Grazing and residence of the marine gastropod *Lacuna vincta* on cultivated kelp

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Abstract

The marine snail *Lacuna vincta* is a generalist mesograzer that is fouling kelp farms in the northern Atlantic. Often found on the blades of naturally occuring kelp, *L. vincta's* larval dispersal and ability to migrate post-metamorphosis allow it to encounter and settle upon cultivated kelp blades located in the upper water column. Once settled, *L. vincta* graze and lay eggs on kelp, causing losses in profit for some farmers and kelp processors when eggs are too costly or difficult to remove. The patchy distribution of *L. vincta* within and between kelp farms led us to test snail preferences between 1) "healthy" (nutrient-enhanced) and "stressed" (unenhanced) farmed *Saccharina latissima* (sugar kelp) and between 2) farmed *S. latissima* and *S. angustissima* (skinny kelp). We measured grazed area and number of snails residing on kelp between treatments and compared grazing between large and small size classes, though snail size was not tested statistically. Trial 1 in the first experiment and trials 1 and 2 in the second showed significant differences in grazing area while others did not, however there were more snails of the large size class found on both the nutrient-enhanced kelp in the first experiment and on the *S. angustissima* in the second. We also found a strong relationship between the amount of *L. vincta* snails present and the amount of kelp area grazed in both experiments. These results suggest that herbivory preference due to the differences in nutritive content and between *S, lastissima* and *S. angustissima* work alongside many other factors that attract *L. vincta* to some kelp blades and not others. This study contributes to best management practices for farmers when designing kelp farms and choosing which species to cultivate.

Keywords: macroalgae, seaweed, kelp, snail, herbivory, species interactions, grazing

Statements and Declarations

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1. Introduction

The interactions between marine herbivores and seaweeds are complex due to the physical and chemical factors acting on both species in the predator-prey relationship. In areas of the Arctic, Pacific, and North Atlantic coasts, the marine prosobranch gastropod *Lacuna vincta* (family Littorinidae) is a generalist mesograzer that can be found on a variety of macrophytes (and sometimes sea grasses) in the low intertidal and subtidal zones. These snails have a strong preference for kelps, especially sugar kelp, *Saccharina latissima*, partly due to its open and broad shape (Smith 1973; Fretter and Manly 1977; Johnson and Mann 1986). For the kelp *S. latissima,* however, *L. vincta* is the primary, and in some cases, only herbivore to inflict lasting damage to blades (Fralick et al. 1974; Brady-Campbell et al. 1985). *L. vincta* grazing has led to destructive fragmentation of benthic natural kelp beds, and even larger losses of biomass when combined with intense wave energy (Fralick et al. 1974; Krumhansl and Scheibling 2011). Even when *L. vincta* herbivory does not lead to kelp mortality, the snails' preference for feeding on the vegetative margins of kelp blades (where there are fewer polyphenolic anti-herbivory compounds) can cause canopy loss that may affect entire algal communities (Johnson and Mann, 1986).

Biofouling assemblages in kelp farms are often different than those found in natural kelp beds (Corrigan et al. 2024). Effects of *L. vincta* settlement, herbivory, and egg-laying are just starting to be seen amongst kelp farmers in the Gulf of Maine (personal communication, Liz MacDonald, Atlantic Sea Farms Seaweed Supply Director), who currently grow mostly *S. latissima* and, increasingly, its close relative *Saccharina angustissima*, or skinny kelp. Kelp farmers and processors have communicated that the snails are easy to brush off kelp, however their eggs adhere strongly to the kelp blades and are difficult to remove post-harvest. Farmers may harvest early, at the first sign of snail eggs, which results in lower yields of kelp biomass and therefore loss of income. Kelp blades with attached snail eggs cannot always be processed for the highest-value products because extra washing and remediation are costly. Even without the presence of eggs, blades of *Saccharina longicruris* grew significantly less wide than their snail-free counterparts just by *L. vincta* grazing (Johnson and Mann 1986). There is little evidence surrounding the snails' interactions with farmed kelp, which in temperate regions, grows from rope lines suspended two meters below the surface of the water in near-shore subtidal areas. Though kelp farmers are encouraged to situate farms in at least 5.5 m of water at mean low tide to avoid biofouling by benthic organisms (Flavin et al. 2013), *L. vincta* have year-round larval dispersal events and can migrate via currents as post-metamorphic juvenile snails using mucus threading and foot-raising (Lebour 1937; Smith 1973; Martel and Chia 1991b), which allow them to encounter kelp suspended in farm areas. Additionally, the removal of kelp farms in Maine occurs in the spring, when water temperatures are still too cold to support most invertebrate biofouling (Grebe et al. 2019), however *L. vincta* are highly active in winter months (Brady-Campbell et al. 1985).

A challenging issue for kelp farmers on both U.S. coasts is that snail infestations are hard to predict—some farms experience large cohorts of snails settling on their blades while others have very few, possibly a result of farm proximity to currents carrying larvae or to natural kelp beds that host *L. vincta* populations. Within farms, snail distribution is patchy. Gathering information about factors that attract *L. vincta* to settle on some kelp blades and not others may become more important as kelp aquaculture increases in the state of Maine, an industry that has seen an increase to over one million wet pounds of kelp landed during harvest season in 2022 from just 54,000 pounds in 2018, and which continues to rapidly grow (Maine Department of Marine Resources, Robidoux and Good 2023).

Kelp health may affect herbivore preferences for grazing and settlement, either making blades more susceptible to predation or more nutritionally attractive to grazers (Van Alstyne et al. 2009). A proxy often used for assessing kelp health is nitrogen, the most limiting nutrient for coastal kelp growth (Roleda and Hurd 2019). Factors such as water motion, temperature, light, carbon dioxide, and air exposure can all affect kelp's ability to uptake nitrogen (Roleda and Hurd 2019), which can vary within a single farm and growing season (Rugiu et al. 2021). Within farms, there can also be variation in drag and tension due to wave and current directions, storm events, and amount of kelp biomass on grow lines (Fredriksson et al. 2023). This could lead to a variation in stress on the kelp itself, potentially making blades on some areas of a farm more vulnerable to predation than others. In Maine, farm-raised *S. latissima* measured for its C/N ratios have ranged from 9.4 (± 0.7) to 23.4 (± 10.8), with lowest ratios in March and highest in May and June (Grebe et al. 2021a). Results from studies that look at grazing pressure by herbivores as a function of chemical composition have been mixed, due to variations between parts of a kelp blade (Johnson and

Mann 1986), variations between kelp species, and environmental differences from year to year (Van Alstyne et al. 2001; Simonson et al. 2015b).

Saccharina latissima and *S. angustissima* are the most-farmed kelp species in Maine (Maine Department of Marine Resources). While *S. latissima* is common and is distributed widely from ~40°N to ~71°N in the North Atlantic (Wilson et al. 2019), *S. angustissima* is endemic to a small area of Maine's coastline that receives extreme amounts of wave exposure (Augyte et al. 2018). *S. angustissima* was long considered a morphological strain of sugar kelp, however Augyte et al. (2018) showed enough genetic divergence between the two to establish *S. angustissima* as its own species, *Saccharina angustissima*. There is no known research on the feeding preferences of herbivores between *S. latissima* and *S. angustissima*.

The goal of this study was to determine whether there is a difference in *L. vincta* preference between 1) nutrient-enhanced (nutrient-fed) and unenhanced (nutrient-deprived) *S. latissima*, and 2) *S. latissima* and *S. angustissima*. We also consider the grazing impacts of juveniles compared to adult snails. This research contributes to best management practices for nursery managers during kelp cultivation, as well as for farmers deciding which kelp species to cultivate and best locations to apply for farm leases.

2. Materials and Methods

2.1 Substrate preference experiments

Two experiments, each composed of four trials, were conducted to assess *L. vincta* preference between (1) nutrient-enhanced and unenhanced *S. latissima* and between (2) *S. latissima* and *S. angustissima*. Both choice-feeding assays were conducted in laboratory tanks with an experimental design adapted from Chenelot and Konar (2007) (number of replicates, controls, number of snails, and calculation of grazing marks) and O'Brien and Schiebling (2016) (calculation of grazing marks, size of kelp tissue used in experiments, analysis of C/N ratios and polyphenol content). Kelp for all trials in both experiments was cultivated in the Gulf of Maine, USA, from wild-sourced hatchery seed using methods described by Flavin et al. (2013). Except for 2022 trials in Experiment 2 (which was collected in Muscongus Bay, Maine,) all kelp was collected from the same farm, which was positioned east of Ram Island in Saco Bay at an exposed location with a seafloor depth of 15.2 m (43.469779 °N, 70.350026 °W).

2.2 Snail collection and treatment

Lacuna vincta snails for every trial in both experiments were collected by hand from a small cove next to East Point Sanctuary in Biddeford Pool, Maine (43.4449 °N, 70.3398 °W). This site is fully exposed to the Gulf of Maine, however large rocky outcroppings help to break incoming waves and create calmer nooks and tidal pools where a variety of macroalgae species grow and intertidal organisms find refuge. Larger snails (3-6 mm shell length) were used in the experiments conducted in Spring 2022. During Spring 2023, smaller snails (1-3 mm shell length) were used in the experiments to qualitatively evaluate potential differences in snail size class on grazing (Martel and Chia 1991b; Martel and Diefenbach 1993). Snails were collected approximately 48 hours before the start of each trial and kept in a separate container within a 284 L seawater flow-through tank at the University of New England at the temperature of ambient seawater (~10°C). Twenty-four hours before the beginning of a trial, snails were removed from the seaweed in which they were collected (primarily *Ascophyllum nodosum* and some *Fucus distichus*) and moved to a new tank containing only a single piece of *A. nodosum* that was ~0.3 m long. This acclimation period ensured that snails' behavior did not change drastically by the stress of removing all seaweeds, and to prevent their exposure to *S. latissima* before the experiments. Snails were kept in this final tank until the moment they were added to replicate experimental containers.

2.3 Experiment 1: Nutrient-enhanced and unenhanced *S. latissima* treatments

Identical tanks containing 60 liters of deionized (DI) water and enough Instant Ocean Sea Salt to reach a salinity of 32 ppt were brought to a temperature of 10°C using an AquaEuroUSA aquarium chiller (Model MC-1/4HP). Water was continuously pumped through a Pentair 18-watt UV sterilizer (Model EU18P-W). One tank was used for the nutrient-enhanced kelp treatment, and the other for the unenhanced treatment. Approximately 30 fully-grown sugar kelp blades including their holdfasts were collected from the same farm in the southern Gulf of Maine. Half of the blades were placed in the nutrient-enhanced treatment, and the other half were placed in the unenhanced treatment. Feedings of 8 mL each part A and B of Proline F/2 Algae Food were added to the nutrient-enhanced treatment every seven days, while no additional nutrients were added to the unenhanced treatment. Both tanks were kept on a 12/12 h light cycle. Trials began after a 14-day kelp acclimatization period so that there was a significant difference in C:N ratio between treatments (Table 1). A second trial at 21 days was conducted to encourage a wider difference in the nutrient level between treatments.

2.4 Experiment 2: *S. latissima* and *S. angustissima*

For our second experiment, we tested *L. vincta* preference between *S. latissima* and *S.angustissima.* Unlike the first experiment, we were not trying to establish a difference in nutritive content between the two species and therefore no nutrient media was used. Instead, kelp from each species was held in tanks containing filtered seawater and trials were conducted within three days of each other (Table 1). In the first year of trials, *S. latissima* and *S. angustissima* were collected from farms located ~80 km apart and placed into tanks containing filtered seawater within one day. In the second year of trials, *S. latissima* and *S. angustissima* were collected on the same day from the same farm site in Saco Bay.

Table 1 Schedule of treatments and trials for Experiments 1 and 2 in Spring 2022 and Spring 2023. Experiment 1 tested the herbivory preferences of *L. vincta* on nutrient-enhanced and unenhanced *S. latissima*. Experiment 2 tested the herbivory preferences of *L. vincta* on *S. latissima* and *S. angustissima.*

			Days since *S. latissima* introduced to treatment tanks	Snail size class
Experiment 1: Nutrient enhanced versus unenhanced *S. latissima*	Spring 2022	Trial 1: May 11	14	Large (3-6 mm)
		Trial 2: May 18	21	Large (3-6 mm)
	Spring 2023	Trial 3: April 18	14	Small (1-3 mm)
		Trial 4: April 25	21	Small (1-3 mm)

			Days since *S. latissima* and *S. angustissima* introduced to holding tanks	Snail size class
Experiment 2: *S. latissima* versus *S. angustissima*	Spring 2022	Trial 1: June 14	2	Large (3-6 mm)
		Trial 2: June 16	4	Large (3-6 mm)
	Spring 2023	Trial 1: May 4	1	Small (1-3 mm)
		Trial 2: May 7	4	Small (1-3 mm)

2.5 Experimental design

A 272.5 L closed-system tank was filled with filtered seawater which was continuously pumped through a chiller and kept at 10°C. Each of thirteen small plastic replicate containers (23 cm long, 15 cm wide, 13.5 cm deep) was filled with two liters of DI water that had been brought to a salinity of 32 ppt using Instant Ocean Sea Salt and aerated overnight with air stones. The plastic replicate containers were suspended in the larger tank of chilled water so that no water was exchanged, but the water within each replicate could reach and be kept at 10°C. A 5.08 cm^2 "punch" was used to cut 13 identical squares of kelp from each treatment. To distinguish the kelp squares, notches were cut in different areas of the tissue for each treatment before placing in replicate containers. Once completed, each replicate contained one square of each treatment (Fig. 1). Twenty snails were released at the same time into the center of each container through a small length of PVC, thus beginning each trial. Each trial lasted 24 hours once snails were introduced.

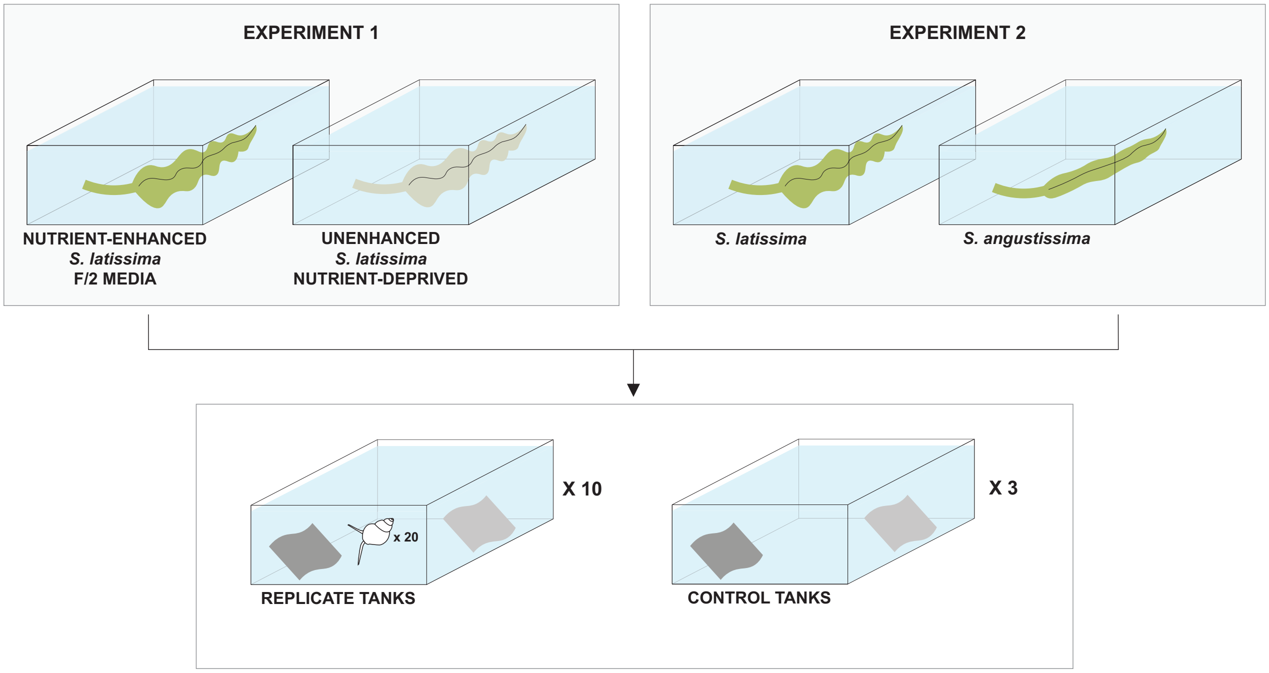

Fig. 1 Experimental design for *L. vincta* preference experiments. In the first experiment, treatments were nutrient-enhanced and unenhanced *S. latissima*. In the second experiment, treatments were *S. latissima* and *S. angustissima*. For both experiments, twenty *L. vincta* snails were offered tissue from both treatments in ten replicate containers. Three controls contained no snails. Four trials of each experiment were conducted

2.5.1 Grazing

At the end of each experiment, each kelp square from the ten non-control replicates and three control replicates was photographed on a light board with a ruler (Fig. 2). The grazed area of each kelp square was then calculated from the photograph as a percentage of total area using a combination of Adobe Photoshop (to adjust image contrast and highlight grazed medulla areas against darker cortex) and ImageJ software (to measure total area of grazing marks).

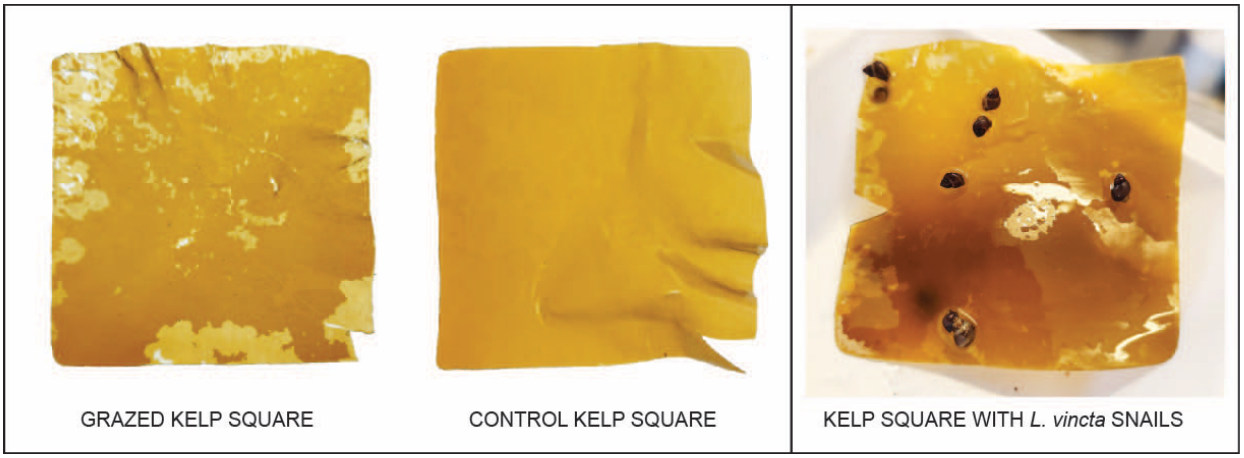

Fig 2 From left to right: Example of a grazed kelp square from a non-control replicate; a square from a control replicate that contained no snails; and a square with *L. vincta* snails actively grazing.

2.5.2 Hourly settlement counts

Trials ran for 24 hours. For 12 of the 24 hours, on the hour, snails were counted. The hours snails were counted varied from trial to trial based on “overnight gaps” which are shown in graphed results (Supplementary Figs. 1 and 2). For each hour, a percentage was calculated from the number of snails on each kelp square divided by the number of living snails. Snail deaths were rare during trials, with only 11 snail deaths out of a total of 1600 snails used, across eight trials over two years (a mortality rate of 0.6%).

2.5.3 Chemical constituents of *S. latissima* for Experiment 1

Individual blades used for snail preference trials were also used for C/N sampling. Three samples from each treatment were prepared and analyzed every week for three weeks. One week before trials began and at the beginning of each trial, three rectangular sections of *S. latissima* from each treatment (nutrient-enhanced & unenhanced) were cut (avoiding the midrib, meristem, and blade tip) and allowed to dry in an oven at 60°C for 48 hours. Dried sections were ground in a mortar and pestle to homogenize each sample, and approximately 4.5 mg of powder from each sample was packaged in a tin capsule. In the first year of trials, kelp tissue samples were sent to the University of New Hampshire Stable Isotope Lab and analyzed on an Isoprime isotope ratio mass spectrometer

(IRMS). In the second year of trials, samples were sent to the UC Davis Stable Isotope facility where they were analyzed on an Elementar vario EL cube elemental analyzer interfaced to an Elementar VisION IRMS. At both facilities, kelp tissue was analyzed for $\delta^{13}C$, $\delta^{15}N$, total carbon, and total nitrogen to determine if there was a significant difference between nutrient-enhanced and unenhanced *S. latissima* treatments.

In our second year of trials (Spring 2023), *S. latissima* was prepared for polyphenol content analysis at the same time as it was being packaged for C/N analysis. Rectangular sections of kelp from each treatment (nutrient-enhanced and unenhanced) were cut (avoiding the midrib, meristem, and blade tip) and allowed to dry in an oven at 60°C for 48 hours. Dried pieces were ground in a mortar and pestle and ≥1.5 g of each sample was packaged in Ziplock bags and sent to Creative Biomart, Inc. for total polyphenol content analysis. For each sample, 0.5 g was weighed, and 10 mL of distilled water was added. The sample was then incubated in a boiling water bath at 100°C for 30 minutes, cooled to room temperature, diluted to 50 mL, and filtered. Total polyphenols were determined using the Folin-Ciocalteu method and quantified using a standard curve of gallic acid. From the filtrate, 1 mL was extracted and to this 1 mL of Folin-Ciocalteu reagent and 3 mL of 7.5% $NaCO_3$ solution were added. The sample was then diluted to 10 mL with distilled water, mixed well, and allowed to develop at room temperature for 30-60 minutes. Absorbance was measured at 765 nm and total polyphenol content was reported as mg/g.

2.6 Statistics

Skewness tests were done for mean paired differences for all continuous data grouped by experimental trial. All trials showed no significant skew ($p > 0.05$). Student's t-tests were used to compare C/N and polyphenol content between treatments. Paired sample t-tests were used to compare treatments within each replicate in all experiments for both percent of kelp squares grazed and the number of snails present on each kelp square after 24 hours. Fully interactive analyses of covariance (ANCOVAs) were conducted to determine the relationship between the percent of kelp squares grazed and the number of snails on kelp squares after 24 hours. To conduct ANCOVAs, all four trials from each experiment were grouped by experiment and tested for normality. Graphs of residuals showed a good model fit with only minor deviation in extreme tails. Counts of snails residing on kelp squares from the final hour only of each trial were used as continuous data for the covariate in ANCOVAs. All statistical analyses were conducted using R 4.1.1 GUI 1.77 High Sierra build using the Rcmdr package version 2.7-1.

3. Results

3.1 Experiment 1: Nutrient-enhanced and unenhanced *S. latissima*

We could not consistently validate a significant difference in C/N between nutrient-enhanced and unenhanced *S. latissima* until kelp blades had been in treatment tanks for 14 days, at which point trials began. We saw a significantly lower C/N ratio in our nutrient-enhanced *S. latissima* in the first (paired t-test, t = -5.6, df = 4, p <0.01), second (paired t-test, t = -4.71, df = 4, p <0.01), third (paired t-test, t = -3.5, df = 4, p <0.05) and fourth (paired t-test, t = -6.5, df = 4, p <0.01) trials (Fig. 3). On average, C/N ratios were 40% lower in *S. latissima* from our nutrient-enhanced treatment tank than from our unenhanced treatment tank. The average total polyphenol content for nutrient enhanced *S. latissima* (n = 6) was 1.92 ± 0.087 mg/g (SE) and for unenhanced *S. latissima* (n = 6) was 2.07 ± 0.048 mg/g (SE). No significant differences were found in polyphenol content between our nutrient-enhanced and unenhanced *S. latissima* treatments in trials 3 and 4 (Student's t-test, t = 2.2, df = 10, p = 0.16), however sample sizes were small and require more replication to draw conclusions. Due to the lag time of analysis of polyphenol content, we were unable to verify or select for polyphenol content of kelp prior to the start of each trial.

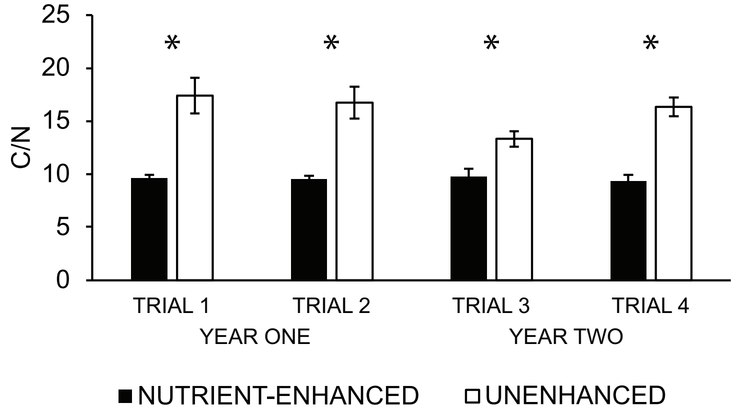

Fig. 3 C/N of nutrient-enhanced and unenhanced (nutrient-deprived) *S. latissima*. Trials one and two are from Spring 2022, and trials 3 and 4 are from Spring 2023. Asterisks indicate significant differences between treatments (p <0.05). Mean ± SE

There only significant difference in grazing marks between nutrient-enhanced and unenhanced *S. latissima* was found in the first trial of Experiment 1 (paired t-test, t = 5.10, df = 9, p <0.001). On average there was 102.6% more area grazed by *L. vincta* on the nutrient-enhanced than unenhanced *S. latissima* squares in the first trial. There were no significant differences found in the remaining trials (p >0.05) (Fig. 4a). After twenty-four hours, we counted on average 80.67% more snails on nutrient-enhanced kelp than unenhanced *S. latissima* in the fourth trial, but this was the only trial where we saw a significant difference (paired t-test, t = 2.30, df = 9, p <0.05) (Fig. 4b). There was only one instance (in trial 2) where overall average snail preference changed over the course of the day (Supplementary Fig. 1). Kelp squares in our control replicates had no grazing marks or evidence of any other damage on their surfaces.

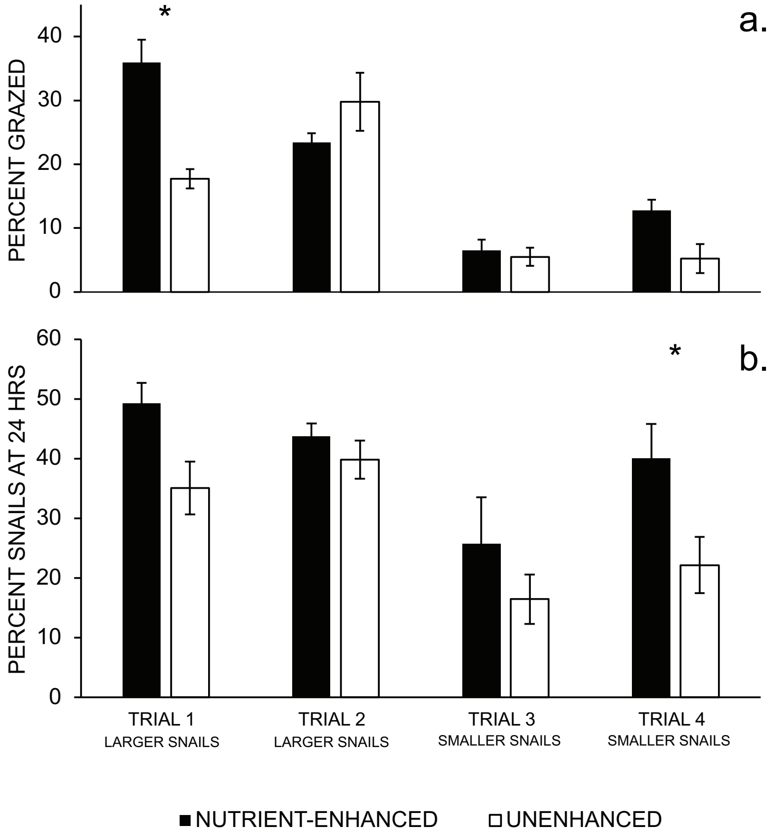

Fig. 4 Bars show (a) percentage of *L. vincta* grazing marks on total surface area of nutrient-enhanced and unenhanced *S. latissima* squares and (b) percentage of *L. vincta* snails on nutrient-enhanced and unenhanced *S. latissima* squares after a twenty-four-hour period. Trials 1 and 2 utilize the same kelp crop from Spring 2022, trials 3 and 4 utilize a kelp crop from Spring 2023. Asterisk indicates trials with a significant difference between treatments from paired t-tests (p <0.05). Mean ± SE

An interactive ANCOVA model for Experiment 1 shows that the percentage of snails on each *S. latissima* square after 24 hours had a significant effect on the percent area grazed throughout all trials (df = 1, F = 38.78, p <0.0001) (Table 2). This relationship is seen in paired t-tests from trials 1 and 4 comparing snail preference for nutrient-enhanced versus unenhanced *S. latissima* (Fig 4a, b).

Table 2. ANCOVA table for fully interactive model of percent area of kelp grazed as a function of treatment (nutrient-enhanced and unenhanced *S. latissima*) with percent snails on kelp at 24 hours as covariate.

	SUM OF SQUARES	**df**	**F**	**p**
Treatment (nutrient-enhanced & unenhanced *S. latissima*)	0.000	1	0.0003	0.986
Percent snails on kelp at 24 hours	0.462	1	38.78	<.0001*
Treatment x percent snails on kelp	0.0080	1	0.6711	0.415
Residuals	0.906	76		

3.2 Experiment 2: *S. latissima* and *S. angustissima*

Differences in percentages of kelp grazed between *S. angustissima* and *S. latissima* were not significantly different in trials 3 and 4. There was significantly more grazing on *S. angustissima* than on *S. latissima* in the first trial (paired t-test, t = -3.05, df = 9, p = 0.014) and second trial (paired t-test, t = -2.6, df = 9, p = 0.029) (Fig. 5a). On average, we saw a little more than twice as much grazing on *S. angustissima* than *S. latissima* in trial 1, and 90.82% more in trial 2. After twenty-four hours we saw no significant differences in the amount of snails on *S. angustissima* and *S. latissima* blades in trials 2, 3 and 4. We counted significantly more snails on *S. angustissima* than on *S. latissima* in trial one (paired t-test, t=-2.71, df=9, p<0.05). Over the entire 24-hour period, patterns in counts of *L. vincta* show a consistently higher average preference for *S. angustissima* than *S. latissima* in trial 1 (Supplementary Fig. 2).

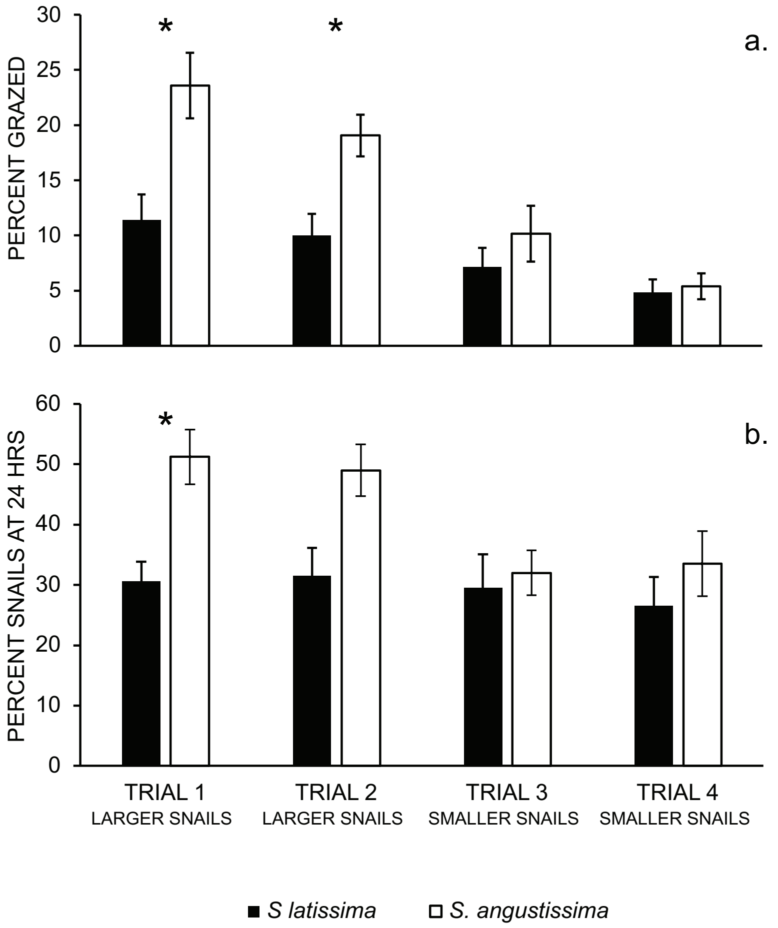

Fig. 5 Bars show (a) percentage of *L. vincta* grazing marks on total surface area of *S. latissima* and *S. angustissima* squares and (b) percentage of *L. vincta* snails on *S. latissima* and S. *angustissima* squares after a twenty-four-hour period. Trials 1 and 2 utilize the same kelp crop from Spring 2022, trials 3 and 4 utilize a kelp crop from Spring 2023. Asterisk indicates trials with a significant difference between treatments from paired t-tests ($p < 0.05$). Mean ± SE

An interactive ANCOVA model shows that the number of snails on each kelp square had a significant effect on the percent area grazed throughout all trials for *S. angustissima* versus *S. latissima* ($p<0.0001$) (Table 3). More of the snails counted on the *S. angustissima* squares appeared to have been actively grazing upon it, supporting significant findings from trials 1 and 2 (Fig 5).

Table 3. ANCOVA table for fully interactive model of percent area of kelp grazed as a function of treatment (*S. angustissima* and *S. latissima*) with percent snails on kelp after twenty-four hours as covariate.

	SUM OF SQUARES	**df**	**F**	**P**
Treatment (*S. latissima* & *S. angustissima*)	0.00313	1	0.9295	0.34
Percent snails on kelp	0.267	1	79.40	<.0001*
Treatment x percent snails on kelp	0.0105	1	3.122	0.081
Residuals	0.256	76		

4. Discussion

Lacuna vincta snails are mesograzers which means they both graze upon and inhabit kelp, often in dense numbers (Chavanich and Harris 2001). Overall, we were able to show a strong relationship between percentages of kelp grazed and percentages of snails present, indicating that snails in our experiments were actively grazing upon the kelp offered, to varying degrees. When increasing resolution to look at trials separately, however, we did not see consistent significant differences in either experiment.

In Experiment 1, only half of the trials show that *L. vincta* have a significantly greater preference for nutrient-enhanced *S. latissima*, either as a food source or for other reasons. Our trials were too short to test for snail egg-laying. However Woods & Podolsky (2007) showed that the egg masses of *Lacuna spp.* rely on their macrophyte hosts as a primary oxygen source. In trial 4 of our first experiment, the significant percentage of snails that were counted on the nutrient-enhanced kelp blades may have chosen them for reasons other than herbivory. Since nitrogen deficiency affects photosynthesis (Mu and Chen 2021), the byproduct of which is oxygen, it is possible that higher oxygen output was an attractive feature of the nutrient-enhanced kelp blades for *L. vincta*. There is not enough consistent evidence to suggest that significant differences in snail preferences can be attributed to the kelps' nutritive content.

Kelp has some chemical defenses against grazers, such as the polyphenolic class of bioactive compounds known as phlorotannins, which are specific to brown algae and have been associated with many applicable functions and characteristics, such as anti-microbial and anti-fungal activity, as antioxidants, as protection from cancer and UV radiation, and more (Kumar et al. 2022). The role of phlorotannins in the thallus of brown algae have been well-studied as anti-herbivory chemical defenses against marine herbivores, however no assumptions should be made about the phlorotannin content of individual kelps because they can vary widely amongst populations (Toth and Pavia 2002), species (Duffy and Hay 1994; Pavia and Toth 2000), parts of the kelp plant (Johnson and Mann 1986; Toth and Pavia 2002), plant access to light and nutrients (Pavia et al. 1999; Pavia and Toth 2000), and between natural and lab-kept plants (Toth and Pavia 2002). Because these chemical defenses are costly to a plant, this variation in phlorotannin content has been attributed to a how a particular kelp allocates its energetic resources, its relationship with its primary grazers, and other environmental factors (Van Alstyne 1988; Hay 1996; Pavia et al. 1999).

Results from our polyphenol content analysis were not statistically significant, likely due to variation between kelp blades and small sample sizes. Our total average polyphenol content was lower than we found in other research (Roleda et al. 2019), however kelp polyphenol levels are typically low in the spring (Schiener et al. 2015) and the Gulf of Maine in 2023 saw below-average levels of nitrates, which can significantly affect phenolic content of seaweeds (Toth et al. 2020). With a longer-lasting experiment and more samples, we expect total polyphenols to decrease as kelp's nutritive content decreases (Targett and Arnold 1998). Generalist mesograzers are hypothesized to be more tolerant of secondary metabolites in plants than large herbivores because they rely on the plants for habitat, are less mobile than larger herbivores and can potentially sequester the plants' toxins to deter predators (Duffy and Hay 1994). Van Alsytne et al. (2009) found that *Littorina sitkana,* a littorinid snail in the Pacific Northwest, preferred to consume algae with higher nitrogen content despite greater amounts of the anti-herbivory chemical dimethylsulfoniopropionate (DMSP), suggesting that some littorinid snails may overlook distasteful chemicals in the presence of high nutritional content. Johnson and Mann (1986) were able to correlate the areas of highest polyphenol content in the bodies of *S. longicruris* blades, the meristematic region, with the least amount of snail grazing. Additionally, they correlated the greatest grazing damage to areas of the kelp, the frilled margins, with the highest nutritional quality (Johnson and Mann 1986). Since we standardized our experiment by only offering snails sections from the vegetative tissue close to the margin of kelp blades, we can be confident that we eliminated most variation in nitrogen and polyphenol content attributable to spatial differences in the plant's body. Testing *L. vincta* preference for different parts of the kelp blade in a future experiment, however, may provide insight for farmers on possible strategies for optimizing harvest of the best quality kelp, with the least amount of biofouling. For example, trimming the often fouled distal-ends of kelp blades during the growing season can lead to reduced risk of biomass lost during storms (Grebe et al. 2021b) and be a potential solution for limiting fouling by snails and other epibionts (Corrigan et al. 2023). A larger-scaled and longer-lasting experiment that tracks polyphenol content as a function of kelp nutritive content due to nitrogen degradation over time would help elucidate results in our nutrient-enhanced versus unenhanced *S. latissima* experiments.

The abiotic conditions of the area in which a farm is located have implications for farmers when it comes to the nutritive and chemical contents of kelp tissue. Seaweeds can launch chemical defenses when being grazed upon by herbivores (Van Alstyne 1988) which may be affected by adverse conditions. For example, the brown seaweed *Dictyota ciliolata* had lower levels of secondary metabolites and was more susceptible to amphipod herbivory after being subjected to one hour of desiccation (Cronin and Hay 1996). Ocean acidification can cause loss of kelp thallus strength by lowering the amounts of structurally important magnesium and calcium (Kinnby et al. 2023). This in turn can have cascading effects on a kelp community when blades are also exposed to grazing damage by herbivores like *L. vincta* (Duggins et al. 2001; Krumhansl and Sheibling 2011). Continuous exposure to seawater temperatures of 14°C and above causes strength reduction in the tissues of *S. latissima* (Simonson et al. 2015a) and in another study *L. vincta* showed no change in preference for *S. latissima* that had been previously held in 21°C seawater treatments (Simonson et al. 2015b). This suggests that *L. vincta* will continue to graze upon kelp that is experiencing lethal or sublethal seawater temperatures, likely exacerbating those deleterious effects. Monitoring of environmental conditions could provide clues for kelp farmers about the stressors affecting kelp sporophytes and how grazing damage by *L. vincta* might impair yields or quality during harvest.

Lacuna vincta's distribution is influenced by algal morphology, which may explain their grazing preference for *S. angustissima* in trials 1 and 2 of Experiment 2 (Fig. 5a). A study off the west coast of Norway (Christie et al. 2007) found that structurally different synthetic algae mimics (bushy, rough, and smooth) placed in an existing natural kelp canopy attracted different fauna. *Lacuna vincta* were found in significantly larger numbers on the broad smooth mimics, suggesting that the habitat architecture of the seaweed is an important factor for this species' recruitment. When comparing two densities (20 sporophytes m^{-1} and 60 sporophytes m^{-1}) of synthetic mimic *Alaria esculenta* fronds on a farm grow line in Ireland, Walls et al. (2017) found significant differences in epibiont community assemblages, which included the presence of *L. vincta*. Other research suggests that *L. vincta* distribution pattern is dictated by the density of snails on a given kelp blade, which when too high, causes snails to migrate to another species (Johnson & Mann, 1986). We chose to offer *L. vincta* small squares of kelp tissue to limit chemical or physical variations between parts of the sporophyte, however snail density may have influenced snail movement within each replicate mesocosm in our experiments. Several studies have found that an individual snail's body size combined with current velocity is partly responsible for settlement and movement in *L. vincta* populations, and that, in some cases, movement to more favorable algal communities or areas of a kelp sporophyte may be a decision on the part of the snail, especially in areas with low water current velocity where snails are not easily dislodged (Martel and Diefenbach 1993; Duggins et al. 2001). We designed our experiments to eliminate factors related to habitat architecture, density, and water movement, however it is likely that more significant differences in snail preference between *S. latissima* and *S. angustissima* would be found on a kelp farm in the ocean. *S. angustissima* blades are much narrower and more strap-like than *S. latissima*, and as a result, move differently in water currents and have less surface area across the width of the blade. A next step for this research should include a comparison of *L. vincta* fouling between the two species on a kelp farm. This would also have the added benefit of exploring effects of water movement (Visch et al. 2020) and entire biofouling assemblages on farmed kelp, which can both be factors in the herbivory preferences of a single species (Rohr et al. 2011; Walls et al. 2017).

Lacuna vincta prefer to graze on juvenile rather than adult tissues of some kelp (Chenelot and Konar 2007) suggesting that "toughness" of plant tissue may be an important factor in the snails' grazing preference (Steneck and Watling 1982; Johnson and Mann 1986; Chavanich and Harris 2001; Molis et al. 2015). Because we outplanted all our kelp at the same time and standardized tissue excision, snails were never offered juvenile kelp tissue, however, due to the strap-like shape of *S. angustissima*, we expected to see snails overwhelmingly prefer the thinner and potentially easier-to-graze tissue of *S. latissima*. Plasticity in feeding preference of another Littorinid snail, *Littorina obtusata,* followed plasticity in algal tissue toughness that was taken from areas with intense wave exposure (Molis et al. 2015). *Lacuna vincta* can produce ~3 new rows of teeth every day (Padilla et al. 1996) and exposure to different food sources changes the development of their radular morphology (Padilla 1998). In trials 1 and 2 of Experiment 2, it is possible that the *L. vincta* of the larger size class had a recent history of feeding on a macroalgae with tough tissue, thus conditioning their teeth for herbivory of *S. angustissima*. In future trials, a longer holding period for the snails would help to eliminate this possibility. *S. angustissima* morphology has likely evolved due to extreme wave exposure where it is endemic (Augyte et al. 2017; Augyte et al. 2018). On a kelp farm situated in the upper water column, it is possible that *S. angustissima* is better adapted to handle stress than *S. latissima*, conceivably making it more nutritionally attractive to herbivores. A comparison of nitrogen and polyphenol content between *S. latissima* and *S. angustissima* needs to be done to evaluate any differences.

Another potential reason we saw less overall grazing in the second year of Experiment 2 is timing (Fig. 5, trials 3 and 4). Trials in our first year took place during the second week of June, but in our second year, trials were conducted in the first week of May (Table 1). This difference of ~6 weeks in late spring is a crucial time in the life cycle of both *L. vincta* and kelp, and is the likely reason we see less grazing in our second year. Spawning times for *L. vincta* occur year-round with documented peaks from January to March (Southgate 1981), January to June (Johnson & Mann, 1986), and mid-winter (Martel and Chia 1991a). Larval settlement in natural kelp beds has been documented from June to October (Fretter and Manly 1977), starting in May (Johnson & Mann, 1986), and peaking in spring and late summer (Martel and Chia 1991a). Martel & Chia (1991a) found that metamorphosis from larva to juvenile can occur in as little as 38 days. It is likely that the decline of overall grazing we see here is attributable to larger proportion of smaller size class and likely juvenile *L. vincta* in our second-year trials. In other marine herbivores, total kelp consumption is attributable to body size (Suskiewicz and Johnson 2017). Future research should make *L. vincta* size class a factor within each trial of each experiment, to quantify differences in snail preference that are directly attributable to size and age.

Conclusion

Lacuna vincta is a generalist mesograzer that has been found on a variety of brown, red, and green macroalgae species across many different studies. Until now, there has been no known research into *L. vincta* herbivory preferences of farmed kelp. Because the settlement on and migration to kelp farms by *L. vincta* is becoming problematic for farmers in Maine, it was important to begin investigating the reasons for the patchiness of snails seen amongst and within farms. Where *L. vincta* recruit and settle is a complex combination of biotic and abiotic factors, and more research should be done to disentangle the factors that attract snails to certain kelp blades on farms. We can conclude that the chemical properties of kelp within a farm are not consistently responsible for *L. vincta* herbivory preference in *S. latissima*, however they play a role alongside other environmental factors such as water movement and epibiont assemblages, as well as choices made by kelp farmers, such as sporophyte seeding density and habitat architecture. There is a strong relationship between snail presence and grazing on farmed kelp, and we show that *L. vincta* snails of a large size class have a significant herbivory preference for *S. angustissima*. These considerations will help farmers make informed decisions about where to locate new farms during the leasing process, how best to design layouts for grow lines on farms and which kelp species to cultivate.

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