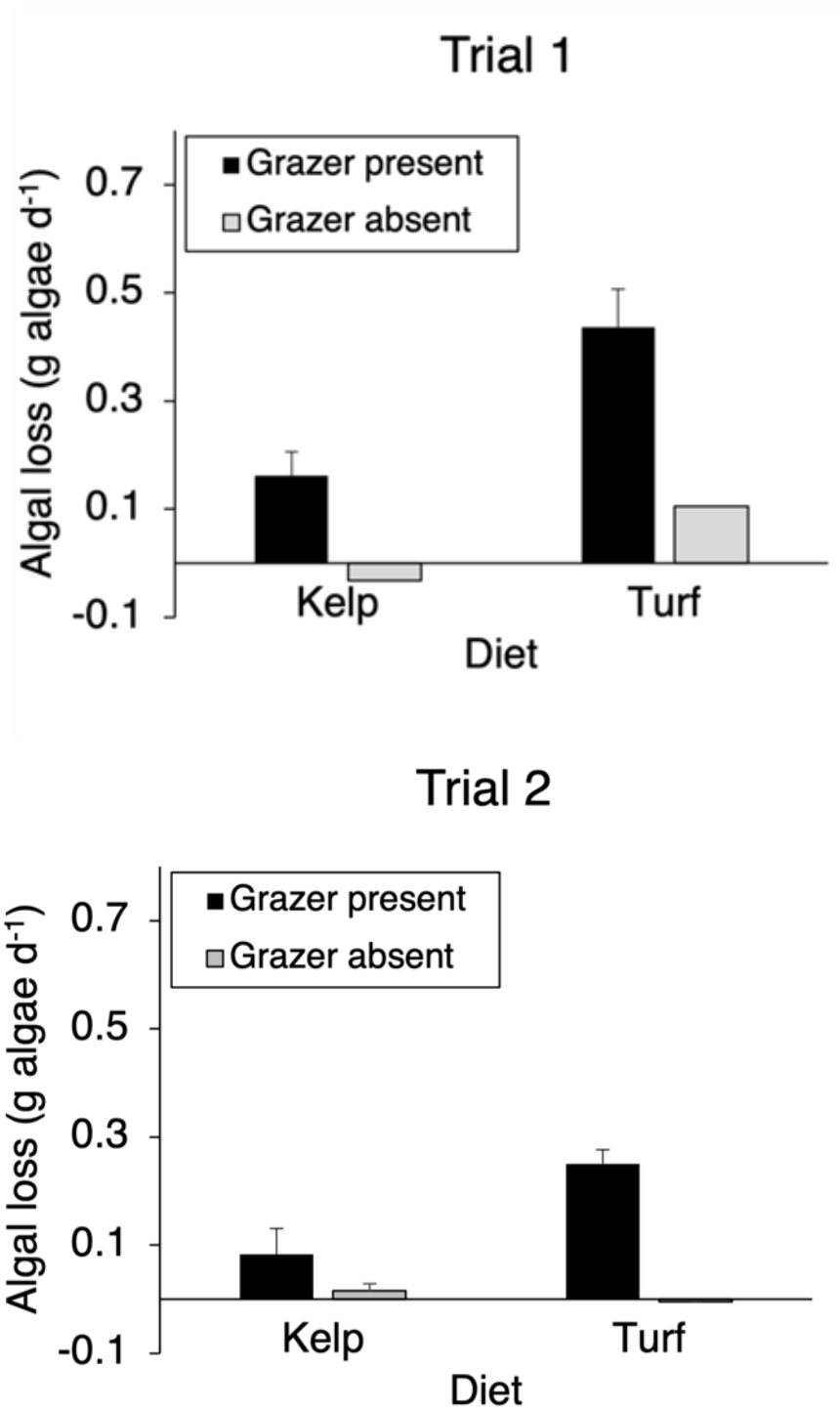


Figure 3. Laboratory choice individual feeding assay. Algal loss of kelp and algal turf (g algae d⁻¹) with *Arbacia punctulata* present and absent over a 4 and 2 day period in Trial 1 and 2, respectively. Errors are SE for n = 6 containers with a grazer present and n = 1 or n = 3 containers (Trial 1 or 2, respectively) with a grazer absent.

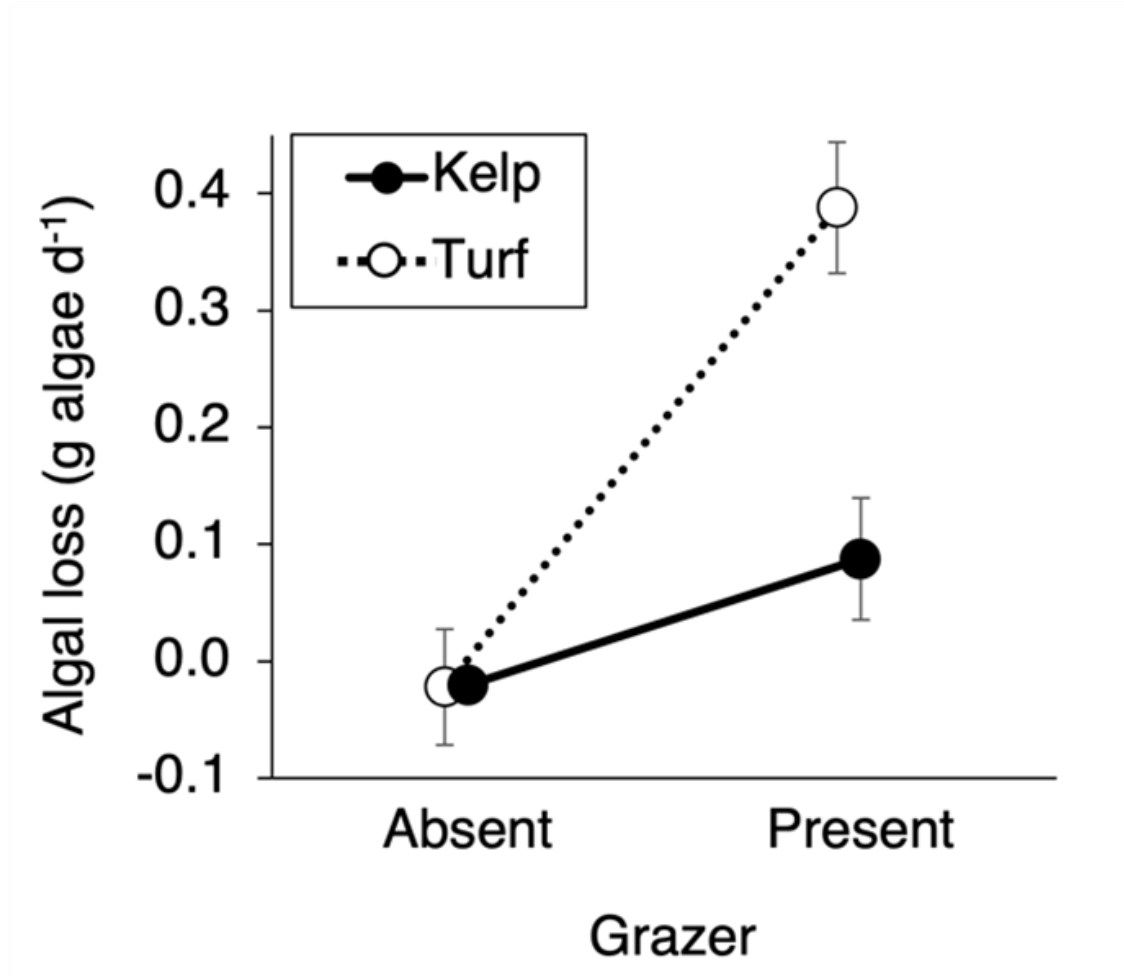


Figure 4. Laboratory no-choice individual feeding assay. Algal loss of kelp and algal turf (g-
algae d⁻¹) with *Arbacia punctulata* present and absent over a 2-day period. Errors are SE for n = 6
containers with a grazer present and n = 3 containers with a grazer absent. A significant interaction
($\alpha = 0.05$) between the grazer and diet treatment is shown ($p = 0.022$) (Table 1).

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