Decision making and risk in *Strongylocentrotus droebachiensis* in competitive and non-competitive foraging environments

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Abstract

Foraging behavior is known to have drastic impacts across the animal kingdom, from the behavior of vertebrates as well as invertebrates. Green sea urchins (*Strongylocentrotus droebachiensis*) are well known omnivorous echinoderms that display a wide diversity of behavioral responses to chemical and tactile stimuli. Green sea urchins likely consider the stimuli of conspecific presence especially in foraging environments where competition can be high. The foraging behavior, specifically ability to reach a food item, of urchins was examined in four distinct trials with urchins under competitive and non-competitive environments with conspecifics after determining the preferred animal protein. Two trials examined the effect of cover type, and the other two considered urchins with no available cover in different water flow regimes. Overall, urchins competing with conspecifics were faster to reach food than those that were alone. However, when cover was available, non-competitive urchins most often did not reach the food item in the time allotted. Urchins likely weigh the risk and benefits of moving towards high value food with the competitive environment and cover type. These results indicate the importance of considering the conspecific environment in urchin behavioral studies and can have implications for aquaculture.

Introduction

Foraging and predator-prey behavior are known to have wide ranging consequences. These consequences can be within a community, as seen with the classic case studies of the otter-kelp-urchin trophic cascade (Estes and Palmisano 1974) and the Yellowstone wolf reintroduction cascade (Ripple and Beschta 2012). Foraging behavior can also impact local species composition (Hobson and Chess 1986). Large foraging impacts are not a result only of vertebrate behavior, as invertebrates are also known to have significant impacts in both biotic (i.e. Allen et al. 2004, Hanson et al. 1990) and abiotic respects (Nkem et al. 2000). This includes marine invertebrates, namely sea urchins (Estes and Palmisano 1974; Dean et al. 1984). Sea urchins are known to be voracious foragers, forming “fronts” akin to a military phalanx as they consume kelp (Dean et al. 1984; L. Harris personal obsv.), whose impacts are density-dependent on certain algae (Benedetti-Cecchi et al. 1998). These impacts likely arise from complex foraging behaviors, and may impact sea urchin aquaculture.

The green sea urchin *Strongylocentrotus droebachiensis* plays a significant role in north Atlantic subtidal ecosystems, particularly in the Gulf of Maine and Canadian Maritimes where it is the only sea urchin species (Witman et al. 1982; Ojeda and Dearborn 1991; Scheibling et al. 2020), and is also a species of great interest in aquaculture and exploitation (Harris et al. 2003; see review by Eddy et al. 2015) and in many areas, not just North America (McBride 2005). Both in and outside these areas, *S. droebachiensis* is one of the primary grazers in benthic hard bottom communities and at high densities can totally alter community structure (Estes and Palmisano 1974; Breen and Mann 1976; Witman 1985; Steneck et al. 2002; Steneck et al. 2013; Steneck. 2020; Scheibling et al. 2020). While sea urchins are generally considered herbivores, they are omnivorous and do best on a diet that includes animal protein (Briscoe and Sebens 1988; Nestler and Harris 1994; Williams and Harris 1998; Eddy et al. 2015; Scheibling et al. 2020). Additionally, despite being covered in a protective layer of spines, urchins of all species have to

contend with predation as they are important prey in their ecosystems (Estes and Palmisano 1974; Pearse 2006; Fergali et al. 2014). Predators tend to have preferences on the size of prey (Scheibling 1996) and there is a wide range of predators for urchins in the 5 - 25 millimeter size range which includes a variety of taxa, from small-mouthed fish and lobsters to crabs and sea stars (Himmelman and Steele 1975).

In spite of having a simple nervous system with no centralized control center, urchins are sensitive to external stimuli and show active behavioral responses to smells, including active movement to food sources (Vadas 1977; Larson et al. 1980; Mann et al. 1984; Propp 1977; Garnick 1978; Lauzon-Guay and Scheibling 2007; Filbee-Dexter and Scheibling 2014; Scheibling et al. 2020). Since sea urchins have a limited photoreceptor system (though possibly more complex than thought: Ullrich-Lüter et al. 2011), they rely on chemosensory and tactile senses to find food. These systems remain largely understudied and could hold key findings to help better understand benthic ecology (Burke et al. 2006). In addition to *S. droebachiensis*, a number of sea urchin species in both temperate and tropical systems tend to aggregate at high densities, which can have significant impacts on benthic community structure (see review by Steneck 2020). Intraspecific interactions within these aggregations and their effects on feeding behavior are also understudied topics. Though the interspecific effects of sea urchins are wide reaching (see discussion above), understanding intraspecific interactions between urchins may be equally valuable. Little is known regarding sea urchin competition, other than individual growth impacts including inhibition of and asymptotic growth (Grosjean et al. 2011). This is likely due to the dominance of larger urchins within the cohort outcompeting small urchins for food, a behavior that has been well documented in captive urchins (Grosjean et al. 2011). Harris et al. (2003) previously reported that there were often differences in growth rates among groups of small urchins, most likely due to intraspecific competition for food.

During experiments on growth and diet, urchins were maintained in stock cultures for future studies and fed a diet of the kelp *Saccharina latissima*. The recirculating system where the animals were maintained also contained sea anemones in the genus *Urticina* which were fed pieces of cooked mussels (*Mytilus edulis*). During sessions of feeding sea anemones, many of the urchins were observed to become active, which included extending their podia, active crawling up the walls of the tank, and spreading out at the tank surface with the oral side facing upwards. They would immediately accept pieces of mussel tissue and consume them.

The urchins also tended to aggregate in groups associated with kelp blades and even where fragments of mussel shells were present. Aggregation has been suggested to have a defensive function to protect smaller individuals from potential predation (Tegner and Dayton 1977; Garnick 1978; Bernstein et al. 1981, 1983). Aggregation may function to hold larger food items to facilitate feeding for groups of individuals, though Nishizaki and Ackerman (2004) found that small urchins did not appear to benefit from aggregations with larger urchins. Urchins also tend to hold inanimate objects like shell fragments on their aboral surfaces, which may have a defensive function (Dumont et al. 2007). Cover, competition, and the general environmental context, likely impacts foraging behavior.

These observations of behavioral responses to animal protein and of aggregating behavior also matched similar patterns consistently observed in the field; this suggested that aggregated urchins would be more responsive to food stimuli than solitary animals. Secondly, we expected that animals with cover and/or a food source would have different responses to an external food source than animals with no food or cover. These hypotheses formed the basis for the studies described below.

Methods

Strongylocentrotus droebachiensis individuals were collected from a subtidal ledge in Gosport Harbor just off Smuttynose Island at the Isles of Shoals on the Maine and New Hampshire border. The animals were maintained in a recirculating sea water system that consisted of two rectangular tanks connected to the same reservoir and pumping system in Spaulding Hall at the University of New Hampshire. Water temperature was maintained at approximately 10°C and salinity was kept at approximately 32o/oo by the addition of deionized water as needed. The input pipes for the tanks were at one end of each sea table and the stem pipes for water exit were at the opposite ends so there was a unidirectional flow. The urchins were fed blades of the kelp *Saccharina latissima*, *ad libitum*. Accumulated fecal pellets were siphoned from the system approximately weekly and the filter bag was changed as it became clogged. When preparations for the experiments described in this study were underway, anemone cultures were transferred to another recirculating system.

Prior to initiating the experimental trials, urchins were offered both raw shrimp and cooked mussel tissue at a distance to determine which elicited the quickest and most active response. The diet that resulted in the fastest reaction amongst the urchins was raw shrimp so it was used in all trials. Once urchins were selected to be used for an experiment in the tank, they were only fed meat during trials and had access to kelp at all other times. Any kelp that may have been removed before conducting the trials was replaced after each trial was finished. Four sets of trials were conducted over a period from February 2019 to March 2020.

During the Spring 2019 semester, urchins were attempted to be trained. As stated previously, through anecdotal evidence, urchins in captivity travel to the top of their holding cages when olfactory cues enter the water. Urchins often present their Aristotle's lantern in preparation for food. We wanted to see if this behavior could be replicated for aquacultural purposes. Small mesh bags full of raw shrimp were suspended on the sides of the urchin holding cages (Figure 1a). Anytime an urchin scaled the wall of its holding cage and reached the small mesh bag, it was rewarded with a piece of shrimp. Going along with this reward system, anytime urchins were seen at the surface of the water presenting their Aristotle's lantern, they were rewarded with shrimp. Statistical analyses were not performed during this study seeing that the data was qualitative in nature.

Trial 1: Six circular mesh cages (diameter 15 cm, height 11 cm) were set up in the recirculating system (Figure 1a). Three cages contained 5 urchins (20 to 25 mm in diameter) and three cages contained a single urchin of similar size. At the beginning of each trial, urchins were aggregated at the down current

end of the cage and a piece of raw shrimp in a mesh bag was attached to the opposite wall of each cage. Once the shrimp entered the water, the urchins were closely observed to see how fast they extended their podia. The extension of podia was deemed a reaction to the olfactory cues entering the water. The urchins were also timed to see how long it took for the first urchin in the competition cages to reach the shrimp and how long it took the isolated urchins to reach the food. Urchins were given a maximum of 30 minutes to reach the bait, if they did not touch the shrimp with their podia in that time frame, this was recorded as a "termination." In this initial experiment six trials were run on different days with only one trial run each day. A shorter experiment to see if competition was the critical factor involved selecting one of the five urchins in the group cages and isolating it as a solitary urchin and the solitary urchin was placed in a cage with four other urchins that were smaller so the experimental animals could be identified (referred to as the "switch" experiment). The trials were then repeated to see if the former isolated animals performed as the aggregated animals had and if the newly isolated animals reacted as the original isolated animals had. This trial was ran in the Spring of 2019, but the end of the semester limited the reversal trial to only three runs.

Trial 2: In the second half of Fall, 2019, the competition experiment from Trial 1 was repeated, but the cages were changed to solid rectangular plastic Sterlite boxes (15 x 27.5 cm), with vexar mesh covering square holes cut in each end to maximize the directional flow, though distance from end to end was longer (15 cm diameter vs 27.5 cm length) (Figure 1b). These raceways also ensured that the food item's chemical signature reached the urchins, and the urchins were being stimulated by only the food item in that cage. The trials were similar to trial 1, in which 5 urchins and one urchin were tested for response times to introduced pieces of raw shrimp. There were eight runs for this repeat of Trial 1. Unlike Trial 1 the time for each replicated raceway was recorded. If no urchin in a raceway reached the shrimp in a 25 minute time period, that replicate was recorded as terminated.

Trials 3 and 4: Trial 3 was the first of two "cover" trials, completed from September to middle October 2019. During these trials, pieces of kelp were left in each tray as cover and as an alternative food source. There were 8 of these trials. Aside from the kelp, these trials were run with the same procedure as Trial 2. Five of these trials were run with two replicates each and the last three with three replicates when all plastic boxes had been fabricated. Trial 4 was similar to Trial 3 and took place the middle of November and into spring 2020, with a 6-week break in December and January; all trials ended in March of 2020 when the university moved to remote operations due to the COVID-19 pandemic. Mussel shell fragments were added to each cage to see if the presence of cover would alter the response times of urchins to food. Kelp was removed as much as possible prior to each run to ensure that physical structure was the lone variable; not another food source. The mussel shell-based trials were run 15 times.

We included in analysis only twenty-three no cover-trials for the solo urchins, and only 44 mussel shell trials for the solo urchins because the other trials were eliminated from analysis due to the following: One urchin stopped and retreated when a small amount of water splashed into its tank as it moved towards the shrimp (no substrate trial, Trial 2). A second did not have an equal distance to cover towards the

shrimp (mussel shell trial, Trial 4), as during the trial, the water flow had moved the shrimp part of the way down the tank.

Analyses: For each trial, the data was averaged for the amount of time it took for at least one urchin in the competitive environments, and a solo urchin in the isolated environments to reach the bait. In JMP, one-way ANOVAs were run for the times it took for the urchins to reach the bait. In Trials 2, 3, and 4, “reaching” was considered an urchin being in contact with the shrimp through podia contact. Student’s T tests were run for pairwise comparisons when applicable; otherwise, an ANOVA/pooled t test was used to understand significance. Across all trials, ANOVAs produced results with $p = x$, and t tests produced $\text{Prob} > F = x$.

Results

When shrimp was introduced to the system, *Strongylocentrotus droebachiensis* individuals projected their tube feet immediately. The crushed mussel did elicit the same response, but the response was not as pronounced as that produced with shrimp. Therefore, shrimp was the bait of choice for all trials. The initial trials were in cylindrical mesh cages that had less consistent flow regimes than the solid trays used in Trials 2-4, but the pattern of urchin responses was consistent in all 4 trials. There were some urchins that did not move or reach the food in the time allotted and those cases were labelled a “termination”. In Trial 1 only the first urchin in each treatment to reach the food was recorded while the times for all replicates were recorded in Trials 2 to 4; an analysis of the first urchin was done for these last trials as well to compare to Trial 1.

Trial 1: The results in all six runs in Trial 1 were consistent with grouped urchins tending to move to food faster than the solitary individuals (Figure 2). This pattern was similar when the solitary urchin was placed with four other urchins and the isolated urchin from the group treatment tended to take more time. The urchins under competition settings showed significantly faster reach times in all trials ($p = 0.0066$). However, the treatments did not differ significantly in terms of reaction time ($p = 0.2328$). The average reaction time for the competition urchins was 10 seconds, and the average reach time for the competition urchins was 3.45 minutes. For the solo urchins, the average reaction time was 18.30 seconds, and the average reach time was 9.78 minutes (Figure 2). The switch analysis resulted in one termination in one of the competition treatments. The solo urchins were slower than the competition urchins. The average reaction time for the competition urchins was 11 seconds, and the average reach time was 9.30 minutes. The average reaction time for the solo urchins was 21 seconds, and the average reach time was 20.30 minutes. However, since only three runs were conducted for the reversal trials, it was not possible to conduct statistical tests and the results only confirm what the other trials demonstrated.

Over the course of the trial, several behaviors were documented. More competition urchins began to climb to the tops of the cages as time progressed. This climbing behavior was not seen in the solo urchins. Intraspecific interactions were noticed in the competition cages with urchins fighting over pieces of

shrimp during the trials. Some of the urchins would pick up detritus from the bottom of the cages with their tube feet and use it to create a barrier against other urchins while eating a piece of shrimp.

Trial 2: Trial 2 was a repeat of Trial 1 but using the revised containers. While aggregated urchins were quicker to the shrimp, the solo urchins reacted more quickly than that seen in Trial 1. On average, solo urchins took 8.13 minutes to reach the shrimp, while competition urchins took only 6.57 minutes. This time difference was not significant ($\text{prob} > F = 0.2871$). Although, these means were out of all three replicates by the total trials, unlike the first of the three replicates to reach the urchin as in Trial 1. For comparison, we calculated these means and ran a respective t-test (solo mean=4.38 minutes, competition=4.88) that showed an insignificant difference in time (0.63824). However, three individual trials of the total eight run (by three replicates) for the competition urchins were terminated due to the urchins exceeding the time limit. No solo urchin trials were terminated. One trial was removed from solo urchin analysis; the urchin had made the way partway to the shrimp but then retreated due to water dripping into the tank.

Trial 3: In Trial 3, urchins that had pieces of kelp tended to hide under the kelp and in general were slower to respond to food. A greater time difference was seen in the solo urchins, which took 12.75 minutes versus the competition 9.12 minutes to reach the shrimp (Figure 4). This difference was not significant ($\text{Prob} > F = 0.3018$). That said, this value for solo urchins was generated from a sample size of four. A high termination rate led to 78.9% of solo urchin trials being terminated while only 2, or 10.5% of the competition trials were terminated (Figure 5).

Trial 4: The most distinct behavioral observations were in Trial 4, perhaps because of the small size of the mussel shell fragments. Many of the urchins would hold the shell fragments over their bodies, even picking up shells midway to shrimp, and they too tended to respond slower to the food stimulus. Solo urchins were frequently observed to entirely cover their bodies with shells and not strongly respond. Termination rates were high (Figure 5), as over 60% of trials were terminated for the solo urchins and 20% for the competition urchins. When the urchins did run, solo urchins took longer at 11.41 minutes, and competition urchins took only 7.75 minutes to reach the shrimp (Figure 4). This difference was significant ($\text{Prob} > F = 0.0237$). One trial was also removed from the solo urchin analysis here: water flow had pushed the shrimp $\frac{1}{4}$ of the way down the container, shortening the container length the urchin had to travel to reach the food.

Across the trials, those urchins that were grouped with conspecifics tended to respond faster to the food stimulus. As seen in Trials 2-4 cover type or availability had little impact with how quickly the urchins reached the food item. Overall, the competitive environment had a significant impact ($\text{Prob} > F=0.0432$) on time to shrimp relative to cover type and availability (Trials 2-4). However, cover type did not significantly impact the urchin time to shrimp in either competitive ($\text{Prob} > F = 0.2986$) or solo ($\text{Prob} > F = 0.1319$) environments (Trials 2-4). Both the competitive environment and cover type strongly impacted termination percentage of a trial (both, $\text{Prob} > F < 0.0001$) (Trials 2-4).

Discussion

Strongylocentrotus droebachiensis showed a series of behaviors that suggest high sensitivity to chemical and physical stimuli, notably the presence of animal food and conspecifics. The most obvious response was extension of podia on the introduction of food, particularly animal protein. Urchins tended to aggregate and to hold both organic and physical objects close to them. These behaviors have been reported for *S. droebachiensis* and other sea urchins previously (Tegner and Dayton 1977; Garnick 1978; Bernstein et al. 1981, 1983; Dumont et al. 2007). In addition, they actively moved in the direction of a food source (Propp 1977; Garnick 1978; Lauzon-Guay and Scheibling 2007).

When disturbed during trials, individuals often stopped and moved back from progress toward the food source, which may be an escape from potential danger (Mann et al. 1984; Vadas et al. 1986; Scheibling and Hamm 1991; Hagan et al. 2002). Another tendency was to move up vertical surfaces as first observed in the holding tank and then during Trial 1, though it was more likely to happen in the presence of conspecifics. The climbing behavior was only observed in the mesh cages and did not occur in Trials 2 to 4 when the cages had solid sides and a more uniform flow regime. *S. droebachiensis* are often found on vertical surfaces and do tend to migrate up from deeper to shallower water (L. Harris, personal obsv.; Scheibling et al. 2020).

In all cases, the urchins showed a faster response to a food source in the presence of other individuals (Figures 2, 3 & 4). The responses were also faster when there was no cover or alternative food source that doubled as cover, like kelp (Figures 2, 3 & 4); when the results of Trial 2, the no-cover trial, were analyzed not inclusively as in Trial 1, the difference in time was not significant. This highlights the impact that assessing individuals (the first of several replicates) versus the whole (the mean of all replicates) can have in behavioral studies (Dingemanse et al. 2010). While sea urchins are generally considered herbivores, they are actually omnivorous and show positive reactions and grow fastest on an omnivorous diet (Lawrence 1975; Briscoe and Sebens 1988; Nestler and Harris 1994; Williams and Harris 1998; Eddy et al. 2015; Scheibling et al. 2020). Urchins predating other animals should earn more attention in future studies, particularly that of the impact of urchin aggregations (see Steneck 2020 review). Invertebrate aggregations are known to have extensive and even catastrophic impacts, such as the infamous locusts (Orthoptera: Acrididae) the control of which earns extensive attention (Peng et al. 2020; Zhang et al. 2019). Sea urchins can also switch from being cryptic to aggregating and causing significant alterations to benthic communities (Ebeling et al. 1985; Steneck 2020).

Unlike the tropical urchin *Diadema antillarum*, which aggregates for defensive purposes diurnally and spreads out to graze nocturnally, *Strongylocentrotus droebachiensis* and other *Strongylocentrotus* species, are cryptic at low densities, but switch to aggregating at high densities. At high densities, *S. droebachiensis* behaves more like migratory locusts and aggregates in feeding fronts that can decimate algal dominated communities (see review by Steneck 2020). The behavior of solo urchins provided cover was as expected for the species at low densities while the urchins in the group treatments were more aggressive at seeking a high value food source.

The results from the timed trials and the switch analysis revealed that competition was a driving factor for the behavior that was seen in the urchins. When urchins were in competition, they were more willing to climb for the bait and they moved faster towards the bait. The climbing behavior was likely not routine based, but competition based. When the urchins were isolated, there was less competitive pressure to reach the bait. Therefore, the solo urchins were slower, in terms of reaction time (Trial 1) and time to reach the bait (Trials 1-4). Not only does this show that urchins alone have varied behaviors to those who are in a competitive setting, but also shows that when studying the species, future studies should consider the effect of how many urchins are being tested at a time.

The switch analysis in Trial 1 revealed that placing competition urchins in isolation led to more lethargic reactions and movements in the form of greater reaction and reach times for both treatments. However, this delayed response may stem from the fewer runs conducted in the switch and because the urchins were still adjusting to their new conditions.

Cover availability impacted urchin foraging behavior. Solitary urchins were more likely to not move if covered with kelp or shell fragments (Figures 4, 5). This led to high termination rates with solo urchins in trials that had available cover (Figure 5). The high termination rates created low sample sizes for solitary urchins, given only 21% were successful in kelp cover and 38% with shell fragments, relative to the nearly 100% success for all competitive urchins across cover availability and type. When the urchins were not given a cover type, there were no terminations in the solo urchins, and a 13% termination rate in the competition urchins (Figure 5).

Urchins seem to be decision making, weighing the cost of movement with the benefit of nutrition, following the foraging model described by Emlen (1966). In the competitive environment, there was a high competition cost: urchins had to compete with conspecifics to ensure high quality food access. This was unlike the urchins in solo environments, which only had to deal with movement cost, and since food, though a lesser quality, was available, urchins minimized movement cost (Emlen 1966). This difference between a solo and a competing predator—the urchin—does not reflect the optimal patch use model of MacArthur and Pianka (1966), but MacArthur and Pianka did not consider the impact of the predator's own predation risk.

Decision making has been seen before in urchins (Vadas 1977) and in other invertebrates, such as caddisflies and mayflies (Kohler and McPeck 1989). While *S. droebachiensis* has been shown to aggregate in response to predator cues (Scheibling and Hamm 1991), competition urchins were more likely to choose food over remaining in an aggregation, while solitary urchins were reluctant to move if they had cover (Figures 4 & 5). When no cover was available (Trials 1 & 2), there was no assurance of protection. Thus, the solo urchins all moved towards and reached the high-quality food.

Prior to initiating a run, all urchins were moved to the down current end of the chambers if not already there; this might have had a greater impact on solitary urchins, especially when cover was available. Recently disturbed solitary urchins may have been more likely to retreat or remain under cover after handling (see Figure 5); handling has been known to discourage behavior in urchins (Vadas 1977).

Leaving the group for food can expose urchins to a higher predation risk, so solitary urchins chose safety. The process of preparing the cages for a trial might be considered a threatening event, even if there was no direct contact as shadows from the experimenters would be detected by the urchins through their light sensitive podia (Yoshida et al. 1984; Lesser et al. 2011). It is also possible that the covering behavior may have been stimulated solely by the room light (Dumont et al. 2007), since long-term white light exposure affects righting and foraging behavior in the congener *S. intermedius* (Yang et al. 2021), a species also sensitive to light intensity (Sun et al. 2019), and many urchins are nocturnal.

The results make sense based on intraspecific interactions previously documented. Grosjean et al. (2011) reported that intraspecific interactions between urchins resulted in impaired growth for less dominant urchins. More dominant urchins compete at a higher rate for resources, causing smaller, less dominant urchins to suffer. Harris et al. (2003) demonstrated that there was variation in growth rates among groups of small urchins, presumably the result of competitive interactions for food. This is likely what drove the behaviors seen in the captive urchins. Dominant urchins are likely those going towards the bait first and climbing the sides of the cage. The trials above should be replicated in the future with marking individuals to understand the dominance hierarchy. Another future study could look at training this behavior into the urchins. Even though reinforcement training was implemented in this study, there was no true training regimen. It was hypothesized that the climbing behavior was being exhibited due to the routine feeding schedule of other organisms in the water tables, causing the sea urchins to associate those smells with feeding time. Discovering that this climbing behavior is trainable would raise major questions for invertebrate biologists, confirming that sea urchins are capable of learning. This climbing behavior may also be useful for urchin aquaculture for cleaning and feeding purposes. If urchins can be trained to climb the sides of their cage during periods of feeding, this would increase feeding efficiency. This would help optimize culture methodology, potentially offsetting the costs of feeding and housing urchins.

Urchins were observed to compete through physical interactions on the way to and after reaching the shrimp. These included stealing pieces of shrimp, overtaking other individuals, and large urchins pinching the tube feet of others using their pedicellaria. In some cases, there would be multiple urchins holding onto the shrimp while traveling. Conspecific competition explains the growth differences seen in the confined spaces of aquaculture (Harris et al. 2003). Intraspecific competition is seen in other cultured species. The commercially important nudibranch *Berghia stephanieae* must be separated by life stage (Monterio et al. 2019). Blacklip abalone (*Haliotis rubra*) in aquacultural settings see great individual size variation attributed to competition for food and shelter space (Huchette et al. 2003). Small Atlantic salmon (*Salmo salar*) individuals can be outcompeted and have the highest incidence of fin damage from conspecific nipping (Noble et al. 2007).

Conclusion

Our work has demonstrated the importance of competition regarding green sea urchin foraging behavior. Sea urchins take longer to reach a food item when alone versus when with others, and when cover is

available, may not even reach the food item or attempt to reach the food item. Interestingly, when the competitive environment is changed for an individual urchin, that urchin's behavior will change and correspond with the behavior expected. Urchins seem to be weighing competition and predation risk, and this should be considered in behavioral studies. This will likely have implications for urchin aquaculture.

Declarations

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Authors' Contributions: LGH and NNS designed the study. LGH acquired funding and supervised the study. NNS, JNO, and SRMW prepared the experimental setup, and collected and analyzed the data. All authors contributed to the writing and revising of the manuscript, led by LGH and JNO. JNO prepared the manuscript for publication, and SRMW prepared the references.

Ethics Approval: As invertebrates were the only organisms used, IACUC approval was not required.

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Figures

Figure 1

Experimental setups for green sea urchins (*Strongylocentrotus droebachiensis*) in an experiment on the impact of competitive and non-competitive environments on foraging behavior. a: Trial 1. b: Trials 2, 3, 4. The left side of b shows a dark cage ahead of the Sterlite urchin run boxes; this cage did contain a sea star for a brief period but was later removed over the course of the trials

Figure 2

(a) Average time it took for green sea urchins (*Strongylocentrotus droebachiensis*) to reach a food source (shrimp) under competitive (5 urchins) and isolated (1 urchin) conditions. Isolated urchins took significantly longer to reach the bait than the urchins under competitive settings ($p = 0.0066$). (b) Average time it took for green sea urchins to react to food stimuli under competitive and isolated conditions as identified by podia extension ($p = 0.2328$)

Figure 3

Average time green sea urchins (*Strongylocentrotus droebachiensis*) took to reach an external food source (shrimp) when competing with conspecifics (competition; 5 urchins) and when alone (solo; 1 urchin). Urchins had no available cover and attempts were made to remove all supplemental kelp food. There was no significant difference in time between solo and competition urchins (prob > F = 0.2871)

Figure 4

Average time green sea urchins (*Strongylocentrotus droebachiensis*) took to reach an external food source (shrimp) when competing with conspecifics and when solo. Urchins were under varying cover: kelp, providing both an alternative food source and a cover type with non-significant impacts (Prob > F=0.3018); mussel shells providing just a cover type and no food. Mussel shells impacted time to shrimp (Prob > F= 0.0237). Due to high termination rates in the solo urchins under mussel, a sample size of only four was recorded

Figure 5

Termination rates of experimental trials examining the impact of competitive environment and cover type on the foraging behavior of green sea urchins (*Strongylocentrotus droebachiensis*). No bar is present for the solo urchins under no cover because no terminations occurred. The competitive environment and cover type overall affected termination (both, $\text{Prob} > F < 0.0001$), with specifically no cover differing from both kelp (0.0001) and mussel shell (<0.0001). Bars that share letters are not significantly different