THE EFFECT OF TURBIDITY ON THE FORAGING BEHAVIOR OF TWO NEARSHORE CRABS

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Abstract:

Multiple studies have shown that increased turbidity can result from both natural and anthropogenic activities. These spikes in turbidity can significantly affect predator-prey interactions and foraging behavior. To test how increased turbidity affects the foraging behavior of the crabs *Pachygrapsus crassipes* and *Pugettia producta*, we performed a choice experiment between chemically versus visually appealing prey in ambient versus turbid conditions. We determined that turbidity did not hamper the crabs' ability to forage or how long it took to choose a stimulus in general. However, when examining the crab's decision speed by stimulus type, turbidity did cause the crabs to take longer choosing the chemical stimulus and to more quickly choose the visual stimulus. We did not observe a decrease in visual foraging under turbid conditions as other studies have documented. This indicates that increased turbidity does not have a strong effect on the foraging behavior of these nearshore crabs.

Keywords: *Marine Ecology | Turbidity | Invertebrates | Foraging | Kelp Crabs | Shore Crabs | Choice Experiment*

Introduction

It is well known that visual predators have a difficult time foraging in turbid waters since the light that penetrates the water's surface is scattered, thus lowering visibility (Lunt and Smee, 2015). While variation in turbidity occurs naturally from biological sources like algal blooms, turbidity can also be increased by anthropogenic activities such as boat traffic or coastal development that suspends sediment in the water (Garrad and Hey, 1987; Moss, 1977).

Sudden surges in turbidity can influence the predator-prey interactions in many aquatic ecosystems. For example, it was found that increased turbidity decreases the reaction distance of smallmouth bass and their prey exponentially (Sweka and Hartman, 2003). This reduces feeding efficiency by predators that rely on visual prey cues in comparison to those that are reliant on chemical prey cues (Lunt and Smee, 2015). Additionally, increased turbidity can impair reef fishes' ability to respond to chemical cues (Wenger et al. 2011). Previous research has established that chemosensory detection is the primary method used by Atlantic Rock Crabs (*Cancer irroratus*; Rebach, 1948). Furthermore, variation in response time to different stimuli has been observed in Striped Shore Crabs (*Pachygrapsus crassipes*). These crabs take longer to respond to chemical stimuli than to visual stimuli, and this response to chemical cues, similar to many other stimulus
responses, may be subject to change in varying environmental conditions (Hiatt, 1948). However, studies have not examined how turbidity might alter the foraging behavior of these crabs or the mechanism behind their selection of food.

Studies on turbidity are rarely conducted on invertebrates and even more rarely on herbivores. Relatively little is known regarding how turbidity affects their feeding or response to stimuli. Therefore, we tested how turbidity affects the foraging of two different species of crab, specifically observing whether there were changes in the use of visual versus chemical stimuli and the time required to locate food. Of the two species we used in our experiment one was an omnivore, the shore crab *Pachygrapsus crassipes*, and the other was an herbivore, the Kelp crab (*Pugettia producta*). *P. producta* are known to use chemical stimuli to detect their food, the Giant Kelp (*Macrocystis pyrifera*) therefore, we hypothesized that *P. producta* would rely on chemical cues rather than visual cues when foraging (Zimmer-Faust and Case, 1982). We also hypothesized *P. crassipes* would favor the visually appealing prey, as they respond more quickly to visual cues (Hiatt, 1948). However, given that the *P. crassipes* is an omnivore, they might utilize different mechanisms for foraging depending on the prey item. We aimed to examine these aspects of foraging by putting the crabs through a two choice Y-maze and having them choose between a chemically appealing and a visually appealing food item. These trials were performed in both ambient and turbid water to determine if the abiotic factor of turbidity would alter their choices and behaviors.

We predicted that turbidity would impede foraging behavior for *P. crassipes* and *P. producta* since utilizing visual and chemical sensory organs would be difficult under turbid conditions as other studies have demonstrated (Sweka and Hartman, 2003; Lunt and Smee, 2015; Wenger et al. 2011). We also predicted that *P. crassipes* and *P. producta* would both rely more on chemical cues than visual cues in turbid water. The amount of time it takes to make a decision was expected to increase across both species and prey types due to this difficulty in detecting prey. We predicted that crabs would be more reactive to visual stimuli than chemical stimuli taking less time to make their decision across both ambient and turbid treatments due to the difference between how visual and chemical stimulus are perceived by the crabs (Hiatt, 1984; Zimmer-Faust and Case, 1982). However, we expected that *P. crassipes* would respond faster to stimuli than *P. producta* since *P. crassipes* has been noted as a highly alert and active species (Hiatt, 1948).

**Methods**

To quantify turbidity we constructed a Secchi disc, approximately 30cm in diameter, from Plexiglas and a PVC pipe that was marked at every 10 cm (Steel and Neuhauser, 2002). The distance at which the disc disappeared from sight was the turbidity measurement of the site. We took measurements at Mason’s Marina, Bodega Harbor, California, and at eelgrass beds in Westside Park, Bodega Bay, California and finally at the dock of Bodega Harbor, California. Three measurements were taken at each site. Then we simulated the highest field turbidity in the laboratory in order to mimic an increased turbidity due to anthropogenic impact. To simulate the turbidity, we gathered water from unused seawater faucets, which contained suspended sediment. By diluting this with ambient seawater, we mimicked the turbidity measurement taken in the field. Large quantities of turbid water were created so that none of the turbid water was re-used to prevent sediments from settling out and contamination by chemical cues from prey items. Turbidity measurements were performed in lab by using a miniaturized Secchi disc horizontally across the length of the maze (Steel and Neuhauser, 2002). For our experiment, ambient turbidity was a visible
distance greater than 1.5m and increased turbidity was a visible distance of 30 cm.

We collected Pachygrapsus crassipes from Horseshoe Cove (N=13), Westshore Road just outside the entrance to the Bodega Marine Lab road (N=13), and Campbell Cove (N=13; resulting in 39 total). One crab was gravid and was not used in the experiment (Final N=38). Pugettia producta were collected from Spud Point Marina (N=9) and Pinnacle Gulch (N=9). However one crab died mid-trial so the data from this individual were not used (Final N=17). Crabs were starved for at least 24 hours before any tests were run. For P. crassipes we used Sea Lettuce (Ulva lactuca), collected from Campbell Cove, as the algal food and crushed Black Turban Snail (Tegula funebralis), collected from Horseshoe Cove, as the animal prey. The Ulva and 3-crushed Tegula were used in both chemical and visual cues with the Ulva standardized to an approximate 10 x 10 cm square. For P. producta we used the Giant Kelp (Macrocystis pyrifera), collected from Doran Beach and standardized to 16 x 4 cm pieces.

To separate the visual element from the chemical stimuli, we put the prey/food item in a transparent glass jar when testing the visual stimulus so that no chemical cues would be present in the water (Figure 1). Additionally, the water in the jar was matched to whichever treatment was being tested at the time. For the chemically appealing prey, we placed the prey item in an opaque mesh cylinder that allowed water to pass through, thus carrying chemical cues but preventing the prey item from being seen (Figure 1). In order to test whether the crabs utilize chemosensory cues over visual cues we put the two stimuli in different wings of a Y-maze with dimensions 80 x 55 cm (Figure 2). To ensure that visual cues from outside the Y-maze were not distracting the crab, laminated black sheets were placed along the walls of the maze (Figure 2). To ensure that chemical cues diffused throughout the maze, a slow flow of water was generated using inlets behind the prey items and an outlet behind the crab (Figure 2). The decision of which stimulus was placed in which wing was randomly decided by the flip of a coin and recorded to check for side bias.

The food stimuli were placed in the Y-maze for at least two minutes before the crab was placed in the start arm of the Y-maze, away from the two arms with the stimuli. Flow between the two arms of the maze was uniform and was the same across all trials. A mesh barrier was put in front of the crab to allow the crab to acclimate, while preventing access to the rest of the maze. The crabs were held behind the barrier for approximately 30 seconds before the barrier was removed. In pilot tests, we found that crabs would not make a choice if they did not decide within the first 2 minutes. Therefore, if the crab did not make a choice within 2 minutes, the outcome was considered a “no choice” trial. In addition, the crab was considered to have made a choice when it attempted to handle the prey item with its chelipeds by tapping the glass jar or picking at the mesh. Before the test was run, the crab’s carapace width was measured and its sex was recorded in order to see if there was an effect of either on their choice or the time it took to make the choice. Each crab was tested once in both turbid and ambient conditions and the time it took to make a decision was recorded.

We used a binomial test and the Chi squared test to determine if the choices the crabs made were non-random and to determine which stimulus drives their foraging behavior (Table 1). The binomial test was also used to determine whether the crabs had a consistent preference for one side of the maze due to unknown confounding factors, which would bias our data. For both of these tests we used a 50-50 distribution as our expected outcome. Additionally, we performed an Analysis of Variance (ANOVA) to test whether variation in decision time was influenced by three factors: the stimulus the crab chose, the level of
turbidity, and the crab species (along with the interactions between these factors; Table 2).

Results

Sensory Preference of Crab Species
When pooling data across both treatments and food choices we found that *P. producta* showed no significant difference between the number of individuals that were attracted to chemical cues over visual cues (Figure 3; Binomial Test, p=0.3145). *P. crassipes* individuals, however, showed a significant difference with 29 of 45 individuals attracted to visual stimulus over chemical stimulus (Figure 4; Binomial Test, p=0.0362). We also cross-referenced our records of randomization (which side of the maze stimuli were assigned to) with the crab’s choices and determined that there was no consistent trend for crabs to favor one wing of the maze over the other (Binomial Test, p=0.623).

Effects of Turbidity on Foraging Behavior
To quantify if turbidity impeded foraging behavior we compared how many crabs made a choice in ambient versus turbid conditions. We found that the number of individuals that made “no choice” increased non-significantly under turbid conditions for the *P. crassipes-Tegula* trials (Figure 5; Chi-Squared Test, df=3, N=19 X²=5.158, p=0.1606; Table 1). For the *P. crassipes-Ulva* the amount of “no choice” individuals decreased, but was a non-significant trend (Figure 5; Chi-Squared Test, df=3, N=19 X²=5.579, p=0.1340). *P. producta* also showed a non-significant decrease in “no choice” individuals in turbid water relative to ambient conditions (Figure 6; Chi-Squared Test, df=1, N=17, X²=0.529, p=0.4669).

Choice of Stimulus Type
Of the crabs that did make a choice and displayed foraging behavior in both ambient and turbid water, the number of individuals that utilized chemical over visual stimulus in the turbid treatment varied between species and prey items. For *P. crassipes*, the number of individuals that were attracted to the chemical stimulus in the *Ulva* trials tended to increase under turbid versus ambient conditions, whereas the number of individuals that were attracted to chemical stimulus in the *Tegula* trials tended to decrease (Figure 7). However neither trend was statistically significant (Chi-Squared, df=3, N=16, X²=0.857, p=0.8359). Similar to the *P. crassipes-Ulva* trials, the frequency of scent choices for *P. producta* tended to increase under turbid versus ambient conditions but was also non-significant (Figure 8; Chi-Squared, df=1, N=7, X²=0.457, p=0.4991).

Changes in Response Times
As a measure of foraging efficiency we examined the time it took each individual to choose a prey item in turbid and ambient treatments. The time the crabs took to choose was not affected significantly by turbidity in either species (Figure 9: 3-way ANOVA, F₆,₅₅=1.2197, p=0.2744; Table 2). However, what stimulus the crab was most attracted to, chemical (scent) or visual (vision), had a significant effect on decision time with the crabs attracted to scent taking 1.8 times longer than those that were attracted to visual cues (Figure 9: 3-way ANOVA, F₆,₅₅=10.7211, p=0.0019). We found that water quality had a significant interactive effect with the type of stimulus the crab was attracted to. The average response time of crabs attracted to scent increased 25 seconds in turbid waters and the average response time of crabs attracted to visual cues decreased by around 7 seconds in turbid waters (Figure 9: 3-way ANOVA, F₆,₅₅=4.938, p=0.0114). None of the other interactions between factors had a significant effect (3-way ANOVA, F₆,₅₅=4.938, p>0.1). Additionally, the species of crab significantly affected the response time: *P. producta* took on average 18 seconds longer than *P. crassipes* (Figure 9: 3-way ANOVA, F₆,₅₅=5.2966, p=0.0253).

Discussion
The effect of turbidity on the foraging behavior of these crabs was much more complex than we expected. Our data did not support our hypothesis that turbid waters would impede *P. crassipes* foraging behavior nor did it support the hypothesis that a similar effect would be observed in *P. producta*. The elevated turbidity did not impede the crabs’ foraging behavior by eliciting more “no choice” trials as we predicted. Instead, the elevated turbidity affected other facets of their foraging behavior, as discussed below.

Efficiency is an important aspect of foraging behavior that was heavily impacted by elevated turbidity in other studies (Sweka and Hartman, 2003). Since our setup did not allow us to measure efficiency in terms of prey successfully consumed, we used the time it took the crab to detect the stimulus and find the prey item as an indication of how turbidity impacted its foraging efficiency. Our hypothesis that the time crabs took to find food would increase with turbidity was partially supported. There was no effect of turbidity alone on the crabs’ response time. However, crabs did take significantly longer to respond to a chemical stimulus than a visual one. There was also a significant interactive effect between turbidity and stimulus choice, indicating that the effect of turbidity on the crab’s response time differed depending on the stimulus chosen. The significant difference in the time individuals took to choose one of the two stimuli might be due to a lower threshold of response for visual stimulus. This lower threshold for detection could arise if any visual stimulus detected results in a response whereas chemical stimulus requires a specific concentration to elicit a response (Pearson et al. 1979). In turbid conditions, crabs that were attracted to visual cues took much less time than those in ambient conditions. In contrast, crabs that were attracted to chemical cues took much more time to respond in turbid conditions than in ambient conditions. Perhaps this is due to visual cues being more obscured in turbid water so that any detection will provoke an immediate response. Furthermore, it might take longer for chemical cues to reach a concentration above the crab’s threshold due to increased particles in turbid water. These opposing trends could explain why we did not see a significant effect of turbidity alone on response times and only found the interactive effect with the stimulus choice.

Our hypothesis that *P. crassipes* would have a slower response time than *P. producta* was supported by our data. This corroborates the idea that organisms that rely on different mechanisms for prey detection, such as vision versus chemosensing, will behave differently. We predicted that that *P. crassipes* should be more attracted to chemical stimulus in the turbid water and *P. producta* would follow a similar trend. However, these hypotheses were unsupported as there was no significant difference between the numbers of individuals that were attracted to scent under ambient versus turbid treatments. This could be a result of equal interference for both chemical and visual stimuli as a couple of studies have found that suspended sediment can interfere with chemical signals, even impairing an individual’s choices (Wenger et al. 2011). Our hypothesis regarding *P. producta* primarily utilizing chemosensory detection in foraging behaviors was unsupported as the distribution of individuals that were most attracted to scent did not deviate significantly from a random distribution. This could be explained by the concentration of chemical cues not surpassing the threshold necessary for response in either treatment. Our hypothesis that *P. crassipes* would primarily employ visual detection across both prey types and turbidity conditions was supported, confirming that *P. crassipes* is a
visual forager, as other studies have found (Hiatt, 1948).

This mixture of supported and unsupported hypotheses clearly demonstrates that the relationship between foraging behavior and turbidity is not uniform across feeding modes, let alone within the same feeding mode (i.e. omnivory vs. herbivory). While previous studies indicate that visual foragers such as pinfish suffer a decrease in efficiency in turbid waters (Lunt and Smee, 2015), our experiment found that *P. crassipes* was a visual forager and their efficiency remained relatively unaffected by the increase in turbidity. This difference in the influence of turbid conditions on efficiency might be a result of different sensory physiologies in vertebrate versus invertebrate predators. For example, reef fishes have low visual resolution at a distance, whereas fiddler crabs have eye structures that impart better resolution in the vertical direction (Marshall et al., 2003; Zeil and Hemmi, 2006). However, our study species’ visual abilities have not been examined so whether their abilities differ greatly from other visual foragers remains unknown.

Our study on the effect of turbidity on the foraging behaviors of these two crab species may not be comparable to other studies of different species under turbidity conditions as our crab species use their macroalgal food, *Ulva* and *Macrocystis*, for both food and shelter (Hiatt, 1948; Zimmer-Faust and Case, 1982). This could mean that crabs’ choices are fueled by a desire for shelter rather than foraging behavior alone. Additionally, there are other confounding factors present such as potentially residual chemical cues in the seawater lines that might have interfered with the crabs’ choices. While the flow between both arms were uniform, the maze was not tested for any eddies that might form as a result of the current which could affect how much of the chemical cue the crabs received. It is also unknown whether the level of turbidity used would elicit significant changes in the behavior for these crabs.

Since the choices of both species were unaffected by increased turbidity, it indicates that these crabs, are affected differently by turbidity than some aquatic vertebrates, such as small mouth bass (Sweka and Hartman, 2003). Our results suggest that turbidity does not impact these crabs as strongly as other visual foragers, particularly in terms of their behavior. This asymmetric effect could increase the abundance of crabs and their relative importance in these coastal ecosystems. This change could in turn cause a cascading effect that alters the composition of coastal communities. Further studies are needed to address how elevated turbidity can impact coastal ecosystems, including effects on patterns of consumer foraging.

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**References**

Abrahams, M. V. and Kattenfeld, M. G. 1997. The role of turbidity as a constraint on predator-prey interactions in aquatic


### Tables and Figures

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Table 1. Summary table of Chi-squared test results. P-values that are significant are in bold.

Table 2. Summary table of 3-way ANOVA of response times. P-values that are significant are in bold.

Figure 1. Experimental Apparatus. Visually appealing prey was presented in a glass jar (left), while chemically appealing prey was enclosed in the mesh tube (right). In this photograph crushed snails (*Tegula*) are present in both containers.
**Figure 2.** Experimental Apparatus. The Y-maze was fitted with black laminated paper to prevent visual cues from outside the maze. Inlets at the rear of the maze provided slow water flow, which drained from the outlets in the center of the photograph. A *P. producta* trial with turbid water is being run in the photograph.

**Figure 3.** The frequency of choices between visual and chemical stimulus by *P. producta* from both ambient and turbid treatments. Data for this figure were pooled together for both ambient and turbid treatments.
Figure 4. The choice in stimuli for *P. crassipes* individuals. For this figure, data were pooled across both water treatments and prey types.

Figure 5. The frequency of the choice versus no choice outcomes for *Pachygrapsus crassipes* individuals in ambient and turbid treatments with *Ulva* or *Tegula* prey items. “No choice” indicates that the individual failed to perform foraging behavior when placed in the Y-maze for the 2-minute trial.
Figure 6. The frequency of the choice or no choice outcomes for *Pugettia producta* individuals in different treatments. “No choice” indicates that the individual failed to perform foraging behavior when placed in the Y-maze for the 2-minute trial.

Figure 7. Frequency of *Pachygrapsus* individuals that made a choice between the visual and chemical stimulus in both ambient and turbid for both prey items. Shows the frequency of that choice in each treatment.

Figure 8. Frequency of *Pugettia* individuals' choices between the visual and chemical stimulus in both ambient and turbid water treatments.
**Figure 9.** The average response time of crabs for each treatment, prey type, and stimulus chosen. Responses for *P. crassipes* are shown on the left, and responses for *P. producta* are on the right. Scent treatments are shown with black bars, and vision treatments are shown with gray bars. Error bars are based on standard error.