Temporal and spatial refugia modify predation risk for invasive crabs in rocky intertidal habitats (#91492)

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Temporal and spatial refugia modify predation risk for invasive crabs in rocky intertidal habitats

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Populations of the invasive Asian shore crab, *Hemigrapsus sanguineus*, now dominate the rocky intertidal of southern New England. High abundances suggest the recent invader may have experienced enhanced success as a result of enemy release. While larvae and juveniles may serve as a food source for ecologically important species, little is known about predation of mature *H. sanguineus,* or the influence of habitat on predation pressure. To assess natural predation rates of adult *H. sanguineus,* crabs were tethered in the intertidal at Clarks Cove in New Bedford, MA. Crabs were left *in situ* for half of a daytime or nighttime tidal cycle then observed for signs of predation. Results of separate high and low tide trials show adult crabs were preyed upon at both high and low tide, though at a significantly higher rate during high tide during both daytime and nighttime, suggesting predation by aquatic species is greater than that by terrestrial species. To investigate the role of habitat as refuge from predation, a laboratory experiment manipulated the complexity of habitat provided to crabs in the presence of native fish predators. Results indicate better refuge is provided by more complex shelter. Together, findings suggest fish, crabs, and/or diving birds are important predators for *H. sanguineus* in the invaded range and that habitat refuge acts to reduce predation pressure.

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Abstract

Populations of the invasive Asian shore crab, *Hemigrapsus sanguineus*, now dominate the rocky intertidal of southern New England. High abundances suggest the recent invader may have experienced enhanced success as a result of enemy release. While larvae and juveniles may serve as a food source for ecologically important species, little is known about predation of mature *H. sanguineus,* or the influence of habitat on predation pressure. To assess natural predation rates of adult *H. sanguineus,* crabs were tethered in the intertidal at Clarks Cove in New Bedford, MA. Crabs were left *in situ* for half of a daytime or nighttime tidal cycle then observed for signs of predation. Results of separate high and low tide trials show adult crabs were preyed upon at both high and low tide, though at a significantly higher rate during high tide during both daytime and nighttime, suggesting predation by aquatic species is greater than that by terrestrial species. To investigate the role of habitat as refuge from predation, a laboratory experiment manipulated the complexity of habitat provided to crabs in the presence of native fish predators. Results indicate better refuge is provided by more complex shelter. Together, findings suggest fish, crabs, and/or diving birds are important predators for *H. sanguineus* in the invaded range and that habitat refuge acts to reduce predation pressure.

Introduction

A prominent factor thought to facilitate the proliferation of invasive populations is enemy release (Heger & Jeschke, 2018), wherein non-native species benefit from a reduction in natural predators, competitors, and parasites in the naïve systems they invade (Colautti et al., 2004). While enemy release may confer an advantage to non-native species (Antonini et al., 2019; Roznik et al., 2020), invasion success is dependent on a myriad of ecological and environmental interactions within native communities (Weis, 2010; Prior et al., 2015).

Across taxa and environments, the availability of temporal and spatial refuge can act to constrain predation risk (Prugh & Golden, 2014; Palmer et al., 2022; Suraci et al., 2022). Habitat structure, the arrangement of biotic and abiotic substrate that supports plant and animal communities (Carvalho & Barros, 2017), can mediate interactions between predators and prey by providing spatial refuge in which prey can more easily avoid capture (Warfe & Bermuta 2004; Lei, Lin & Zhang, 2014; Mendez, Schwindt & Bortolus 2015; Pozzebon, Loeb & Duso, 2015). In addition to habitat-specific structural refuge, predation risk can change over time (Sperry et al., 2008). For example, risk and refuge for prey can exhibit diel variation (Clark, Ruiz & Hines, 2003). More to the point, the availability of refuge is a consequential determinant of predation risk (Smith et al., 2019), but rarely explored as a factor influencing enemy release (Soifer & Ackerman, 2019).

Evidence suggests a recent invader to the rocky shores of the North American Atlantic coast, the Asian shore crab, *Hemigrapsus sanguineus*, may have experienced enhanced success as a result of enemy release. The abundance of *H. sanguineus* in invaded habitats can far exceed densities found along the native Asian-Pacific region (Takahashi et al., 1985; Lohrer et al., 2000). Today, Asian shore crabs are the most abundant intertidal crab species in southern New England and Long Island Sound (Kraemer et al., 2007; O'Connor, 2014), and can reach densities of >300 crabs m^{-2} at some locations (O'Connor, 2018). The species' success since its introduction to the northeast US in the 1980s is thought to be explained, in part, by reduced impact of natural enemies compared to the populations in native habitats (Pushchina & Panchenko, 2002; Brousseau et al., 2008).

Invasive Asian shore crabs benefit from significantly lower prevalence of parasitic infection (Lohrer, 2001; Blakeslee et al., 2009), out-compete resident crab species, and may have fewer crab competitors along the eastern US (Sakai, 1976; Jensen, McDonald & Armstrong, 2002; Kraemer et al., 2007; Hobbs, Cobb & Thornber, 2017). In other systems, native predators can act as biological resistance against the growth of invasive populations, with several examples including non-native crabs (Noé et al., 2017; Tiralongo, Messina & Lombardo, 2021). The relationship between the invasive Asian shore crab and native predators, however, remains ambiguous in the absence of direct field experimentation and laboratory tests with adult crabs. Additionally, factors that modify predator-prey relationships, like spatial and temporal refuge, should be more fully explored to clarify the factors influencing enemy release in invaded systems.

For benthic aquatic species, the availability of refuge can have a strong effect on survival (Coull & Wells, 1983; Scharf, Manderson & Fabrizio, 2006; Nunes, Sampaio & Barros, 2015) and community structure (Margiotta et al., 2016; Hesterberg et al., 2017). Habitat structure can provide spatial refuge from predation by limiting the ability of predators to access prey (Toscano & Griffen, 2013). Asian shore crabs inhabit highly complex rocky intertidal habitats (Gilman & Grace, 2009); if predator-prey dynamics can be modified by habitat refuge then invasive populations across different coastal habitats may experience different degrees of enemy release.

Intertidal environments are particularly unique because they can be accessed by fish only during the high tide period of the tidal cycle, providing a substantial temporal refuge from marine predators at low tide. In contrast, predator-prey dynamics during periods of low tide are underexplored. Despite serving as an important link between marine and terrestrial ecosystems, coastal mammalian and avian predators have been largely overlooked by research on intertidal systems (Quammen, 1984; Wootton, 1992; Carlton & Hodder, 2003). Terrestrial mammals including rats, minks, skunks (Amos, 1966), shrews (Churchfield ,1990), raccoons (Ricketts et al., 1985), mice (Drever et al., 2000), and even foxes (Fay & Stephenson, 1989) are all observed to feed on intertidal invertebrates. Similarly, coastal birds, like gulls, are apex predators that can affect the distribution of intertidal organisms and impact the density of species like crabs (Dumas & Witman, 1993; Ellis at al., 2007). Yet the impact of bird predation is rarely considered in studies of New England's rocky intertidal zone, particularly in relation to highly mobile prey (Menge, 1976; Edwards, Conover & Sutter, 1982). In addition, most intertidal studies have been conducted during daytime. Thus, our knowledge of predator activity during low tide and nocturnal times is severely limited. The influence of habitat structure, and relative predation throughout the tidal and diel cycle, should be considered when assessing a species' risk or release from enemies.

In its native range, *H. sanguineus* is known to be consumed by two species of sculpins, *Myoxocephalus stelleri* and *M. brandti* (Pushchina & Panchenko, 2002). Species thought to prey on invasive *H. sanguineus* include those that utilize the rocky intertidal zone to forage, and species that are adapted to eating hard-shelled benthic invertebrate prey, including fish and likely bird species (Epifanio, 2013). Of the potential predators of invasive Asian shore crabs present throughout its range in northeast North America, only predation by fish on juveniles has been examined. Native coastal fish including tautog (*Tautoga onitis*), cunner (*Tautogolabrus adspersus),* scup (*Stenotomus chrysops*), and grubby (*Myoxocephalus aenaeus*) are all documented to consume *H. sanguineus* megalopae in the laboratory (Rasch & O'Connor, 2012). Striped killifish (*Fundulus majalis*) also readily consumed planktonic larval stage (megalopae) *H. sanguineus* in the lab but did not feed on small (sexually immature) crabs (Kim & O'Connor, 2007). However, little is known about predation on larger, sexually mature *H. sanguineus.*

Tautog*, Tautoga onitis*, is a temperate reef fish that plays an important role in the structure of nearshore marine communities as a specialized predator of hard-shelled benthic invertebrates including crabs (Liem & Sanderson, 1986; Clark et al., 2006). Tautog is a major component of recreational catch and a valuable commercial fishery resource from Massachusetts to Virginia (Steimle & Shaheen, 1999). The species occurs in coastal environments from Nova Scotia to South Carolina and is most abundant from Cape Cod to Chesapeake Bay (Dorf & Powell, 1997; Steimle & Shaheen, 1999), occurring throughout the North American invasive range of *H. sanguineus*.

Tautog is a member of the Labridae family, named for their terminal protractile mouths and jaw morphology associated with hard-prey diets (Liem & Sanders, 1986). The species reaches a maximum size of 90 cm (about 6 kg) (Collette & Klein-MacPhee, 2002), and feeds predominantly on mussels and other shellfish, including Atlantic rock crabs (*Cancer irroratus*), Jonah crabs (*Cancer borealis*) and small American lobsters (*Homarus americanus*) (Smith, 1907; Steimle & Ogren, 1982; Richards, 1992). Cunner, *Tautogolabrus adspersus*, is another Labrid fish which is abundant along the inshore temperate waters of the Gulf of Maine (Bigelow & Schroeder, 1953) and consumes a wide variety of invertebrate prey, including crabs (Liem &

Sanderson, 1986; Bowmen et al., 2000). Both Labrid species have high affinity for benthic structure and aggregate around substrate like rocks and docks (Olla, Bejda & Martin, 1975; Auster, 1989). Tautog and cunner begin foraging soon after sunrise and feed until evening twilight (Olla, Bejda & Martin, 1975). They follow the flood tide up above low water levels to forage in the intertidal zone and find their prey visually using a scan-and-pick foraging strategy (Olla et al., 1974; Deacutis, 1982), then return to deeper water during the ebb tide (Bigelow & Schroeder, 1953).

Limited studies on the gut contents of wild fishes, including tautog and *Fundulus spp.* killifish, *F. majalis,* and mummichog, *F. heteroclitus*, since the establishment of the invasive Asian shore crab provide evidence that *H. sanguineus* are consumed in nature, but at relatively low frequencies compared to other food items (Clark et al., 2006; Brousseau et al., 2008). In one laboratory choice experiment, tautog consumed juvenile *H. sanguineus*, but less often than native prey species of mud crabs (family Panopeidae) and blue mussels, *Mytilus edulis* (Savaria & O'Connor, 2013). Conversely, other laboratory experiments found cunner, tautog, and black sea bass (*Centropristis striata*) preferentially preyed upon *H. sanguineus* when given the choice with other local crab species (native mud crab *Panopeus herbstii*, and resident European green crab *Carcinus maenas*), and that substrate influenced predator preference (Heinonen & Auster, 2012). These native fish are well-equipped to influence the abundance of sexually mature *H. sanguineus,* however, that dynamic has not yet been investigated and questions remain about the role of spatial and temporal refuge as a potential mechanism to facilitate enemy release.

The purpose of this study was to measure predation of sexually mature Asian shore crabs in the field to examine temporal refuge from predation risk and use laboratory experiments to assess the influence of spatial refuge on predation. This investigation includes a series of field tethering experiments to test relative predation of adult *H. sanguineus* at high tide and low tide, during daytime and nighttime. Tethering is a useful method to compare relative predation intensity (Moody & Aronson, 2007; Glazner, Ballard & Armitage, 2021). In addition, a series of laboratory feeding trials were conducted to test the influence of high and low levels of habitat refuge on predation of sexually mature *H. sanguineus* by the fish predator *T. onitis*.

Materials & Methods

Field experiment

Crab collection and housing

Male (n = 28) and female (n = 6) sexually mature *Hemigrapsus sanguineus* (15 - 22 mm in carapace width, CW) used for tethering experiments were collected at the study site in Clark's Cove, New Bedford, Massachusetts (41°35′40.33″N, 70°54′37.45″W) by hand at low tide and outfitted with tethers 12 – 24 h prior to experimentation. Crabs were held individually in 113 L aerated aquaria, with water sourced directly from Clark's Cove, and kept at ambient conditions (temp 20.5 - 24.5 °C, salinity 33-34), housed adjacent to the field site at the University of Massachusetts School for Marine Science and Technology Seawater Lab. Outfitting crabs with tethers beforehand ensured that the tether was retained and did not impede mobility.

The tethering apparatus was constructed using 0.3 m of monofilament fishing line (6.8 kg test strength) secured to the crab by looping around the transverse plane of the body between the 2nd and 3rd walking legs. The line was tied at the dorsal midline and the knot was secured with a drop of cyanoacrylate glue. Crabs were reliably recovered using this tethering method and the tether was not shown to cause damage to the crabs when subjected to simulated wave energy in the lab.

Field tethering procedure

Field tethering experiments were conducted in the lower intertidal zone of Clark's Cove, New Bedford, MA (41°35′40.33″N, 70°54′37.45″W) June 28 - August 26, 2020 (Table 1) at +0.29 m above mean low water. Previous investigations at the study site showed crabs were most abundant at that tidal elevation (Towne, Judge & O'Connor, 2023).

To prepare the field site for tethering experiments, all rocks and cobble were removed from a 1 m diameter circle, so that only flat sandy substrate was available to the tethered crab. At the time of experimentation, the free end of the tether line was attached to the top of a 10 cm stake embedded in the sediment. Two experimental replicates (plot A and B) were established >10 m apart. The experiments took place during low tide and high tide, during daytime (daylight hours) and nighttime (after sunset). Tethered crabs were left in situ for half of a daytime or nighttime tidal cycle (beginning three hours before low/high tide and ending three hours after low/high tide). Crabs were considered to have been eaten by predators if missing at the end of the trial. Each crab was used for a single trial, and surviving crabs were returned to the wild, outside of the area where this work was performed.

Field tethering analysis

To test whether tide (high / low) and time (daytime / nighttime) influence predation of adult crabs, predation was examined using binomial regression. The dependent variable (predation) was coded as binary data (predation = 1; no predation = 0). The test determined the probability that a crab would be eaten based on the independent variables tide (high / low), and time (daytime / nighttime). The interaction between each of the independent variables (time and tide) were not significant and therefore excluded from the final model. Other independent variables including trial position (plot A or B), trial date, tide time, tidal height, crab sex, moon phase, and their interactions were tested with an expanded binomial regression, and were not found to significantly influence predation, so they were also excluded from the final analysis. Significance of factors was evaluated with analysis of deviance using the anova() function of the car v3.1-2 package in R (Fox and Weisberg 2019). All statistical analyses performed in this study were done using R v4.0.0 (R Core Team, 2020).

Laboratory experiment

Crab and fish collection

The twenty-seven *Tautoga onitis* (25.5 – 37 cm total length) used in the laboratory experiment were caught in New Bedford Harbor, MA using unbaited traps May 13 – June 4, 2021. Fish were collected during annual trap surveys conducted by the Massachusetts Division of Marine Fisheries; traps were checked at least every three days. Fish were transported in a 50 L insulated cooler with fresh seawater and continuous aeration. Fish were held in groups of < 10 for a two-week acclimation period ahead of experimentation. During acclimation, fish were fed crabs and cracked clams to satiation. Fish and crabs were housed, and experiments were conducted, in 1.8 m diameter tanks (tank floor area = 2.6 m^2) continuously supplied with ambient seawater from Clarks Cove, New Bedford (water temp 20.5 - 24.5 °C, salinity 33-34) and artificially lit to match natural light-dark cycles. Tanks were cleaned daily. Fish were provided pieces of large PVC pipe (10.2 cm diameter) for shelter during acclimation. Each fish was used for a single trial, then returned to the wild.

The 720 *Hemigrapsus sanguineus* (14 – 20 mm) used in these tests were collected from the rocky intertidal in Clark's Cove 12 - 24 h prior to experimentation. Crabs were held in one tank in mesh-sided 0.5 L Tupperware containers in groups of <6 crabs. Crabs were not fed during this time. Only non-gravid crabs with all ten limbs were used in this study. Each crab was used for a single experiment.

Lab experiment treatment construction

Habitat structure provided during the lab experiment was constructed from concrete pavers (L = 40 cm, W = 20 cm, H = 5 cm). The experiment included a No Refuge control treatment without structure, as well as a control treatment without a fish predator. Low Refuge Habitat consisted of two pavers laid flat on the bottom of the tank (Fig. 1). High Refuge Habitat consisted of two pavers, modified with the addition of twelve quartzite river stones (2-3 cm) glued to one long edge of the pavers using saltwater resistant Seachem cyanoacrylate Reef Glue™ which created 1984 cm^3 of refuge space under each paver (Fig. 1).

All materials were rinsed with fresh water and allowed >24 h to air dry before use. The glue was given >24 h to cure. Stones remained glued in place throughout the duration of the experiment.

Each tank was outfitted with a shelter for the fish made of three large PVC tubes (10.2 cm diameter), suspended 8 cm above the tank floor in the center of the tank (Fig. 1). Fish utilized the inside and the outside of the PVC tubes as shelter. These PVC tubes were not accessible to the crabs. Fish were maintained and housed under University of Massachusetts Dartmouth Institutional Animal Care and Use Committee protocol # 21-02 approved July 19, 2021.

Lab experimental procedure

Experimental tanks were randomly assigned habitat treatments. Nine trials were conducted for each habitat treatment (High Refuge, Low Refuge, No Refuge, and no fish control). One fish was used per trial and allowed 24 h to acclimate in the experimental tank prior to the experiment, during which time the fish was not fed. Tautog require 8 h to process and evacuate food (Olla et al., 1974). To begin the experiment, habitat treatments were lowered into the tanks (pavers placed >0.5 m away from each other and from tank walls) and 20 crabs were added to the tank. A dip net was used to quarantine the fish for 15 min to allow the crabs to acclimate to the experimental tank. Fish were then given 6 h to feed. Results of pilot work showed, when starved for 24 h, a Tautog (35 cm total length) could consume between 20 and 30 *Hemigrapsus sanguineus* (10 mm - 18 mm CW) in 6 h. All trials were conducted during daylight hours, approximately 0700 – 1300.

At the end of each trial, the surviving crabs were counted. Fish were returned to storage tanks and observed for an hour after experimentation, then transported in a cooler with sea water to Clark's Cove. No fish showed signs of illness or injury, and all 27 fish used in experiments were released. Tanks were drained and cleaned following each experiment.

Lab experimental analysis

The proportion of crabs eaten was calculated for all trials. To test if habitat refuge treatments influenced the proportion of crabs eaten, all habitat treatments were compared using a one-way ANOVA. A Tukey post hoc test was then performed to determine any differences among levels of habitat complexity. Other independent variables including fish size, water temperature, and experimental tank (A, B, C, D) were tested using an expanded ANOVA model, none of which had significant influence on the proportion of crabs eaten, so were excluded from the final analysis. Data met the assumptions of normality and homogeneity of variance. Significance of factors was evaluated with type-III sums of squares using the R package car (Fox and Weisberg 2019).

Results

Field tethering

One male and one female crab were found damaged (lost multiple limbs) after experiments, and although injuries were likely the result of predation attempts by a small predator, injured crabs were excluded from the analysis. Of the remaining 32 crabs, seventeen were missing and presumed eaten, and fifteen crabs were recovered unharmed. The proportion of crabs missing during daytime high tides was 0.83 (n = 6); nighttime high tides was 0.89 (n = 9), daytime low tides was 0.22 (n = 9), nighttime low tides was 0.25 (n = 8) (Fig. 2). There was a significantly higher probability of predation at high tide compared to low tide (df = 30, X^2 = 30.330, p < 0.001), while daytime or nighttime did not influence the probability of predation (df = 29, X^2 = 30.245, p = 0.77) (Table 2).

Laboratory experiment

In the control (no fish) treatment, all crabs survived without injury. Predation in laboratory feeding trials varied significantly with habitat complexity (p < 0.001) (Fig. 3, Table 3). The proportion of crabs eaten was significantly lower in the presence of High Refuge Habitat (mean = 0.18, SD = 0.13, median = 0.15) compared to both Low Refuge Habitat (mean = 0.64, SD = 0.13, median = 0.70) (p <0.001) and No Refuge (mean = 0.71, SD = 0.16, median = 0.65) (p <0.001). There was no difference in predation between the Low Refuge Habitat and No Refuge treatments (p = 0.63) (Fig. 3, Table 4). One fish consumed all 20 crabs available in the experiment (No Refuge, fish total length = 31 cm), and one fish consumed zero crabs (High Refuge Habitat, fish total length = 35.5 cm).

Discussion

Predation of *Hemigrapsus sanguineus* was influenced by tide (high tide / low tide) and not affected by time (daytime / nighttime) in field experiments. Crabs had a higher probability of being eaten during high tide than low tide. However, predation at high tide and predation at low tide occurred at similar rates irrespective of time of day. The tethering experiment in the field likely overstated actual predation risk, because the tether apparatus restricted the crabs' ability to flee predators, and the experiment was conducted in the absence of refuge for the crab. Nevertheless, results show predation of adult Asian shore crabs can occur during high tide and low tide, and during daytime and nighttime, suggesting that diurnal as well as nocturnal marine and terrestrial species can prey on the invasive Asian shore crab.

Tautog and cunner were likely the primary fish species responsible for predation at high tide during this study. The native fishes are specialized for consuming hard-shelled invertebrates in the intertidal zone during high tide (Olla et al., 1974), and are known to feed on crabs, including *H. sanguineus* (Clark et al., 2006). At the study site, beach seines deployed during daytime high tides in August 2020 found 5 species of fish (Table 5), of which tautog and cunner were the only candidate species for preying on benthic adult crabs. Additionally, in >20 h of video footage recorded of tethered crabs for pilot work (July 18 – August 23, 2020) there were three predation attempts observed during daytime high tides and all appeared to involve tautog and/or cunner (pers. obs.). Other species, that are unlikely to prey on adult crabs, including the American puffer and Alewife were observed in footage, and found in beach seines, but were not seen interacting with crabs (Table 5; pers. obs.).

When predation occurred during high tide field experiments, the free end of tether line was found broken and masticated, which is consistent with feeding morphology of Labrid fishes that masticate prey with knob-like teeth lining their mouth and pharynx (Liem & Sanderson, 1986, Collette & Klein-MacPhee, 2002). Most crabs in the field experiments were entirely consumed, most likely by Tautog which can swallow small crustaceans whole and use their pharyngeal teeth to crush larger prey (Collette & Klein-MacPhee, 2002). Two crabs in the tethering experiment were found alive but missing limbs after the trial. Those incidences better reflect the feeding strategy of a smaller fish predator like cunner which use their highly evolved jaw morphology to shear and crush food items (Collette & Klein-MacPhee, 2002).

Higher probability of predation during high tide may, in part, be explained by what is known about the behavior of the Asian shore crab. Both male and female *H. sanguineus* are highly mobile and can travel up to 16 m over a single day (Brousseau et al., 2002). Thought to be most active at high tide, laboratory experiments conducted during daytime found crabs were more likely to move under and out from under shelter when submerged in water (Towne, Judge & O'Connor, 2023). Activity at high tide may expose crabs to visual predators, like tautog and cunner, which use a scan-and-pick foraging strategy to feed in the intertidal zone (Dew, 1976; Deacutis, 1982) where the crabs occur (Brousseau et al., 2002; Epifanio, 2013; Towne, Judge & O'Connor, 2023).

Given greater relative predation at high tide, periods of low tide appear to offer, to some extent, temporal refuge from predation. While at lower levels, predation did occur during field tethering experiments at low tide, demonstrating that species that are not strictly aquatic also pose a predation risk to adult *H. sanguineus*. Other invertebrate species could have been responsible for the predation observed in this study at high tide or low tide. European green crabs, *Carcinus maenas*, Atlantic rock crabs, *C. irroratus*, and blue crabs, *Callinectes sapidus*, co-occur with Asian shore crabs on the US east coast (DeRivera et al., 2005). Additionally, other resident crab species have been found in intertidal surveys conducted at the location of these field experiments (Z. Towne, 2020, pers. comm.). The European green crab avoids competitive interactions with Asian shore crabs (Hobbs, Cobb & Thornber, 2017). Blue crabs, however, are known to exert biotic resistance to limit the density and distribution of other invasive invertebrate species like European green crabs (DeRivera et al. 2005), as well as zebra mussels (Molloy, Powell & Ambrose, 1994), and whelks (Harding 2003). Blue crabs are expanding their range northward due to increasing water temperature in the Gulf of Maine (Johnson, 2015) and increasingly overlap with the invasive range of *H. sanguineus* in North America. The antagonistic interactions between Asian shore crabs and blue crabs (MacDonald et al., 2007) deserve further exploration to understand *H. sanguineous* as prey under current and future conditions. Large Asian shore crabs are also known to cannibalize sub-adult conspecifics (Crane & O'Connor, 2021), and while not the dynamic under focus in this study, predation threats for Asian shore crabs are known to change across ontogeny (Kim & O'Connor, 2007), which further complicates questions about enemy release.

Benthic species in rocky intertidal communities are commonly prey for birds (Edwards et al., 1982; Wootton, 1992). Previous experiments that have excluded avian predators from rocky intertidal habitat found the absence of bird predation caused a significant increase in the density of intertidal crabs like *Cancer borealis* (Ellis et al., 2007). Predation of invasive *H. sanguineus* specifically by avian predators has not been well documented but merits additional investigation. Several species of shorebirds were noted at the site where field tethering experiments were conducted; cormorants (family Phalacrocoracidae) and gulls (family Laridae) were observed feeding in the intertidal during daytime low tides but none were seen consuming crabs (A. Marcelino, 2020, pers. comm.). Similarly, the relationship between Asian shore crabs and coastal mammals has yet to be investigated. Animals like rats, skunks, and racoons are known to consume intertidal organisms (Carlton & Hodder, 2003) and have been observed at the experimental location (pers. obs.), and so may be responsible for the low tide predation observed here. Further research should include field studies that specifically measure the impact of non-fish predators and the variation in predation risk and refuge throughout the tidal cycle, which could have an effect on the degree of enemy release experienced by invasive Asian shore crabs.

In the field experiments conducted here, the probability of predation was similar during daytime and nighttime. This is counter to the hypothesis that predation risk would be constrained to the daytime period of the diel cycle, because of the propensity of high tide predators to restrict their activity to daytime. For example, tautog cease feeding at night (Dew, 1976; Deacutis, 1982; Collette & Klein-MacPhee, 2002).

Predation during nighttime high tides indicates consumption by nocturnal piscine or crab predators. The American eel, *Anguilla rostrata*, feeds at night (Collette & Klein-MacPhee, 2002) and is ubiquitous in coastal habitats throughout the Gulf of Maine (Sheppard & Block, 2013). While notorious for being an indiscriminate predator and scavenger of animal food items, large eels are known to feed on crustaceans (Ogden, 1970) which may explain the predation measured during nighttime high tides. Potentially increased nighttime activity by *H. sanguineus*, which feed more actively during dark conditions (Spilmont, Gothland & Seuront, 2015), could contribute to predation occurring at night.

Predation at nighttime may have been enhanced because of the proximity of the field experiment to a lighted dock. The dock could have encouraged aggregation of tautog and cunner which are known to affiliate with structures like docks (Olla et al., 1975). Illumination from lights on the dock at night could improve the predators' ability to see prey and forage throughout nighttime, particularly on a dark night, like under cloudy skies or during a new or crescent moon (Table 1). Nevertheless, man-made structures like the dock described here are increasingly common in coastal habitats (Ruiz et al., 2000), and such human influence does affect predation efficiency and prey choice in nearshore ecosystems (Montalvo, 2020).

In the laboratory study detailed here, High Refuge Habitat significantly reduced the proportion of crabs eaten by *Tautoga onitis*. In addition, there was no difference in the proportion of crabs eaten when provided Low Refuge Habitat and when provided No Refuge. Asian shore crabs are most abundant in mid and lower intertidal zone where there is high structural complexity (Ledesma & O'Connor, 2001; Brousseau et al., 2002; Gilman & Grace, 2009; Epifanio, 2013). A limitation of this study is an under-representation of the true complexity of the rocky intertidal zone, which is more often composed of multiple layers of rocks and cobble that could provide more spatial refuge to further minimize the risk from predators (Hesterberg et al., 2017). Nevertheless, evidence presented here demonstrates that *T. onitis* will readily consume adult (sexually mature) *H. sanguineus,* and that the availability of structural refuge modifies the risk of predation.

The availability of spatial refuge from predation greatly impacts predator-prey interactions across marine ecosystems. Other studies of benthic marine communities have demonstrated that prey survivorship increases significantly with habitat that provides refuge (Scharf, Manderson & Fabrizio, 2006). Local site-level differences in habitat quality best explained variation in predation risk along the range of another invasive crab, the green porcelain crab (*Petrolisthes armatus)* (Kinney, Pintor & Byers, 2019). Similarly, physical-biological interactions like the effect of refuge on predation tested here appear to enhance the degree of enemy release experienced by Asian shore crabs.

Given the high density of invasive Asian shore crabs, relative to other intertidal crab species (O'Connor 2014, 2018), *H. sanguineus* appears particularly adept at avoiding predation. The high abundance of *H. sanguineus* in many coastal communities throughout the invaded range suggests that predators do not strongly impact the population size of this species, perhaps, in part, because of the temporal and spatial refuge within rocky intertidal habitats. Unlike other resident crabs, *H. sanguineus* has a high tolerance for sharing refuge with conspecifics (Hobbs, Cobb & Thornber, 2017) and is more active than other resident crab species (Saxton et al. 2020). These characteristics, combined with cryptic coloration and anti-predatory behaviors (Kim & O'Connor, 2007; Savaria & O'Connor, 2013), may confer an advantage against predation, even at high densities.

Adult *Hemigrapsus sanguineus* can be eaten throughout the diurnal and tidal cycles in the rocky intertidal zone, although refuge strongly modifies predation threat by a common fish predator, *Tautoga onitis*. Not all the predation observed in field studies can be explained by diurnal fish predation; other predators like nocturnal fish or terrestrial mammals could also prey on the invasive crab. This study suggests invasive Asian shore crab predation risk can be modified by habitat refuge, and therefore populations across different coastal habitats may experience different degrees of enemy release by different suits of predator. Subsequent research could combine the factors examined here, predation and refuge, to directly test if predation pressure experienced by adult *H. sanguineus* populations is different among coastal habitats with varying structural complexity.

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Figure 1

Low Refuge Habitat and High Refuge Habitat treatments in the laboratory experiment with concrete pavers.

Low Refuge Habitat and High Refuge Habitat treatments in the laboratory experiment with concrete pavers. Paver underside: dark gray area shows the underside of the 20 x 40 cm paver used to construct habitat; light gray circles represent individual quartzite river stones (2-3 cm) glued to the underside of the paver on one side. Experiment profile: dark gray represents habitat pavers and light gray represents space available to crabs underneath pavers.

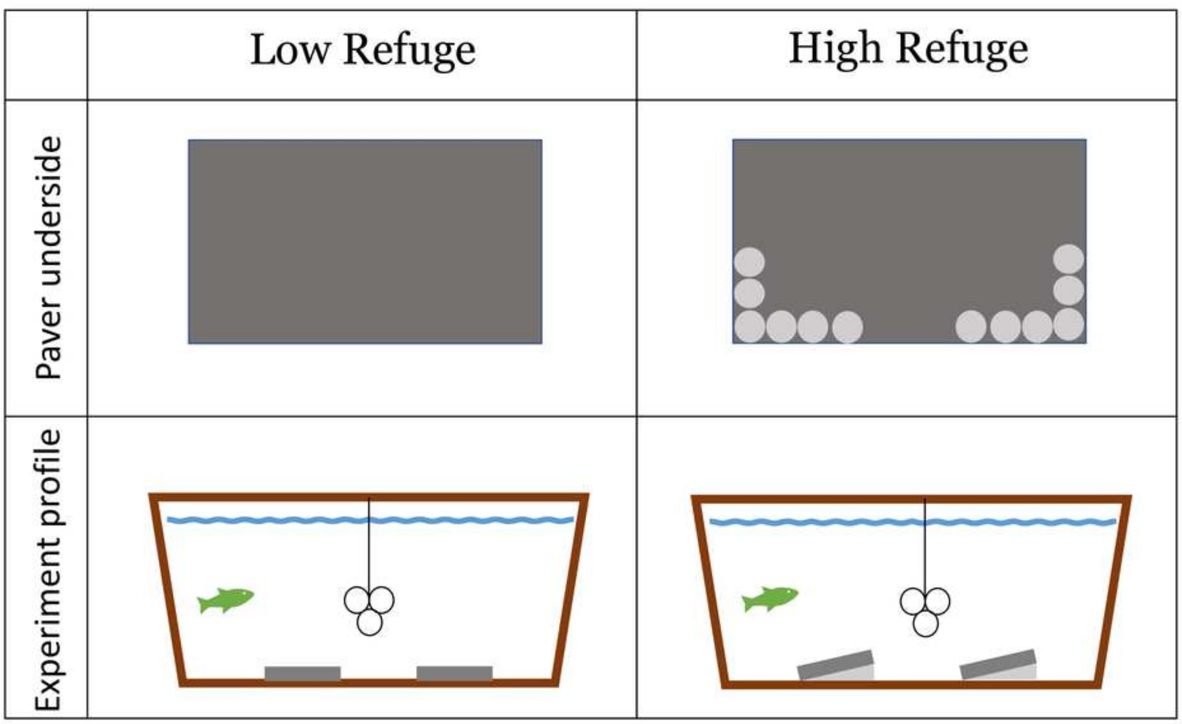

Figure 2

Results of tethering experiments in the field

Results of tethering experiments in the field. Proportion of crabs eaten during daytime high tide (n = 6), daytime low tide (n = 9), nighttime high tide (n = 9), and nighttime low tide (n = 8).

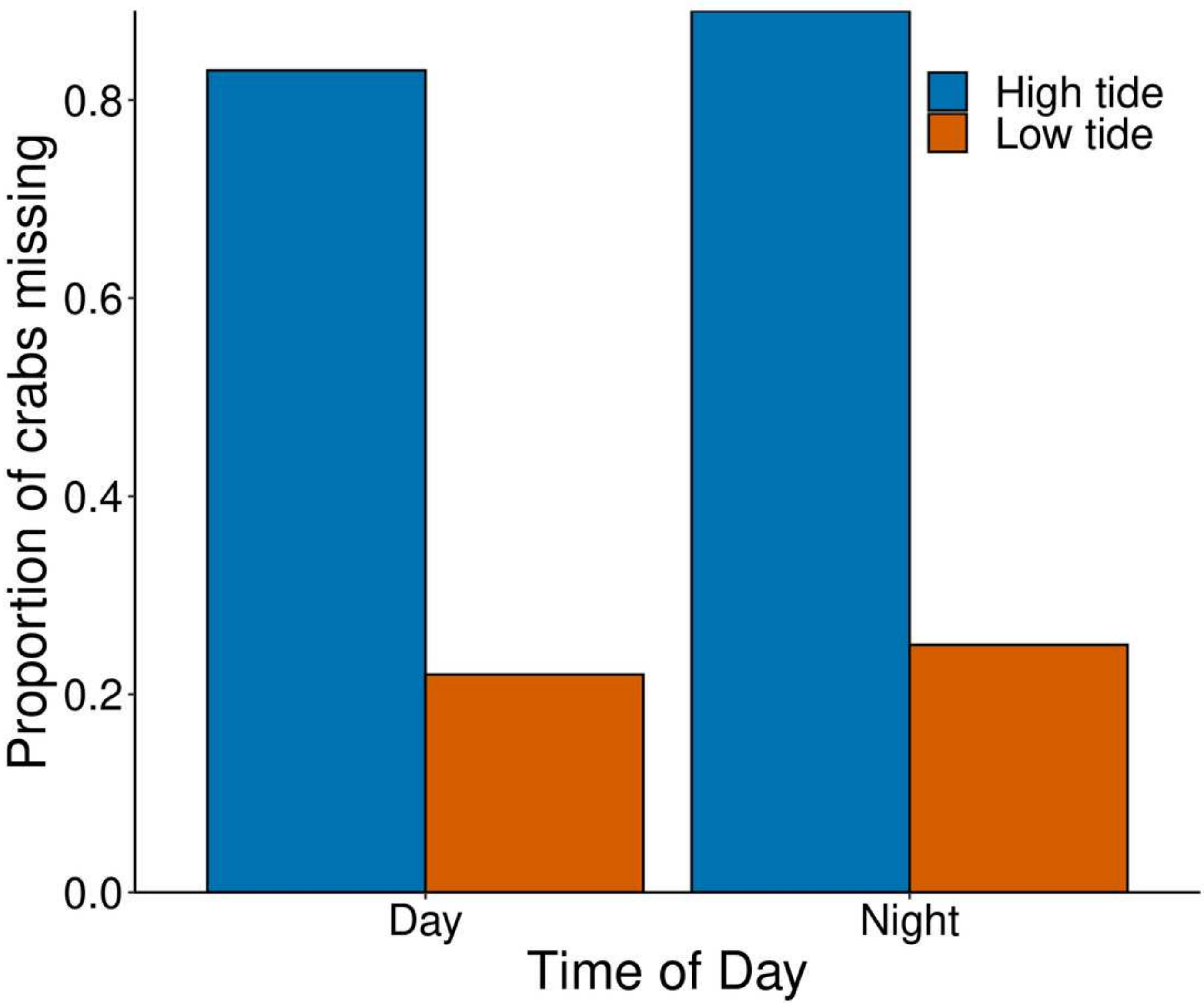

Figure 3

Results of habitat complexity experiments in the laboratory.

Results of habitat complexity experiments in the laboratory. Box and whisker plot showing the proportion of crabs missing with No Refuge, Low Refuge Habitat and High Refuge Habitat. Boxes indicate 25th percentile (Q1), median, and 75th percentile (Q3). Whisker lines extend to maximum and minimum values. Habitat treatments that share a letter were not significantly different (Tukey $p < 0.001$). Sample size was equal for all habitat treatments ($n = 9$).

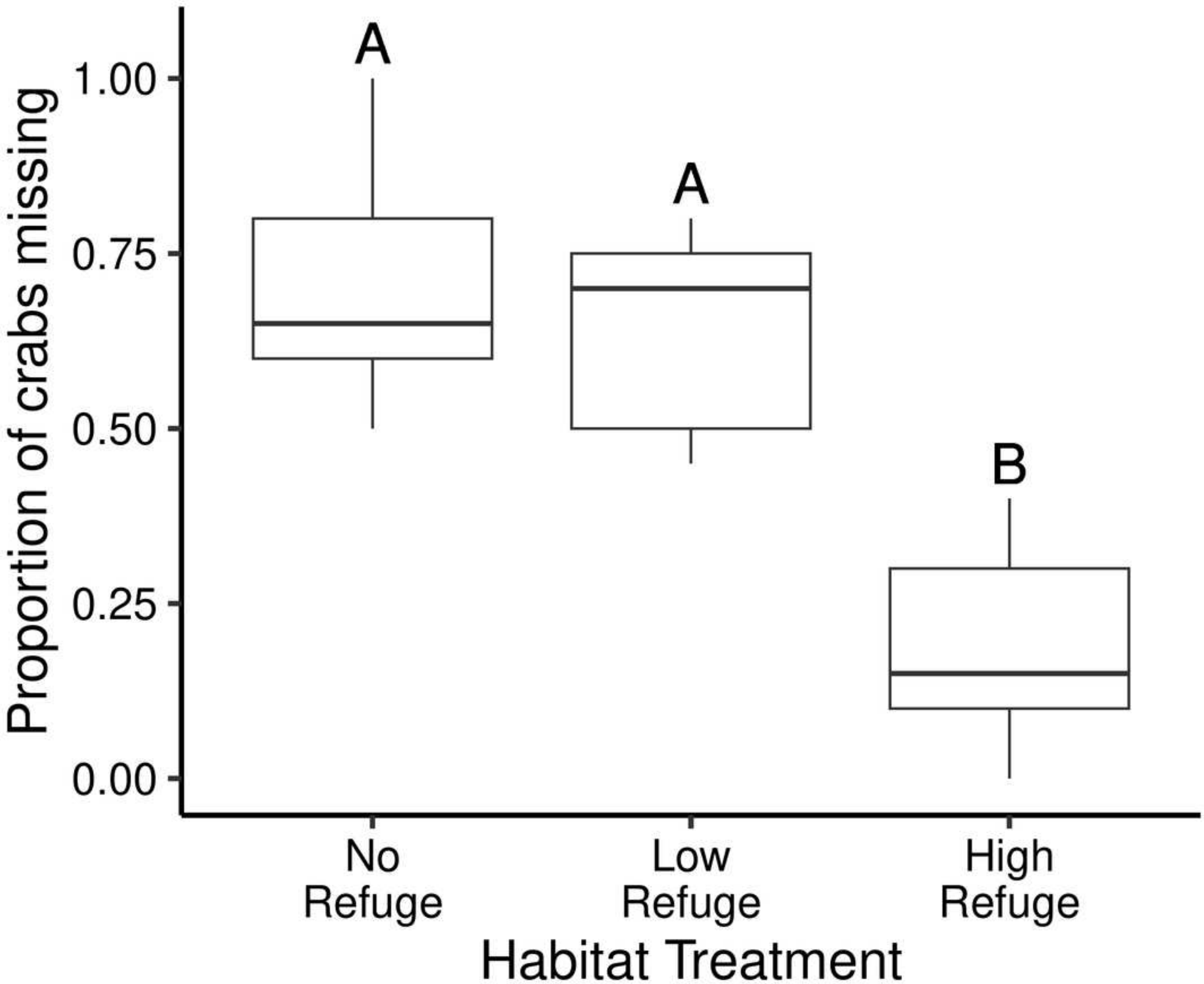
A
A
B
1.00
0.75
0.50
0.25
0.00
Proportion of crabs missing
No Refuge
Low Refuge
High Refuge
Habitat Treatment

Table 1(on next page)

Details of field experiment conditions.

Details of field experiment conditions. Dates experimental trials were conducted in 2020, the time (Day or Night), tide (High or Low), predicted tidal height (difference from mean low water level in meters, source: US Harbors Padanaram, South Dartmouth, MA), moon phase (jpl.nasa.gov/edu), and cloud cover (personal observation).

Trial #	Date	Time	Tide	Tidal Height	Moon Phase	Cloud Cover
1	28-Jul	Day	Low	0.1	N/A	Clear
2	28-Jul	Night	Low	0.2	Waxing Gibbous	Cloudy
3	29-Jul	Night	High	1.3	Waxing Gibbous	Clear
4	30-Jul	Day	High	1.0	N/A	Clear
5	3-Aug	Day	High	1.1	N/A	Clear
6	4-Aug	Day	High	1.1	N/A	Cloudy
7	12-Aug	Night	High	1.0	Waning Crescent	Cloudy
8	13-Aug	Day	Low	0.2	N/A	Cloudy
9	14-Aug	Day	Low	0.2	N/A	Clear
10	18-Aug	Night	Low	-0.1	Waning Crescent	Cloudy
11	19-Aug	Night	Low	-0.1	New Moon	Cloudy
12	19-Aug	Day	Low	-0.1	N/A	Cloudy
13	20-Aug	Night	Low	-0.2	Waxing Crescent	Clear
14	21-Aug	Day	Low	-0.2	N/A	Clear
15	24-Aug	Night	High	1.3	Waxing Crescent	Cloudy
16	25-Aug	Night	High	1.3	1st quarter	Cloudy
17	26-Aug	Night	High	1.2	Waxing Gibbous	Clear

Table 2 (on next page)

Results of field experiment binomial regression.

Results of field experiment binomial regression testing the probability that a crab would be eaten based on the independent variables tide (high / low), time (daytime / nighttime).

Parameter	DF	Deviance Resid.	DF	Resid. Dev	Pr(>Chi)
Tide	1	13.91	30	30.33	< 0.01
Time	1	0.09	29	30.25	0.77

Table 3 (on next page)

Results of laboratory experiment one-way ANOVA.

Results of laboratory experiment one-way ANOVA testing the effect of habitat complexity treatment on predation.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Treatment	2	1.43	0.72	35.99	< 0.001
Residuals	24	0.48	0.02		

Table 4(on next page)

Laboratory experiment post-hoc Tukey Test.

Laboratory experiment post-hoc Tukey Test to determine differences in crab predation among habitat complexity treatment.

Treatment	diff	lwr	upr	p adj
Low-High	0.46	0.29	0.63	< 0.001
None-High	0.52	0.35	0.69	< 0.001
None-Low	0.06	-0.11	0.23	0.63

Table 5(on next page)

List of species found during beach seines at the field site in Clark’s Cove, New Bedford August 2020.

List of species found during beach seines at the field site in Clark’s Cove, New Bedford August 2020. Two hauls with a 10 m net, conducted at high tide, 9:50 am, +3.6ft predicted tidal height (difference from mean low water level in feet, source: US Harbors Padanaram, South Dartmouth, MA), N is the total number of individuals collected.

Common Name	Species	N
Cunner	*Tautogolabrus adspersus*	1
Tautog	*Tautoga onitis*	2
Alewife	*Alosa pseudoharengus*	44
Atlantic silverside	*Menidia menidia*	56
Northern puffer	*Sphoeroides maculatus*	3