5-2019

Do Indirect Predator Cues Affect Behavior of the Freshwater Clam Sphaerium simile?

Jesse Bruce Eichler
Montclair State University

Recommended Citation

Eichler, Jesse Bruce, "Do Indirect Predator Cues Affect Behavior of the Freshwater Clam Sphaerium simile?" (2019). *Theses, Dissertations and Culminating Projects*. 283.
https://digitalcommons.montclair.edu/etd/283

Abstract

Freshwater bivalves provide important ecosystem services, like filtering water and cycling nutrients. Predators affecting the behavior of bivalve prey, therefore, could potentially impact the structure and function of ecological communities. Because little is known about the antipredator responses of sphaeriid clams, I examined the behavior of juvenile and adult freshwater clams, *Sphaerium simile*, when exposed to two types of indirect predator cues: effluent of a crayfish (*Orconectes rusticus*) and damaged conspecific clams. Adult clams responded to crayfish effluent by significantly reducing burrowing behavior. Juvenile clams, however, buried indiscriminately regardless of experimental treatment and significantly more often/more quickly than adults. These results suggest that invasive crayfish predators could cause reduction in adult *S. simile* activity that in turn might affect community and ecosystem function.

MONTCLAIR STATE UNIVERSITY

Do Indirect Predator Cues Affect Behavior of the Freshwater Clam Sphaerium simile?

By Jesse Bruce Eichler

A Master's Thesis Submitted to the Faulty of Montclair State University

In Partial Fulfillment of the Requirements for the Degree of

Master of Science

May 2019

College of Science and Mathematics

Department of Biology and Molecular Biology

Thesis Committee

[redacted]

Dr. Scott Kight

Dr. Paul Bologna

Dr. Matthew Aardema

Do Indirect Predator Cues Affect Behavior of the Freshwater Clam *Sphaerium simile*

A THESIS

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

By

Jesse Eichler

Montclair State University

Montclair, NJ

May 2019

Acknowledgements

I would like to thank Montclair State University's Department of biology for the facilities used for the housing and care of the clams and crayfish. I would like to thank Tiana Bonventre, Dylan Jones, Lauren O'Neil, and my father Dean for assisting in the capture and transport of specimens. I would like to thank my fiancée Cathie Ruesch for her support and insight throughout this entire process. I would like to thank my committee for their support, time and insight. Finally, I would like to thank Dr. Scott Kight for his guidance, positive attitude, and infinite patience.

Table of Contents

Chapter Title **Page**

Abstract 1

Thesis Signature 2

Title Page 3

Copyright Page 4

Acknowledgements 5

Table of Contents 6

List of Figures 7

Introduction 8

Materials and Methods 12

- Collection and maintenance 12
- Behavioral Trials 13
- Video Analysis 14
- Statistical Analysis 14

Results 15

- Percent burrowed 15
- Time to burrow 15
- Size 15

Discussion 18

- Conclusion 21

Literature Cited 22

Figures 25

Figures

Figure 1 – Example of S. simile with unique color ID representing 4234. (Photograph: Jesse Eichler)

Figure 2 – Example of clam arrangement at beginning of trials (Photograph: Jesse Eichler)

Figure 3 – Relationship between percent burrowed individuals (Juvenile) in different experimental treatments.

Figure 4 – Relationship between percent burrowed individuals (Adults) in different experimental treatments

Figure 5. Relationship of time to burrow (Juveniles) in different experimental treatments

Figure 6. Relationship of time to burrow (Adults) in different experimental treatments

Introduction

Predator-prey interactions directly and indirectly affect the populations of both predator and prey species, with consequences that potentially affect the function and structure of the larger community (Carpenter & Kitchell, 1988; Lodge, Kershner, Aloi, & Covich, 1994).Prey species face selective pressures that result in the evolution of antipredator responses. Some prey species actively flee from predators, others may avoid detection, and some species can develop induced defenses like painful spines or bitter tasting secretions as exhibited by some insects (Bowers, 1992; Schmidt, 1990; Ydenberg & Dill, 1986). Induction of such defenses comes at a cost; energy spent on defense is energy that could be used for reproduction(Lima, 1998). Hence even when predators are not successful in killing prey, the response to predation risk may be sufficient to alter the ecosystem. For example, Power et al. (1986) demonstrated that when piscivorous bass (*Micropterus salmoides* and *M. punctulatus*) were introduced into different stream pools, grazing minnows (*Campostoma anomalum*) began to avoid pools containing the predators, resulting in an increase of algae in those pools.

As a mostly sessile group, bivalves generally cannot employ motile means of escape from predators. Instead employing other forms avoidance such as burrowing and reduced ventilation (Lin & Hines, 1994; Nakaoka, 2000). Adaptations to increase handling time are common as well, including changes in shell morphology which make shells difficult to crush(Boulding (1984), as well as increased byssus production, making removal difficult (Leonard, Bertness, & Yund, 1999). Predators that may remove bivalves from the sediment surface experience longer handling and processing times to dislodge bivalves via excavation or removal from byssal attachment, making bivalves an energetically costly food item (Klocker & Strayer, 2004).

Literature on shell morphology can be unclear on whether bivalve shells have adapted in response to predation, but studies have found that shell morphology does affect predation risk regardless; shell thickness as well as shape help to discourage predators by increasing handling time of specimens that are to difficult to crush(Boulding, 1984). Many mollusc-eating crabs, such as *Liocarcinus puber* and *Carcinus maenas(ROPEZ, 1968),* have developed dimorphic claws, a crushing claw used to break shells and a cutting claw for catching and holding prey (Vermeij, 1977). Burrowing bivalves in particular exhibit little to no adaptation against crushing by crustacean predators, likely due to their infaunal lifestyle; while crustaceans are capable of excavating sediment, they are more successful foraging on the surface. Heavy ornamentation of the bivalve shell as well as less blade-like cross sections would also hinder burrowing efficiency (Boulding, 1984; Stanley, 1970). For such bivalves, burrowing behavior is the main line of defense against predation.

Bivalve prey detect their predators through several different sensory processes, using diverse cues that can originate from either the predator or from conspecific individuals (Flynn & Smee, 2010; Leonard et al., 1999).Bivalves may receive chemosensory input from the surrounding water through the osphradia, two patches of sensory epithelium located below the posterior adductor muscle. (Haszprunar, 1987; G. L. Mackie & Bailey, 2007). Cues from predators that are starved (Côté & Jelnikar, 1999), predators that have fed on bivalves (Griffiths & Richardson, 2006), and cues from injured conspecifics are used by different species of bivalves to assess risk of predation. For some species, the magnitude of response to a predator is proportionate to the concentration of predator-related chemical cues, as there is an initial immediate response of zebra mussels to predator cues, followed by an adjustment of the response to match the level of threat (Antoł, Kierat, & Czarnoleski, 2018). Bivalves can also respond to changes in their orientation and possibly acoustic stimuli (Budelmann, 1992) in the environment through the statocyst, a fluid filled organ lined with cilia containing a statolith, a small mineral inclusion (McMahon & Bogan, 1991).Studies by Roberts (2015) on the mussel *Mytilus edulis* and Kastelein (2008) on cockles *Cardium edule* demonstrated that these species exhibit reduced siphoning behavior when exposed to certain sound frequencies. Some bivalve species use photoreception for predator detection; exhibiting a behavioral shadow response when a shadow is cast over the animal, typically a shell closing response and retraction of the siphons (Morton, 2008).

In the present study, I examine the behavior of the bivalve *Sphaerium simile* when exposed to predator cues. *Sphaerium simile* is classified in the *Sphaeriidae,* a family of freshwater ovoviviparous clams (G. Mackie, 1978). *Sphaerium simile* is distributed throughout North America, generally inhabiting the sediments of lentic systems, and often found in large aggregates of conspecifics. *Sphaerium simile* is the largest species of the genus in North America with individuals growing up to 20 mm at the widest part of the valve (G. L. Mackie & Bailey, 2007). Juveniles of the species are brooded in specialized gill pouches (so-called “marsupial sacks”) with up to four offspring at different stages of development existing in the parent clam until release of each offspring at approximately 5-8 mm in size (G. L. Mackie & Bailey, 2007; Zumoff, 1973).

It is important to understand the potential costs of anti-predator adaptations in *S. simile* because burrowing bivalves perform ecological functions that affect water clarity, nutrient cycles, and oxygenation. For example, filter feeding by bivalves removes particles from the water column (Kasprzak, 1986), thereby increasing water clarity which in turn increases light penetration resulting in increased primary productivity (Newell & Koch, 2004). Larger particles may also be ingested by some species through alternative feeding, such as pedal deposit feeding(G. L. Mackie & Bailey, 2007). Deposition of nutrients like phosphorus in bivalve feces and pseudofeces might also cause increases in primary production (Nakamura & Kerciku, 2000). Shells of bivalves also provide space for epiphytic and epizoic colonization, as seen in some epipelic species of *Pisidium* (Beckett, Green, Thomas, & Miller, 1996; G. L. Mackie & Bailey, 2007), thereby influencing the distribution of microorganisms in the ecosystem. Bioturbation of the sediment via the physical act of burrowing also increases oxygen content and releases nutrients such as nitrogen from the sediment (Beckett et al., 1996).

One potential predator of *S. simile* in North America is the rusty crayfish *Orconectes rusticus*, a species of crayfish native to the midwestern United States (Klocker & Strayer, 2004), which has been introduced into areas north and east of the ancestral home range both accidentally through escapes from aquaculture facilities and deliberately by pet owners and fisherman (Lodge, Taylor, Holdich, & Skurdal, 2000; Taylor & Redmer, 1996).Outside of the historical home range, *O. rusticus* is an aggressive (Reisinger, Elgin, Towle, Chan, & Lodge, 2017) fast growing species that displaces other native crayfish species, and may hybridize with native congeneric species (Perry, Lodge, & Feder, 2002). Introduction of *O. rusticus* into naive communities often results in competition with native crayfish and reduces populations of food species, thereby negatively impacting biodiversity (Lodge et al., 1994). In areas where bivalve populations coexist with smaller crayfish species, introduction of *O. rusticus* may cause increased bivalve predation as *O. rusticus* have relatively larger chelae that facilitate excavation and processing (Klocker & Strayer, 2004).

Orconectes rusticus, like most crayfish species, uses olfaction (Moore & Grills, 1999) to locate prey. Locating prey through chemosensory cues appears to be a learned behavior, as crayfish exhibit an increased feeding response to chemical cues from prey species they have encountered before (Hazlett, 1994). Crayfish generally forage for food at night, walking along the sediment. When food is identified, crayfish use the chelae and walking legs to handle and initiate processing of food items, moving food particles to the mandibles for grinding and consumption (Brown, 1995). Crayfish are polytrophic, feeding on almost any organic matter, alive or dead (King, 1883). This relatively indiscriminate feeding behavior can impact food webs at many different levels (Lodge et al., 1994; Momot, Gowing, & Jones, 1978). However, crayfish prefer to consume animal protein when available (Momot, 1995),and can significantly impact densities of both gastropods and bivalves (Perry, Lodge, & Lamberti, 1997).

The present study examines whether indirect predator cues affect behavior of the freshwater clam *S. simile.* In addition, I compared the responses of adults versus juveniles to address the possibility of developmentally-associated antipredator behavior in this species. Although little is known about antipredator behavior in freshwater bivalves, marine bivalves like *Macoma balthica* and *Cerastoderma edule (Griffiths & Richardson, 2006)* have been observed to burrow in the presence of predators. I therefore expected *S. simile* to exhibit a burrowing response in the presence of *O. rusticus*. Because *O. rusticus* do not readily excavate Sphaeriid and Unionid bivalve prey (Klocker & Strayer, 2004) burrowing in the presence of crayfish would suggest an adaptive response..

Methods

Collection and Maintenance. *Sphaerium simile* were collected at a privately-owned pond in Byram Township, NJ (40°59'22.5"N 74°40'37.4"W) in May of 2018 using a dip net along the eastern shore. Clams were found burrowed in sandy sediment that was artificially introduced during the construction of the spring-fed pond. Clams were transported to the laboratory in large plastic buckets and thereafter housed in a 38 L aquarium containing aged tap water and no substrate to facilitate cleaning, maintenance, and selection of individuals for trials. Subjects were fed once each week with commercial API® Algae Eater wafers, crushed with a mortar and pestle to distribute food particles throughout the aquarium.

Two to seven days prior to observations, each clam was measured across the widest point of the valve from anterior to posterior using an electronic caliper to the nearest 0.01mm and marked with a distinct ID using a Sharpie® permanent marker (Fig. 1). Crayfish used as stimulus animals in this study were collected from the Wallkill river in Ogdensburg, NJ (41°05'13.1"N 74°35'41.4"W) using a dip net. Crayfish were found concealed under rocks during the daytime. Crayfish were housed in a 38 L aquarium containing aged tap water, Sakrete ® natural recreational sand as substrate and broken terra cotta pots to provide shelter. Crayfish were fed commercial Hikari® Crab Cuisine food every two days. The water in all aquaria was treated with chemical, biological, and mechanical filters as well as bi-weekly 20% water changes with aged tap water.

Behavioral Trials.

In general, each observational trial took place in a 100 mm diameter 350 ml watch glass. Each watch glass was filled with approximately 175 cm^3 sand as a burrowing substrate, with an additional 180 ml of aged tap water. In each trial, nine clams were selected by the observer (passively based on conspicuousness) from the stock tank and behavior recorded for one hour via time lapse videos (at a rate of one frame per second) to assess burrowing and crawling behavior. The clams were transferred from the stock tank using 25.4 cm forceps and individuals were arranged in a 3 x 3 grid (Fig. 2) in the center of the watch glass as this arrangement allowed for easy tracking and recording of individuals.

Each independent group of nine clams was exposed to only one of three possible treatments: control, predator-cues, or distressed conspecific-cues. Clams in control treatments were observed in aged tap water only. Clams in predator-cue treatments were observed in water collected from the crayfish tank immediately before each trial began.

Clams in distressed conspecific-cue treatments were observed in aged tap water in the presence of two damaged conspecifics placed on one side of the watch glass. Immediately before each distressed conspecific trial, the two stimulus clams were damaged by placing pressure on the valves with a mortar until the shell cracked. Damaged clams were still alive during the experiments, but immediately euthanized by freezing at the end of the trial. Adults and juveniles were placed into different groups in which all nine individuals were of the same developmental stage. Adults were characterized by being over 8 mm wide, the size class at which reproductive activities become possible (Zumoff, 1973). Clams below this size threshold were considered to be pre-reproductive juveniles.

Time lapse recordings were taken using a Campark® ACT74 action camera mounted on a tripod above the watch glass to capture a clear view of all individuals and their movement during the trial period. Recordings were then transferred to a computer for video analysis.

Video Analysis. A single human observer viewed all video recordings and transcribed relevant behavioral events that occurred during a trial, including whether and when burrowing behavior occurred. When a clam exhibited burrowing behavior, burrowing time was defined as the time that had elapsed between the beginning of the trial and when a clam had ceased burying any further. Timestamps on the video frames were used to measure burrowing time in minutes.

Statistical Analysis. All statistical analyses were performed in JMP Pro (v 14.0) statistical software (SAS Institute, Cary, North Carolina, USA). Results were analyzed with factorial ANOVA using the JMP least squares fit model platform. *Post-hoc* comparisons of least square means were conducted in JMP with the Tukey HSD procedure with $\alpha = 0.05$. Sample size for each analysis was conservatively determined by the number of trial replicates, not the total number of individual clams observed to account for the possibility of interactions among the nine clams in each watch glass. Behavioral data were therefore averaged for each replicate.

Results

Percent Burrowed.

ANOVAs were conducted separately for juveniles [F (2,14) = .1726, p= .8436, Fig 3] and adults [F (2, 26) = 19.8044, p < .0001, Fig 4]. There was a significant effect of trial on proportion of clams burrowed in adults (p < .0001). In general, clams were significantly less likely to burrow in predator treatments than control or distressed conspecific treatments.

Time to Burrow.

ANOVAs were conducted separately for juveniles [F (2,14) = 0.6657, p = .5319, Fig 5] and adults [F (2, 21) = 2.1952, p= .1388, Fig 6] for influence of treatment on mean time to burrow. There was no significant effect of treatment on burrowing time. In general, juvenile clams burrowed faster than adult clams across all treatments.

Size. ANOVAs were conducted separately for juveniles and adults to compare differences in body size of individuals selected for different treatments. There were significant differences in mean body size between treatments for both adults [F (2,24) = 6.9454, p = .0042) and juveniles [F (2,12) = 6.8806, p = .0102). Average size was significantly different between control and distressed clam treatments for adults and juveniles (p< .0042 and p < .0102 respectively), but not between predator-cue and either treatment. This is most likely the result of human bias for larger, more conspicuous specimens during selection. However, it is unlikely that this influenced the experimental outcomes of the study because the behavior of clams did not differ between the control and distressed treatments.

Discussion

The results of this study were unexpected, particularly the depressed burrowing behavior of adult clams in the presence of a predator. Adult clams were least likely to bury themselves when placed in water that previously housed crayfish. Juvenile clams, however, were very likely to bury regardless of experimental treatment. Juvenile clams also buried themselves more rapidly than adults in all treatments.

That adult clams exposed to predator cues were significantly less likely to bury than all other treatments was in contrast to my prediction that the presence of a predator would stimulate burrowing behavior. Burrowing is expected to reduce the likelihood of predation because clams in the substrate presumably require more energy and handling time for the predator to excavate and process relative to prey located on the sediment surface (Klocker & Strayer, 2004; Nyström & Pérez, 1998).Indeed, other species of clam are known to respond to predator cues, burrowing when exposed to a predator or injured conspecific. For example, the Baltic clam (Tellinidae) , *Macoma balthica* and common cockle (*Cardiidae*) *Cerastoderma edule* increase burrowing depth in response to effluent from the predatory crab *Carcinus* maenas (Griffiths & Richardson, 2006) while *Mercenaria mercenaria* responds to both predator signals as well as injured conspecifics (Smee & Weissburg, 2006). The razorshell clam *Ensis directus* is known for particularly rapid burrowing time, moving from a prone position atop the sediment surface to completely buried in less than 30 seconds (Drew, 1907).

However, it is possible that the depressed burrowing behavior of adults in the present study is a function of physiological processes. Czarnołęski (2010) suggested that chemical cues can have a different effect on physical processes in zebra mussels (*Dreissena polymorpha)*, which responded to predator cues (injured conspecifics and effluent from predators that were fed mussels) by reducing crawling speed and distance. The result was surprising, as it was previously thought that increased byssus production was responsible for slower movement in the mussels; but this was not the case because byssus production was halted, suggesting that increased attachment strength is not a viable strategy in response to an immediate threat from a predator (Czarnołęski et al., 2010). Antol et al (2018) subsequently demonstrated suppression of metabolites in zebra mussels as an immediate response to predator cues, with the response modulated to match predation risk. Perhaps for these species reduced risk of detection is more adaptive than resistance to attack (Czarnołęski et al., 2010). If so, the lack of burrowing behavior exhibited by the clams in the present study could be due to a decrease in mobility that reduces emission of metabolites detectable by predators. Anecdotally, clams in the other two (non-predator) treatments were more apt to extend the foot and touch the sediment, even when a burrowing event did not follow. A similar study by Ishida and Iwasaki (2003) found that the solitary intertidal mussel *Hormomya mutabilis (Mytilidae)*, reduced crawling speed in the presence of predators, suggesting that the action of opening the valves and extending the foot provides predators with both visual and olfactory cues. An additional study by Czarnołęski et al. (2011) found that crayfish (*Orconectes limosus*) congeneric to those in the present study used chemosensory cues to detect prey, including bivalves, further suggesting that lowered emission of chemical cues by clams in the present study would have adaptive significance.

Different bivalve species use different cues to assess predation risk, such as cues from the predator itself, cues from injured conspecifics, or a combination of both (Griffiths & Richardson, 2006; Nakaoka, 2000; Tallqvist, 2001). In the current study, clams responded to water presumably containing an olfactory cue(s) from a predator. In the absence of a predator cue, clams in the control treatment and distressed clam treatment buried in greater proportions, coincident with the presumed absence of risk, whereby clams can increase metabolism while burrowing without being detected. It is worth noting that these results are limited to cues from a crayfish predator, and other clam responses might be observed if a different type of predator were present, such as a duck, gull, boring snail, or fish. Future studies of antipredator behavior in this species would therefore benefit from a multi-predator context.

A predator-mediated reduction in clam physiological processes could have ecological consequences, as bivalves perform several important ecological roles including filtration, nutrient cycling, and as a habitat themselves for smaller organisms like epiphytic algae (Beckett et al., 1996; Vaughn & Hakenkamp, 2001). Bivalves affect water clarity by filtering the water column, processing phytoplankton, bacteria, and other organic matter (Strayer 1999, Vaughn 2001). Sphaeriid clams also remove organic matter from the sediment, through the process of deposit feeding (Vaughn & Hakenkamp, 2001). They also affect nutrient cycling in their habitats through deposition of feces and pseudofeces (Vaughn & Hakenkamp, 2001). By reducing activities such as filtering and burrowing, clams become less effective as a filtering system within their environment, possibly causing a decrease in water quality (Newell & Koch, 2004). With increasing populations of invasive predator species like *O. rusticus*, significant reduction in bivalve filtering could have significant negative impacts on ecosystems with large bivalve communities. Unfortunately, in the present study the video camera resolution was not sufficient for direct observation and quantification of the siphoning behavior of individual clams. In the future, a study of siphoning behavior during predator exposure could help elucidate the effect that an abundance of predators might have on water quality in environments with *S. simile* populations.

Contrary to the observed behavior in adults, juvenile clams exhibited similar burrowing behavior in all three treatments. In two studies of substrate preference, Gale et al. (1971, 1973) discovered that species (*S. striatinum, S. transversum*) of sphaeriid clams congeneric to the species in the present study preferred a mud substrate, followed by sandy mud. Perhaps burrowing regardless of threat level is a more general adaptation against predation in juveniles, as the lighter pigmentation of juvenile valves may produce higher contrast against the dark mud substrate in which they tend to burrow, making them easier to detect by visual predators. Innate burrowing regardless of predation risk might also be adaptive for juvenile clams, because smaller clams are more vulnerable to predation at the sediment surface by crayfish than larger clams with thicker shells (Klocker & Strayer, 2004). Klocker (2004) observed this phenomenon in a study comparing *O. rusticus* and *O. limosus*, where both crayfish species preferred to eat exposed bivalves smaller than 7 mm, while buried individuals were generally undisturbed by crayfish and larger clams sustained damage only on the outer margins of the valves. It is also possible that predation is not a factor driving juvenile burrowing behavior at all. Juvenile *S. simile* may bury in order to feed on small particles of inorganic matter in the sediment similar to juvenile unionids (Yeager, Cherry, & Neves, 1994). Although average size was significantly different between control and distressed clam treatments in the current study, this was due primarily to bias during selection of subjects and there were no corresponding differences in burrowing behavior between treatments.

Similarly, selection favoring juveniles that burrow could also influence the evolution of burrowing time if juveniles that burrow quickly reduce predation risk. The physical act of burrowing is also easier for smaller clams, as their smaller shells have a slimmer cross section on the leading edge during burrowing, requiring less energy to burrow than required for burrowing adults (Levine, Hansen, & Gerald, 2013; Stanley, 1970).

It is important to consider the timescale on which clams exhibit behavior when interpreting the results of the present study. Trial times for the experiment were limited to one hour, and therefore all observed behaviors occurred only during that period. This limited the data collection on other aspects of behavior that may have occurred during longer exposure to predator cues. Clams may require several days to alter their behavior in response to a predator. For example, the Baltic clam *Macoma balthica* and the common cockle *Cerastoderma edule* increase burrowing depth in the presence of crab predators over a period of several days (Griffiths & Richardson, 2006). Certainly changes in shell morphology in response to specific predator types, as seen in blue mussels *Mytilus edulis (Leonard et al., 1999)* and Zebra mussels (Hirsch, Cayon, & Svanbäck, 2014) take place on timescales far larger than the scope of the present study. Morphological changes to the size, shape, and weight of the valves during growth and development could also influence antipredator behavior, including likelihood or speed of burrowing. It would therefore be helpful to observe clam behavior during longer experimental trials and observational periods. A much longer study would permit measurement of changes in factors like shell morphology and reproductive output under different predator conditions.

There are many studies about the predators of marine bivalves and their responses (Delavan & Webster, 2012; Flynn & Smee, 2010; Griffiths & Richardson, 2006; Tallqvist, 2001) but many freshwater studies focus only on invasive species (Antoł et al., 2018; Czarnoleski et al., 2011; Hazlett, 1994; Perry et al., 1997; Saloom & Scot Duncan, 2005) predator effects on bivalve distribution. Generally speaking, there is more to be learned about predator response in freshwater bivalves. Further information on the nonlethal effects predators may have on bivalve communities would lead to a better understanding of how predator-prey dynamics shape freshwater ecosystems.

Literature Cited

Antoł, A., Kierat, J., & Czarnoleski, M. (2018). Sedentary prey facing an acute predation risk: testing the hypothesis of inducible metabolite emission suppression in zebra mussels, Dreissena polymorpha. *Hydrobiologia, 810*(1), 109-117.

Beckett, D. C., Green, B. W., Thomas, S. A., & Miller, A. C. (1996). Epizoic invertebrate communities on upper Mississippi River unionid bivalves. *American Midland Naturalist*, 102-114.

Boulding, E. G. (1984). Crab-resistant features of shells of burrowing bivalves: decreasing vulnerability by increasing handling time. *Journal of Experimental Marine Biology and Ecology, 76*(3), 201-223.

Bowers, M. D. (1992). The evolution of unpalatability and the cost of chemical defense in insects. *Insect chemical ecology: an evolutionary approach. Chapman and Hall, New York*, 216-244.

Brown, P. B. (1995). Physiological adaptations in the gastrointestinal tract of crayfish. *American Zoologist, 35*(1), 20-27.

Budelmann, B. U. (1992). Hearing in nonarthropod invertebrates *The evolutionary biology of hearing* (pp. 141-155): Springer.

Carpenter, S. R., & Kitchell, J. F. (1988). Consumer control of lake productivity. *BioScience, 38*(11), 764-769.

Côté, I. M., & Jelnikar, E. (1999). Predator-induced clumping behaviour in mussels (Mytilus edulis Linnaeus). *Journal of Experimental Marine Biology and Ecology, 235*(2), 201-211.

Czarnołęski, M., Müller, T., Adamus, K., Ogorzelska, G., & Sog, M. (2010). Injured conspecifics alter mobility and byssus production in zebra mussels Dreissena polymorpha. *Fundamental and Applied Limnology/Archiv für Hydrobiologie, 176*(3), 269-278.

Czarnoleski, M., Müller, T., Kierat, J., Gryczkowski, L., & Chybowski, Ł. (2011). Anchor down or hunker down: an experimental study on zebra mussels' response to predation risk from crayfish. *Animal behaviour, 82*(3), 543-548.

Delavan, S., & Webster, D. (2012). Predator and flow influence on bivalve clam excurrent jet characteristics. *Journal of Experimental Marine Biology and Ecology, 432*, 1-8.

Drew, G. A. (1907). The Habits and Movements of the Razorshell Clam, Ensis Directus, Con. *The Biological Bulletin, 12*(3), 127-140.

Flynn, A., & Smee, D. (2010). Behavioral plasticity of the soft-shell clam, Mya arenaria (L.), in the presence of predators increases survival in the field. *Journal of Experimental Marine Biology and Ecology, 383*(1), 32-38.

Gale, W. F. (1971). An experiment to determine substrate preference of the fingernail clam, Sphaerium transversum (Say). *Ecology, 52*(2), 367-370.

Gale, W. F. (1973). Substrate preference of the fingernail clam, Sphaerium striatinum (Lamarck)(Sphaeriidae). *The Southwestern Naturalist*, 31-37.

Griffiths, C., & Richardson, C. (2006). Chemically induced predator avoidance behaviour in the burrowing bivalve Macoma balthica. *Journal of Experimental Marine Biology and Ecology, 331*(1), 91-98.

Haszprunar, G. (1987). The fine morphology of the osphradial sense organs of the Mollusca. III. Placophora and Bivalvia. *Phil. Trans. R. Soc. Lond. B, 315*(1169), 37-61.

Hazlett, B. A. (1994). Crayfish feeding responses to zebra mussels depend on microorganisms and learning. *Journal of Chemical Ecology, 20*(10), 2623-2630.

Hirsch, P. E., Cayon, D., & Svanbäck, R. (2014). Plastic responses of a sessile prey to multiple predators: a field and experimental study. *PloS one, 9*(12), e115192.

Ishida, S., & Iwasaki, K. (2003). Reduced byssal thread production and movement by the intertidal mussel Hormomya mutabilis in response to effluent from predators. *Journal of Ethology, 21*(2), 117-122.

Kasprzak, K. (1986). Role of Unionidae and Sphaeriidae (Mollusca, Bivalvia) in the eutrophic Lake Zbęchy and its outflow. *Internationale Revue der gesamten Hydrobiologie und Hydrographie, 71*(3), 315-334.

KASTELEIN, R. A. (2008). Effects of vibrations on the behaviour of cockles (bivalve molluscs). *Bioacoustics, 17*(1-3), 74-75.

King, F. (1883). The food of the crayfish. *American Naturalist, 17*, 980-981.

Klocker, C. A., & Strayer, D. L. (2004). Interactions among an invasive crayfish (Orconectes rusticus), a native crayfish (Orconectes limosus), and native bivalves (Sphaeriidae and Unionidae). *Northeastern Naturalist, 11*(2), 167-178.

Leonard, G. H., Bertness, M. D., & Yund, P. O. (1999). Crab predation, waterborne cues, and inducible defenses in the blue mussel, Mytilus edulis. *Ecology, 80*(1), 1-14.

Levine, T. D., Hansen, H. B., & Gerald, G. W. (2013). Effects of shell shape, size, and sculpture in burrowing and anchoring abilities in the freshwater mussel Potamilus alatus (Unionidae). *Biological Journal of the Linnean Society, 111*(1), 136-144.

Lima, S. L. (1998). Nonlethal effects in the ecology of predator-prey interactions. *BioScience, 48*(1), 25-34.

Lin, J., & Hines, A. H. (1994). Effects of suspended food availability on the feeding mode and burial depth of the Baltic clam, Macoma balthica. *Oikos*, 28-36.

Lodge, D. M., Kershner, M. W., Aloi, J. E., & Covich, A. P. (1994). Effects of an omnivorous crayfish (Orconectes rusticus) on a freshwater littoral food web. *Ecology, 75*(5), 1265-1281.

Lodge, D. M., Taylor, C. A., Holdich, D. M., & Skurdal, J. (2000). Reducing impacts of exotic crayfish introductions. *Fisheries, 25*(8), 21-23.

Mackie, G. (1978). Are sphaeriid clams ovoviviparous or viviparous. *Nautilus, 92*(4), 145-146.

Mackie, G. L., & Bailey, R. C. (2007). *Biology of freshwater corbiculid and sphaeriid clams of North America* (Vol. 15): Ohio Biological Survey Columbus, Ohio.

McMahon, R. F., & Bogan, A. (1991). Mollusca: bivalvia. *Ecology and classification of North American freshwater invertebrates*, 315-399.

Momot, W. T. (1995). Redefining the role of crayfish in aquatic ecosystems. *Reviews in Fisheries Science, 3*(1), 33-63.

Momot, W. T., Gowing, H., & Jones, P. D. (1978). The dynamics of crayfish and their role in ecosystems. *American Midland Naturalist*, 10-35.

Moore, P. A., & Grills, J. L. (1999). Chemical orientation to food by the crayfish Orconectes rusticus: influence of hydrodynamics. *Animal behaviour, 58*(5), 953-963.

Morton, B. (2008). The evolution of eyes in the Bivalvia: new insights. *American Malacological Bulletin, 26*(1/2), 35-45.

Nakamura, Y., & Kerciku, F. (2000). Effects of filter-feeding bivalves on the distribution of water quality and nutrient cycling in a eutrophic coastal lagoon. *Journal of Marine Systems, 26*(2), 209-221.

Nakaoka, M. (2000). Nonlethal effects of predators on prey populations: predator-mediated change in bivalve growth. *Ecology, 81*(4), 1031-1045.

Newell, R. I., & Koch, E. W. (2004). Modeling seagrass density and distribution in response to changes in turbidity stemming from bivalve filtration and seagrass sediment stabilization. *Estuaries, 27*(5), 793-806.

Nyström, P., & Pérez, J. R. (1998). Crayfish predation on the common pond snail (Lymnaea stagnalis): the effect of habitat complexity and snail size on foraging efficiency. *Hydrobiologia, 368*(1-3), 201-208.

Perry, W. L., Lodge, D. M., & Feder, J. L. (2002). Importance of hybridization between indigenous and nonindigenous freshwater species: an overlooked threat to North American biodiversity. *Systematic Biology, 51*(2), 255-275.

Perry, W. L., Lodge, D. M., & Lamberti, G. A. (1997). Impact of crayfish predation on exotic zebra mussels and native invertebrates in a lake-outlet stream. *Canadian Journal of Fisheries and Aquatic Sciences, 54*(1), 120-125.

Reisinger, L. S., Elgin, A. K., Towle, K. M., Chan, D. J., & Lodge, D. M. (2017). The influence of evolution and plasticity on the behavior of an invasive crayfish. *Biological invasions, 19*(3), 815-830.

Roberts, L., Cheesman, S., Breithaupt, T., & Elliott, M. (2015). Sensitivity of the mussel Mytilus edulis to substrate-borne vibration in relation to anthropogenically generated noise. *Marine Ecology Progress Series, 538*, 185-195.

ROPEZ, J. (1968). The feeding habits of the green crab, Carcinus maenus (L.). *Fisheries Bulletin, 67*(2), 183-203.

Saloom, M. E., & Scot Duncan, R. (2005). Low dissolved oxygen levels reduce anti-predation behaviours of the freshwater clam Corbicula fluminea. *Freshwater Biology, 50*(7), 1233-1238.

Schmidt, J. O. (1990). *Insect defenses: adaptive mechanisms and strategies of prey and predators*: SUNY Press.

Smee, D. L., & Weissburg, M. J. (2006). Clamming up: environmental forces diminish the perceptive ability of bivalve prey. *Ecology, 87*(6), 1587-1598.

Stanley, S. M. (1970). *Relation of shell form to life habits of the Bivalvia (Mollusca)* (Vol. 125): Geological Society of America.

Tallqvist, M. (2001). Burrowing behaviour of the Baltic clam Macoma balthica: effects of sediment type, hypoxia and predator presence. *Marine Ecology Progress Series, 212*, 183-191.

Taylor, C. A., & Redmer, M. (1996). Dispersal of the crayfish Orconectes rusticus in Illinois, with notes on species displacement and habitat preference. *Journal of Crustacean Biology, 16*(3), 547-551.

Vaughn, C. C., & Hakenkamp, C. C. (2001). The functional role of burrowing bivalves in freshwater ecosystems. *Freshwater Biology, 46*(11), 1431-1446.

Vermeij, G. J. (1977). Patterns in crab claw size: the geography of crushing. *Systematic Biology, 26*(2), 138-151.

Ydenberg, R. C., & Dill, L. M. (1986). The economics of fleeing from predators *Advances in the Study of Behavior* (Vol. 16, pp. 229-249): Elsevier.

Yeager, M., Cherry, D., & Neves, R. (1994). Feeding and burrowing behaviors of juvenile rainbow mussels, Villosa iris (Bivalvia: Unionidae). *Journal of the North American Benthological Society, 13*(2), 217-222.

Zumoff, C. H. (1973). The reproductive cycle of Sphaerium simile. *The Biological Bulletin, 144*(1), 212-228.

Fig. 1 *Example of S. simile with unique color ID representing 4234. (Photograph: Jesse Eichler)*

Fig. 2 *Example of clam arrangement at beginning of trials (Photograph: Jesse Eichler)*

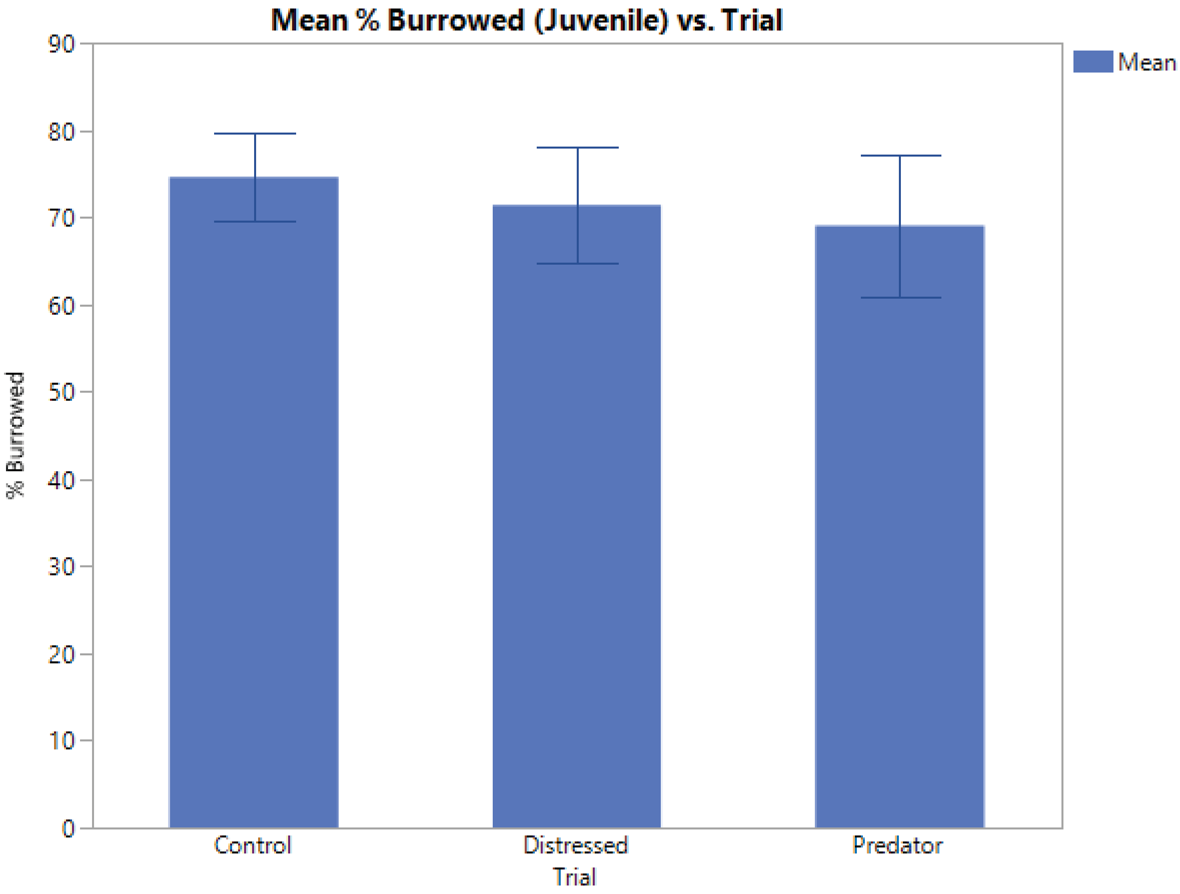

Fig. 3 Relationship between percent burrowed individuals (Juvenile) in different experimental treatments

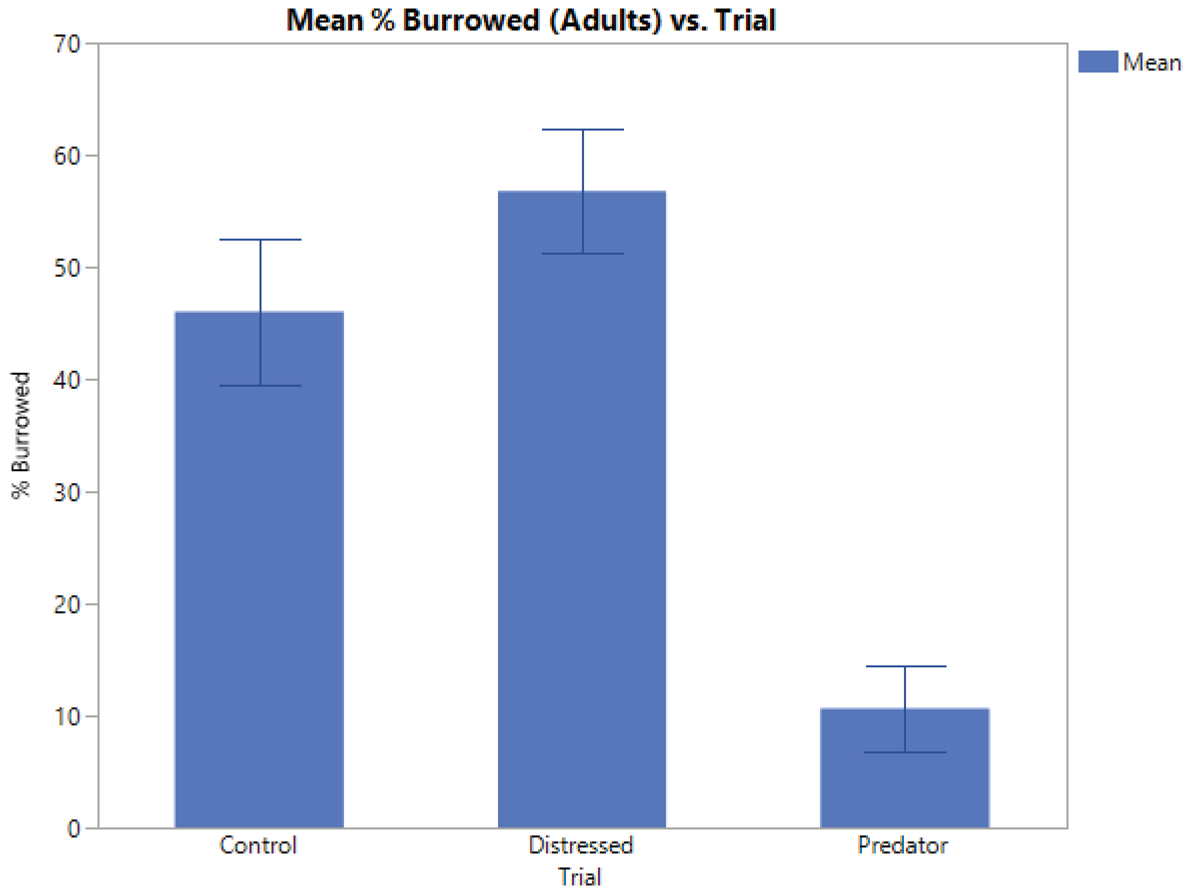

Fig. 4 Relationship between percent burrowed individuals (Adult) in different experimental treatments

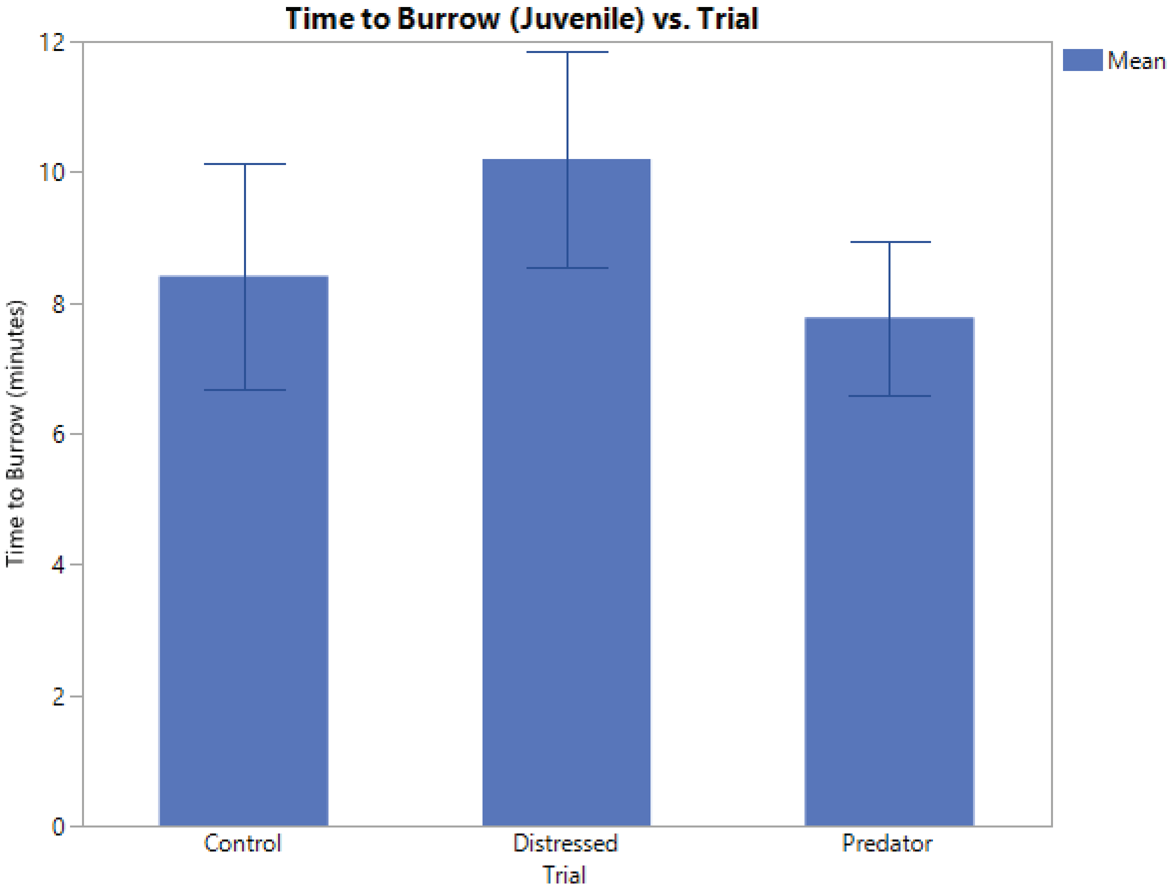

Fig 5. Relationship of time to burrow (Juveniles) in different experimental treatments

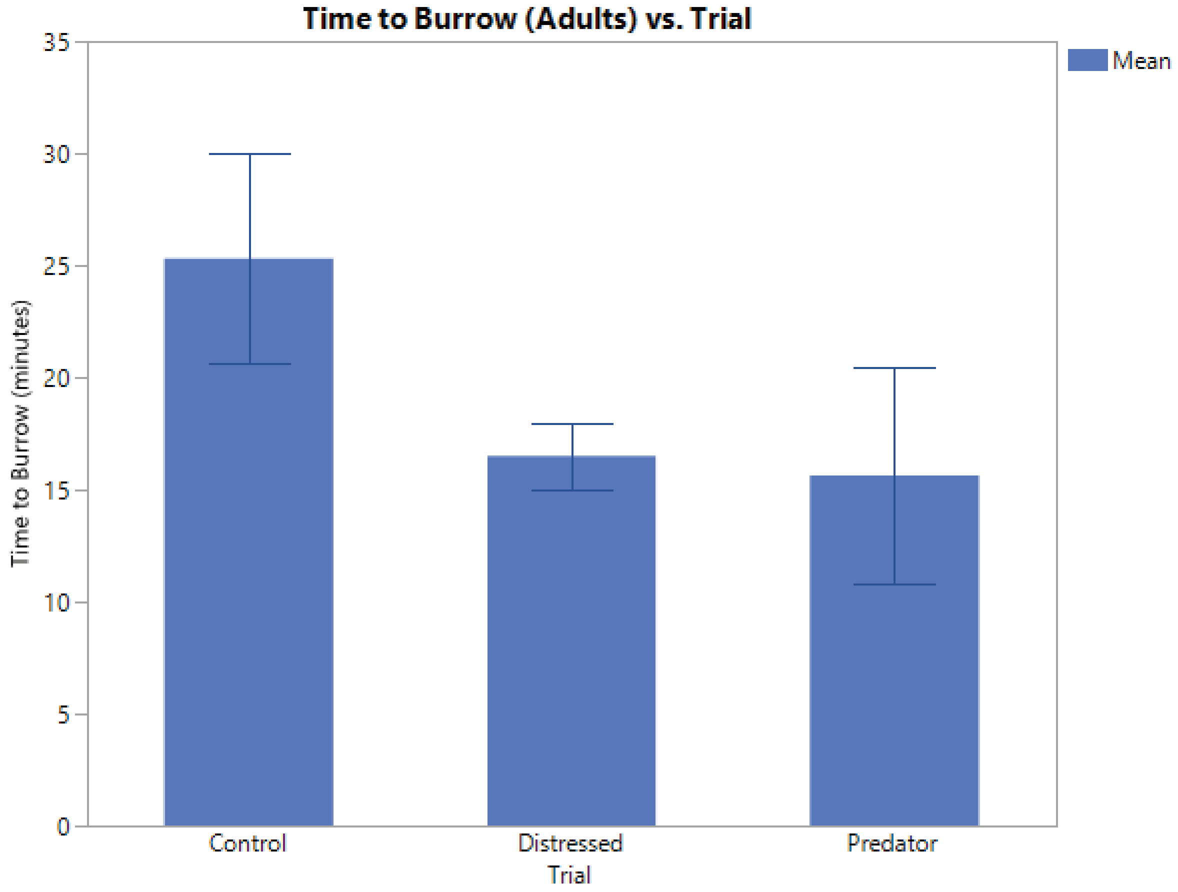

Fig 6. Relationship of time to burrow (Adults) in different experimental treatments