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Ocean Acidification Impedes Foraging Behavior in the Mud Snail *Ilyanassa obsoleta*

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Abstract: Ocean acidification may diminish the response of many marine organisms to chemical cues that can be used to sense nearby food and predators, potentially altering community dynamics. We used a Y-maze choice experiment to investigate the impact of ocean acidification on the ability of mud snails (*Ilyanassa obsoleta*) to sense food cues in seawater. Mud snails have a well-adapted chemosensory system and play an important role in estuarine ecosystem functioning. Our results showed substantially diminished foraging success for the mud snail under acidified conditions, as snails typically moved towards the food cue in controls (pH 8.1) and away from it in acidified treatments (pH 7.6). These results, coupled with previous work, clearly demonstrate the magnitude at which ocean acidification may impair foraging efficiency, potentially resulting in severe alterations in future ecosystem dynamics.

Keywords: snail; cue sensing; estuary; foraging efficiency

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1. Introduction

Elevated carbon dioxide (CO_2) levels in the atmosphere have resulted in a suite of negative environmental impacts. The ocean plays a significant role in mitigating harmful ecological effects from the anthropogenic flux of CO_2 by absorbing ~30% of atmospheric CO_2 [1,2]. However, this influx in CO_2 alters marine chemistry, ultimately resulting in ocean acidification. As such, the average ocean pH is predicted to drop from 8.1 to 7.8 by 2100 [2–4].

The magnitude of seawater pH fluctuations varies by location. Shallow bays and estuaries are highly variable habitats and can fluctuate in pH by 0.5–1 units in a day [5–7]. Because of freshwater input, estuaries are inefficient buffering systems, making them especially susceptible to both short and long-term changes in pH [8,9]. As a consequence, estuaries are acidifying globally; for example, the estuarine pH in Australia decreased by an alarming 0.5 units over 6 years [10]. Estuaries are taxonomically diverse and complex habitats that facilitate ecosystem health and are important nursery habitats for myriad fish and invertebrate species. However, the impact of acidification on the biology of estuarine and intertidal organisms remains poorly understood [10–12].

Negative changes in species abundance, growth, shell production, and physiological performance are well-known consequences of ocean acidification [4,10,13–21]. In addition to these well-known effects, there is increased interest regarding the effects that ocean acidification may also have important trophic interactions, including foraging behavior and predator-prey relationships, which are essential to maintaining ecosystem health [15].

In particular, ocean acidification may alter an organism's ability to detect and respond to critical chemical cues that guide decision-making (e.g., predators, food, mates) [22–24]. For instance, Jiahuan et al. (2018) found that the black sea bream's olfactory transduction was substantially hampered and a significant reduction in the in vivo contents of both

GABA and ACh in elevated CO_2 conditions, altering their behavioral response to certain olfactory cues [25]. Ocean acidification also may impair marine organisms' ability to locate nearby food items.

Acidification likely alters invertebrate decision-making in a similar manner to fish, as they have similar neuroreceptor functioning [26]. For instance, Manríquez et al. [27] showed that *C. concholepas* was less successful in self-righting behavior under more acidified conditions. Additionally, acidification significantly impaired the escape response of *G. gibbosus* [26].

Acidification may also impact invertebrates' ability to locate nearby food items, although this response appears to be species-specific, with only some species negatively affected. For instance, Quierós et al. (2015) identified acidification as a more influential factor in regulating predator–prey interactions compared to temperature for *N. lapillus* [28], and acidification impeded the foraging success of *N. festivus* as well [12]. However, a review conducted by Clemente and Hunt highlighted significant variability in the types of responses discovered by acidification studies on behavior and suggested that multiple mechanisms are likely involved in governing species' responses [29]. Another example of this variability in responses is the finding that the foraging of the scavenger *N. nitidus* was unaffected by acidification, while *H. trunculus* foraging was inhibited [30].

In the present study, we aimed to investigate the effect that acidified conditions would have on the ability of the mud snail *Ilyanassa obsoleta* say to locate nearby food items. The mud snail is a common gastropod found in high densities in estuaries and coastal habitats along the northwest Atlantic coast [31]. Mud snails are omnivorous scavengers and have well-adapted chemosensory systems to locate food, conspecifics, and predators [31–34]. Further, mud snails play an important role in ecosystem functioning, as they influence benthic community structures and nutrient recycling in coastal environments via bioturbation, defecation, and the production of mucus trails [22,31,33].

Despite their abundance and ecological importance, little is known about how mud snails respond to changes in their environment. A recent study by Froehlich and Lord (2020) showed that the escape response of *I. obsoleta*, when exposed to the scent of the predatory mud crab, was diminished in elevated CO_2 environments [22]. These results suggest that ocean acidification impairs the mud snail's ability to detect chemical cues in seawater, similar to the diminished response that predator cues exhibited by other gastropods [35,36]. We sought to build on recent work and determine whether or not ocean acidification would interfere with the ability of mud snails (*I. obsoleta*) to find food, as this could have severe impacts on their success in estuarine ecosystems.

2. Materials and Methods

Our study included three sets of similar experiments conducted over a period of 4 years between fall 2017 and summer 2021, testing the ability of mud snails (*Ilyanassa obsoleta*) to find food under normal and ocean acidification conditions. We collected all mud snails (*Ilyanassa obsoleta*) for these experiments in the intertidal zone of Raritan Bay in Cliffwood Beach, New Jersey, USA (40.45027, −74.21815). The habitat was primarily a mud and sand flat, with a few stands of salt-marsh grasses in the high intertidal zone. The salinity was typically around 25 ppt, and the temperature ranged from 4–24 °C seasonally, and while pH data were sparse in the area, mid-Atlantic estuaries could range from 7.0–8.5 depending on daily, tidal, and seasonal cycles (https://oceansmap.maracoos.org/, accessed on 1 February 2023). After field collection, we transported the snails back to the marine laboratory at Moravian University in Bethlehem, PA, in aerated seawater containers and then stored them in large holding tanks at an ambient pH of ~8.1, the temperature of 25 °C, salinity of 25 ppt, and a 14/10 h light/dark cycle. We did not acclimate the snails to lower pH levels to mimic the rapid, short-term fluctuations of pH levels in intertidal and estuarine habitats [12]. We used all the snails in experiments within two months of field collection. We conducted experiments at three different times with different researchers; this was not the initial design, but each set of experiments followed similar methods, increased the overall sample size, was analyzed separately, and showed similar results (described later); as such, we believe that this actually strengthened our findings.

We created artificial seawater with a salinity of 25 ppt in all experiments by using deionized water and Instant Ocean® Sea Salt. For all control experiments at current ocean conditions, we used an ambient unmodified pH of 8.1. To create our acidified seawater, we used a setup first described by Froehlich and Lord (2020); we pumped carbon dioxide-enriched air into a 12-L seawater tank to produce seawater with a pH of 7.6 (similar "future" ocean pH was used by other studies including Froehlich and Lord 2020) [22]. A CO_2 controller (Autopilot APC8200) activated a solenoid valve to add CO_2 from a compressed cylinder and maintain a steady mix of ambient air and CO_2 at 1200 ppm in a sealed 10-L chamber. Air pumps then pumped this enriched air out to an airstone in the experimental tank. Prior to each experimental trial, we measured seawater pH in the control and acidified treatments with a DeltaTrak® Pocket ISFET pH Meter calibrated with Tris buffers before each measurement.

We examined mud snail foraging using Y-mazes, which is common in choice experiments utilizing a wide range of animals, from mice to fish to snails [28,36–38]. The first set of experiments in 2017 used a block-shaped Y-maze, while the second and third sets of experiments in 2021 used a more streamlined Y-maze (Figure 1), but both used the same general setup. Seawater flowed into the top of the forks of the Y-maze from 10-L header tanks containing the experimental water, then water mixed together and flowed out the base of the Y-maze. The header tank supplying the empty side of the Y-maze contained only seawater, while the tank supplying the food side of the maze contained either a crushed mussel *Geukensia demissa* (2017 experiment) or Hikari Sinking Carnivore® Pellets containing fish and krill ingredients (2021 experiments). Because the goal was to test cue sensing, food was placed in the supply tanks 15 min prior to the start of the experiment, with no food in the Y-maze itself. In all experiments, both the supply tanks had the same seawater treatment (control or acidified).

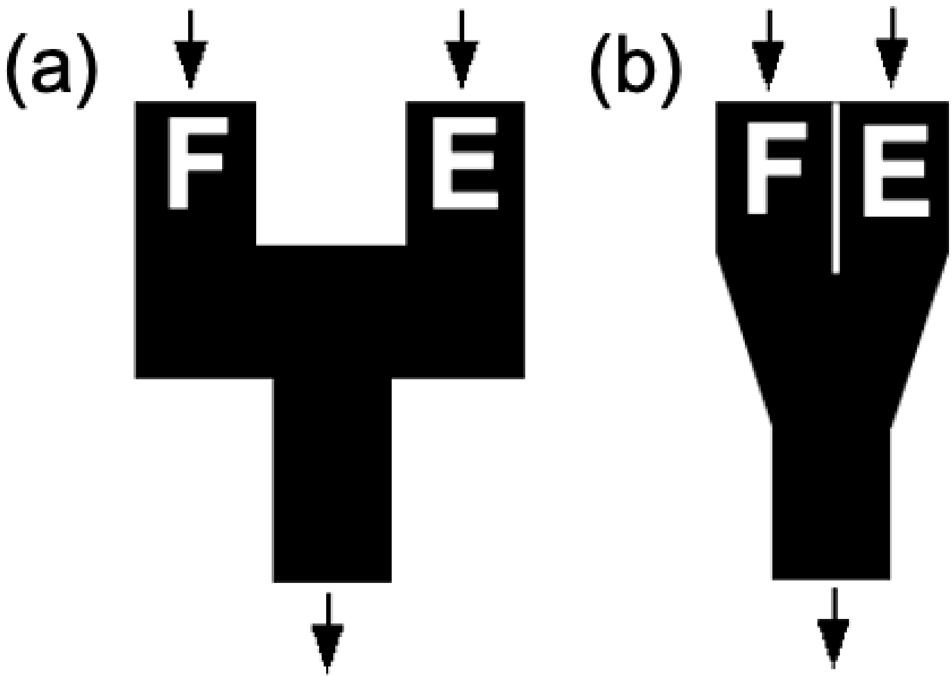

Figure 1. Diagrams of the Y-mazes used in these experiments. The first set of experiments used the block-shaped Y (**a**), while the second and third sets of experiments used the angled Y-maze (**b**). Seawater flowed through the mazes from top to bottom in the diagram, with food-cue water (F) coming from one side and the control water with no cues from the empty (E) side of the fork. Arrows show the direction of water movement in the Y-maze.

In all Y-maze choice experiments, we placed mud snails at the base of the maze and then started a timer when they righted themselves and began to move. Once a snail moved into the food (F) or empty (E) fork, we considered this a choice and ended that trial, recording the decision and the time to make the decision. We also thoroughly cleaned the Y-maze between trials to ensure that the snails did not follow trails or odors from previous trials. Due to different time constraints and different researchers for each set of experiments, the cut-off time after which we ended the trial with "no decision" made by the snail varied by experiment: 20 min for the 2017 experiments (control N = 20, acid N = 20), 10 min for the first set in 2021 (control N = 33, acid N = 33), and 5 min for the second set in 2021 (control N = 16, acid N = 26). This difference is one of the primary reasons that we analyzed each set of experiments separately, even though they had similar designs and showed largely the same patterns.

We entered and sorted all data in Google Sheets, created figures with Microsoft Excel, and performed all data analysis in R [39]. We initially analyzed each set of experiments separately, using a Fisher's exact test in the base 'stats' package in R (R Core Team 2020) to compare the control and acidified treatments for the number of snails that chose the food side of the maze, the empty side, or made no decision. After running these tests for each experiment separately because of the different cut-off times, we combined all the datasets and limited the analysis to snails that made a decision in under 5 min (the shortest cut-off time any experiment used). We ran a Fisher's exact test to compare the number of snails choosing the food or empty sides of the maze in the control and acidified treatments for this subset of data. While each set of the experiments had slightly different methods, because we had already analyzed them individually, we thought it would be informative to conduct this test to assess the dataset in a comprehensive way as well. We also computed the average times that it took the snails to successfully find food in each set of experiments, but we did not compare this statistically because the cut-off times artificially capped the searching time. It would be interesting to focus on movement rates and foraging times, but that was beyond the scope of this study, which we designed to focus on decision-making.

3. Results

All three sets of experiments showed diminished foraging success under acidified conditions, though the magnitude of the response varied. In the 2017 experiment with crushed mussels as a food source (20 min time limit), snails were less successful at finding food in acidified water, but Fisher's exact test indicated that this difference was non-significant ($p > 0.05$; Table A1) (Figure 2a,d). The snails took a longer time to find food in the acidified conditions (444 s) relative to the control treatments (246 s), but this was not statistically significant when compared because only five snails found the food in the acidified treatments.

In the second experiment (2021, 10 min time limit), snails in the acidified treatment were more than five times less likely to successfully choose the food side of the Y-maze (12%) than in the control treatments (67% success) (Figure 2b,e). Additionally, far more snails made no decision in the acidified treatment, with 55% remaining in the base of the Y-maze for the duration of the experiment (compared to 21% in controls). Fisher's exact test showed a significant difference in the snails' ability to locate food between the two treatments ($p < 0.001$; Table A1).

The results for the third experiment (2021, 5 min time limit) were similar to the second, with only 16% of the snails successfully choosing food cues under acidified conditions (compared to 50% in controls) (Figure 2c,f). No snails in the control treatments chose the empty side of the Y-maze, while 42% made this choice in acidified treatments. Similar to the second experiment, Fisher's exact test indicated a significant difference in the snails' decision-making between the two treatments ($p = 0.002$; Table A1).

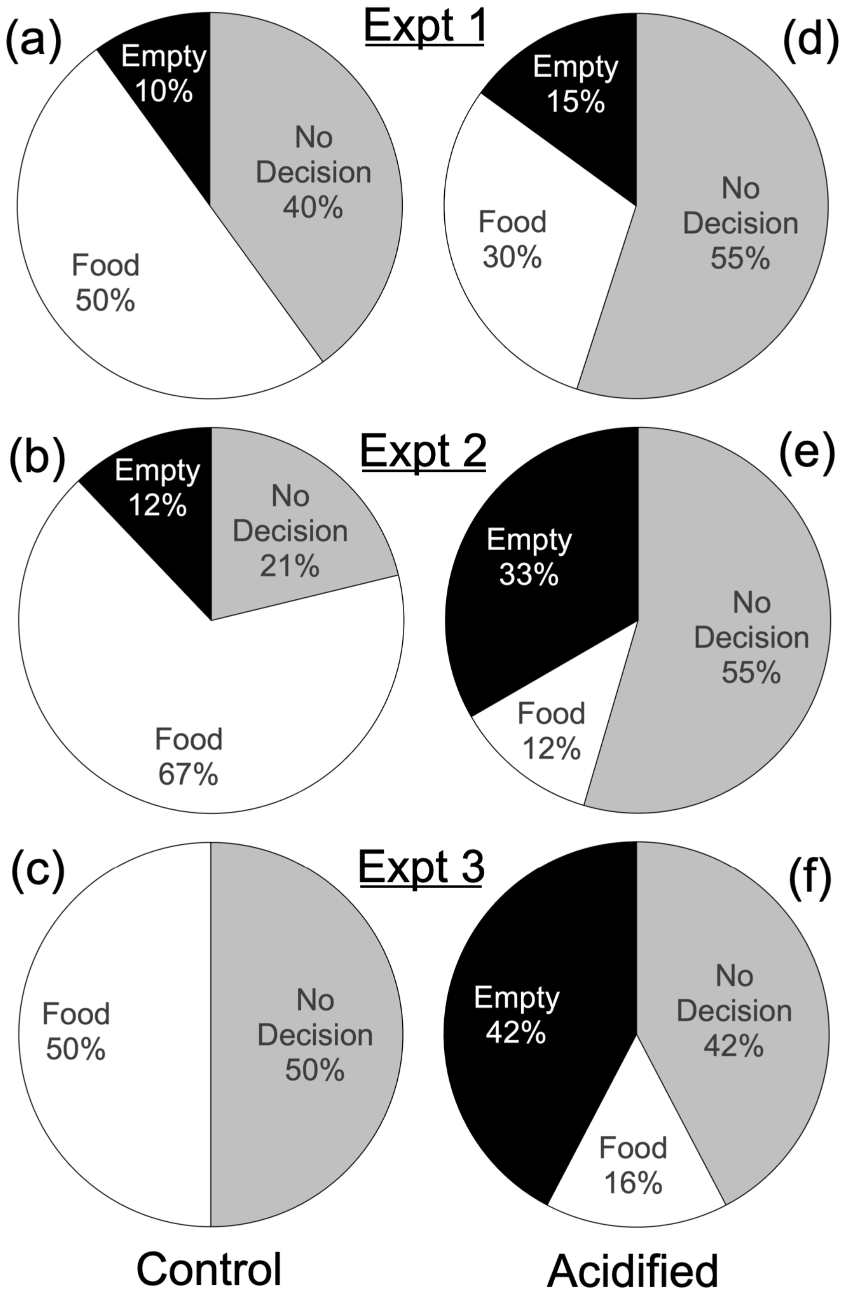

Figure 2. Pie charts showing the decisions of snails under control and acidified conditions in all three sets of experiments. In all 3 sets of control experiments (**a**,**b**,**c**), snails chose the food at least 5 times as often as the empty chamber. This was greatly reduced in acidified treatments (**d**,**e**,**f**), where far fewer snails found the food and more chose the empty side of the Y-maze. Sample sizes were 20 (**a**), 33 (**b**), and 16 (**c**) for the control treatments and 20 (**d**), 33 (**e**), and 26 (**f**) for the acidified treatment.

All three experiments exhibited a similar pattern, with snails in acidified conditions far less likely to make a decision and far more likely to choose incorrectly (Figure 3). Using the combined data from all the trials in which snails made decisions in less than 5 min, we found that 84% of snails chose the food in the controls, compared to only 27% in acidified treatments (Table A1). Fisher's exact test showed this difference to be significant ($p < 0.001$). No obvious changes in general snail foraging behavior were observed, but this was not the main focus of the experiments, which focused on food choice.

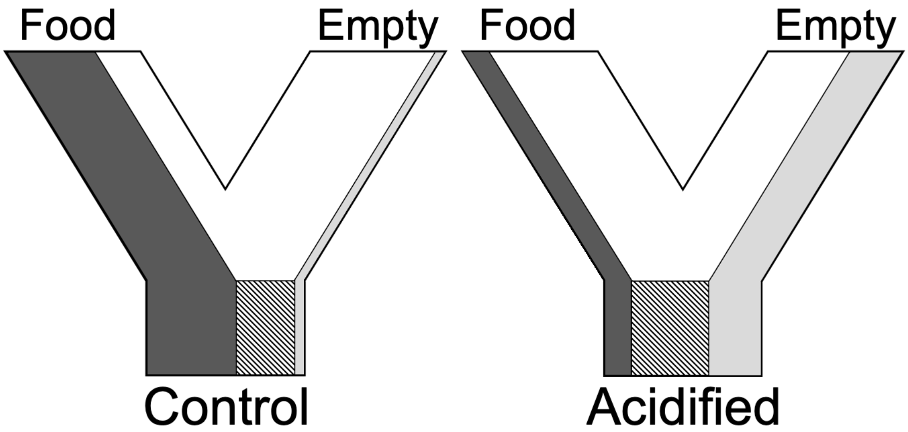

Figure 3. Y-maze schematic diagrams showing the relative proportions of snails that chose the food side of the maze in control and acidified conditions. Dark grey shows the proportion of snails that chose the food, the hashed lines show snails that made no decision, and the light grey shows snails that chose the empty chamber. By combining data from all three sets of experiments (Total control n = 69, acidified n = 79), it is clear that the vast majority of snails choose food in control conditions (60% food, 9% empty, 33% no decision), while more choose the empty side of the maze under acidified conditions (18% food, 32% empty, 51% no decision).

4. Discussion

Mud snail (*Ilyanassa obsoleta*) foraging was impeded under ocean acidification conditions, as snails were far more likely to sense and successfully move toward food cues in the control treatments. Our experiments highlighted the impressive chemosensory ability of *I. obsoleta*, as 87% of the snails that made decisions in control treatments correctly chose the side of the Y-maze that contained water laced with food cues. Across all three sets of experiments, this dropped to only 36% in acidified treatments, meaning that snails were not only struggling to find food but were making the incorrect decision nearly two-thirds of the time. This suggests that they were still able to sense the chemical cue in some way because the expectation was that if they could not sense the cue, they would choose directions randomly (50% each direction). Because they were more likely to make the incorrect decision than the correct one under acidified conditions, it seems likely that they were sensing and responding to the cue in some way but not in the same manner as in the control. Therefore, while it is possible that the chemical cue itself was altered or degraded by the change in seawater chemistry, we find it more likely that the snail's response to the cue was primarily affected.

The differences between treatments were most drastic in the 2021 experiments (second and third sets of experiments), as the success rate dropped from 88% to 27% when moving from the control to acidified treatments. In the first set of experiments in 2017, we observed this same pattern. Still, it was not as drastic or significant, perhaps because we used a different type of Y-maze or because the food (crushed mussels) was not as attractive to them as the fish and krill pellets used in later experiments. Despite the minor differences in protocol between the three sets of experiments, they all showed the same general pattern that acidified conditions substantially impeded foraging behavior.

Our observation that mud snails were usually unsuccessful in finding food under acidified conditions (choosing the non-food cue water) is similar to the many previous findings in acidification research [12,26,40,41]. Notably, in all three of the experiments we conducted, there was an increase in the number of snails that made "no decision" within the time limit of the experiment (Figure 2). This aligns with previous work suggesting that rapid acidification leads to higher levels of inactivity in both *N. festivus* and *N. lapillus* [12,28].

Our results have implications for the mechanisms by which acidification interferes with cue sense because if the snails were unable to sense the food cue, one would expect a 50–50 breakdown between the food and empty chambers of the Y-maze. Because the snails instead moved away from the food cue most of the time, we can surmise that they could sense the cue, but acidification may interfere with signal transduction pathways (as observed in some fish) [25] or with the neural processes involved in decision-making. It is also possible that acidification may have altered the food or chemical cues themselves, though we find this less likely because species-specific responses to acidification in previous studies seemed to suggest an internal mechanism [25]. However, this is largely speculative because of the lack of a well-defined mechanism for changes in species cue-sensing abilities under acidified conditions, both in mollusks and marine organisms more generally. Further research on this topic is necessary to pin down the exact mechanism.

It is not surprising that acidification interfered with food cue-sensing in this species, as previous research on this mud snail indicated a similar effect on their ability to sense predator cues, and other snail species also struggled to sense predators under acidified conditions [15,22,35,36]. These results also align with the growing body of research suggesting that acidification interferes with foraging and/or predator avoidance behavior in a wide range of mollusk, arthropod, and fish species [12,40–43]. These widespread responses suggest that there will be substantial shifts at the ecological level, as cue-sensing plays, an important role in myriad ecological processes including, but not limited to, habitat selection, mate choice, predator avoidance, foraging, aggression, and social hierarchy formation; many of these research areas have yet to be explored with respect to acidification.

For the mud snail, including *I. obsoleta* in particular, the inability to find food in acidified conditions has implications not only for long-term responses to climate change but also for current behavior in dynamic coastal and estuarine environments. In nutrient-rich estuaries and bays and areas that experience coastal upwelling, the pH can drop below 7.6 (used in this study) on an hourly, daily, or monthly basis [44,45]. Because mud snails inhabit a wide range of coastal muddy and sandy environments, they experience these diel and tidal shifts in pH over the same short window of time that we exposed them to in our study. Thus, during periods of low pH, these snails are likely unable to easily find the type of food that requires searching, potentially influencing their diet. Mud snails consume benthic microalgae as well as carrion [46], so they would presumably be better suited to feed on ubiquitous microalgae in low pH conditions where they would struggle to rely on scavenging for larger dead organisms. In the longer term, decreased foraging efficiency by mud snails could minimize their ecological role as bioturbators and scavengers. It is not known the extent to which they use cue-sensing to find high concentrations of benthic microalgae, so impeded cue-sensing may or may not impact their ability to find and utilize this food source. If they do rely more on microalgae and less on carrion for food, then this could potentially cause a shift in microalgal communities, altering the balance between algae-like benthic diatoms and potentially toxic cyanobacteria. While this study did not investigate the role of mud snails in feeding on microalgae, the fact that *I. obsoleta* was superabundant, ecologically important, and low on the food chain suggests that any changes in their populations or foraging strategy could have broad ecosystem-level consequences.

While organisms in laboratory cue-sensing experiments do not always respond in the same way in the field [47], we expected that *I. obsoleta* may be even more strongly impacted in the field where cues were more diffuse than in the Y-maze setting. However, this study system could greatly benefit from field studies assessing snail foraging behavior and diet under different pH regimes. Because they have difficulty sensing predator cues under acidified conditions [22], mud snails will likely struggle in the future if they are unable to behaviorally compensate (e.g., by shifting their diet) for their reduced foraging abilities.

This study clearly demonstrates the extreme degree to which ocean acidification can interfere with decision-making in a marine snail, but future research will ideally need to incorporate multiple trophic levels and/or field experiments to better gauge the ecological impacts. It would also be useful to incorporate other environmental variables, such as temperature and salinity, as these also can influence mollusk foraging behavior and cue-sensing [48]. Foraging experiments could also assess foraging efficiency by quantifying movement speed and the routes that organisms take to a food source in less-controlled settings than a Y-maze. Additionally, testing multiple species may allow us to make accurate generalizations about how groups of organisms are likely to respond to climate change instead of tackling them one at a time. It would be especially valuable to compare the behaviors in organisms from environments with different pH regimes to determine what long-term effects may exist, as it is evident that ocean acidification will have widespread ecological impacts that we are only just beginning to understand.

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Informed Consent Statement: Not applicable.

Data Availability Statement: Raw data can be found on FigShare at: doi.org/10.6084/m9.figshare.21986786.

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Appendix A

Table A1. Snail decisions for each of the three experiments as well as Fisher's Exact Test results for each of the statistical comparisons between control and acidified conditions. The bottom rows show the combined dataset that included all snails that made decisions in less than 5 min across all experiments.

Expt.	Length of Expt.	Treatment	Empty	No Decision	Food	Fisher's Exact Test Results	
						n	*p*
1	20 min	Acid	3	11	6	40	0.55
		Control	2	8	10		
2	10 min	Acid	11	18	4	66	<0.001
		Control	4	7	22		
3	5 min	Acid	11	11	4	42	0.002
		Control	0	8	8		
All decisions under 5 min		Acid	11	n/a	4	47	<0.001
		Control	5		27		

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