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Research Article

Recently established Asian tiger shrimp *Penaeus monodon* Fabricius, 1798 consume juvenile blue crabs *Callinectes sapidus* Rathbun, 1896 and polychaetes in a laboratory diet-choice experiment

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Abstract

Asian tiger shrimp, *Penaeus monodon* Fabricius, 1798 are a newly established exotic species on the Atlantic and Gulf coasts of the United States (US). Their size, estuarine distribution, and diet preference for crustaceans and mollusks in their native range suggest that these shrimp may have significant impacts on a variety of species native to the northern Gulf of Mexico and Southeastern US. However, to date no studies have investigated this possibility. We examined tiger shrimp prey choice in mesocosm predation experiments. In these experiments, blue crabs and polychaetes exhibited the lowest survival rates (<25%) while small flat fish, grass shrimp, and juvenile penaeid shrimp exhibited the highest survival (>60%). In separate video observations tiger shrimp searched for prey by probing the sediment; consequently, juvenile blue crabs *Callinectes sapidus* Rathbun, 1896 that were buried were easily located and consumed. This suggests that demersal or buried prey are more likely to be consumed than species occurring on the sediment surface or in the water column. It is currently unknown how often tiger shrimp may encounter juvenile blue crabs, as tiger shrimp are still rare and adult tiger shrimp are typically caught on commercial shrimping grounds. These preliminary results warrant further examination of tiger shrimp diets and distributions to more fully determine their potential impact on populations of commercially important species.

Key words: invasive species, predation, arthropod, generalist predators

Introduction

In freshwater and marine ecosystems, many successful invasive species are decapod crustaceans (Snyder and Evans 2006; Galil et al. 2011). Notable introductions of invasive decapod crustaceans in the United States include green crabs (*Carcinus maenas* Linnaeus, 1758), Asian shore crabs (*Hemigrapsus sanguineus* De Haan, 1853), and mitten crabs (*Eriocheir sinensis*; Milne-Edwards 1853), as well as a number of crayfish species (Snyder and Evans 2006). Asian tiger shrimp, *Penaeus monodon* Fabricius, 1798 have recently been identified as another potentially invasive decapod species in the eastern coastal US. Tiger shrimp, native to the Indo-West Pacific, are farmed widely in aquaculture ponds (Motoh 1985), and have previously established non-native populations in many locations including West Africa, South America, and the Dominican Republic (Coelho et al. 2001; Aguado and Sayegh 2007; Gómez-Lemos and Campos 2008; Ayinla et al. 2009). It is unknown how previous invasions have affected local species. Tiger shrimp were first reported off the US Gulf Coast in Alabama waters in 2006, and reports of this species in commercial shrimp catches increased slowly in estuarine bays, lagoons, and adjacent sub-tidal littoral zones, and then suddenly peaked at 678 reports in 2011 (Fuller et al. 2014). Although reporting has slowed, tiger shrimp continue to appear in shrimp trawls off the Atlantic and Gulf Coasts and are now considered an established species (Fuller et al. 2014).

The establishment of Asian tiger shrimp in US coastal waters and their current estuarine distribution is of ecological concern because of their extremely large body size and carnivorous diet. Adult tiger shrimp can reach 33 cm total length (TL) (FAO 2016a) in comparison with native brown shrimp, *Farfantapenaeus aztecus* Ives, 1891 and white shrimp, *Litopenaeus setiferus* Linnaeus, 1767 that only reach 23.6 and 20 cm TL, respectively (FAO 2016b, c). Accompanying their large size is a diet width and predatory capacity that differentiates tiger shrimp from native shrimp species. Native penaeid shrimp are primarily omnivorous macrobenthic scavengers that consume infaunal polychaetes, amphipods, tanaids, small bivalves, detritus, and plant matter (McTigue and Zimmerman 1998; Beseres and Feller 2007; Pollack et al. 2008). In contrast, tiger shrimp are primarily carnivorous and consume small crabs, penaeid shrimp, fish, and mollusks in their native range (Thomas 1972; Marte 1980; Motoh 1985). Thomas (1972) reported that in an Indian estuary crustaceans comprised nearly 50% of tiger shrimp diets, followed by mollusks at 20%. Similar to other shrimp species, tiger shrimp juveniles occur in estuarine nursery habitats while adults occupy deeper offshore waters (Motoh 1985). However, along the Northern Gulf of Mexico, adult tiger shrimp are commonly recovered within estuarine bays (NAS 2016). Consequently, tiger shrimp may pose a predatory threat to many estuarine invertebrates, including some commercially important crustaceans, such as white, pink and brown shrimp, and blue crabs. However, because tiger shrimp populations are still small and recovery of live individuals is difficult, this threat has not been evaluated.

In fall 2014, we collected live tiger shrimp from commercial shrimpers in the US Gulf of Mexico. To characterize any impacts that tiger shrimp could have on common native benthic species, we performed a laboratory diet choice experiment using benthic flat fish, polychaetes, both grass and penaeid shrimp, and juvenile blue crabs.

Methods

Animal collection and husbandry

Seven adult tiger shrimp between 15–28 cm TL were obtained by commercial shrimpers in the coastal waters of Alabama and Mississippi, USA. Tiger shrimp were transported to the Dauphin Island Sea Lab (DISL; Dauphin Island, AL) in aerated seawater and maintained in recirculating laboratory mesocosms (2.45 L × 0.52 W × 0.40 H m) that contained a mixture of sand, gravel, and bare bottom, with a few small artificial seagrass units (<0.02 m^2) to provide habitat structure. Tiger shrimp were fed dead mysids, grass shrimp (*Palaemonetes* spp.), and/or blood worms every other day for at least one week before feeding experiments began.

We used benthic animals commonly found in shallow estuarine waters near Dauphin Island as prey to examine the feeding behaviors and diet preferences of tiger shrimp. Animals were collected in nearby estuaries by dip net and a hand-towed plankton beam trawl. Polychaetes were collected by hand and/or sieved from rocky substrate along a nearby beach. Collected organisms were maintained in recirculating laboratory mesocosms (0.60 L × 0.32 W × 0.40 H m) at the DISL for at least 48 hrs before experiments began.

Mesocosm diet choice experiment

We performed a mesocosm experiment assessing tiger shrimp predation preferences on estuarine organisms including: black-cheek tonguefish (*Symphurus plagiusa* Linnaeus, 1766); grass shrimp (*Palaemonetes* spp.); polychaete worms (Capitellidae and Nereidae); juvenile blue crabs (*Callinectes sapidus* Rathbun, 1896); and juvenile penaeid shrimp (*Litopenaeus setiferus* and *Farfanta-penaeus aztecus*). We chose these animals because they were easy to collect, represented a variety of benthic prey behaviors and habitats (infaunal, epibenthic, and demersal), and were representative of animals known to be consumed by tiger shrimp in their native range (Thomas 1972; Motoh 1985). One tonguefish (30–40 mm TL), three grass shrimp, six polychaetes, three juvenile blue crabs (10–25 mm carapace width, CW), and three juvenile panaeid shrimp (25–55 mm TL) were placed in each laboratory mesocosm (0.60 L ×0.32 W × 0.40 H m) containing ~1 cm washed beach sand. These densities were chosen to reflect densities of each species relative to each other in the field and also due to interspecific predation amongst prey species in controls. For instance, polychaetes were consumed by all the other prey species and their consumption in controls was inevitable. Consequently, initial polychaete densities were higher than other prey items to allow a buffer for predation in control treatments. We chose organism size classes based on preliminary observations and other predation experiments using juvenile and adult panaeid shrimp, where juvenile panaeid shrimp (25–55 mm TL) were more likely to be consumed (40–75%; 24 h survival rates) than adult shrimp (80–90% survival rates; JM Hill unpublished data). Since polychaetes were consumed by all animals in the experiment, polychaetes were added to the mesocosms at least five minutes before all other organisms to allow them time to bury. Then all other prey were added and acclimated to the tank for one hour prior to adding one tiger shrimp to each mesocosm. The fivetiger shrimp used in the experiment were 26.5, 15.0, 27.5, 27.0, and 20.6 cm TL, and all but the smallest individual were female. All tiger shrimp were fasted for 24 hours before feeding trials to standardize hunger and ensure tiger shrimp were ready to feed.

Feeding trials (n = 5) were conducted over 24 hours and no tiger shrimp was used more than once. We also conducted 24 hour control trials with all prey species and no tiger shrimp (n = 4). After 24 hours, we removed all remaining animals and sieved all sand through 500µm mesh to find remaining polychaetes or burying organisms. The type and number of missing animals were recorded.

The tiger shrimp treatments represented a choice among five different potential prey items, while control treatments allowed us to determine a background level of survival of the species, which includes mortality due to intraguild predation. Because these five species (potential diet items) represented a choice, these data were not independent and dictate a repeated measures design. However, our data did not fit the assumptions of parametric statistics as the percent survival of each species was non-normal and heteroscedastic despite transformations for which repeated measures ANOVAs are non-robust (Oberfield and Franke 2013) and few nonparametric options exist for unbalanced non-normal repeated measures. Percent survival across prey species in control and tiger shrimp treatments could be analyzed separately via two Friedman's tests, but these comparisons would not adequately address that intraguild predation mortality seen in controls was also likely taking place in tiger shrimp treatments. Therefore, to best (and conservatively) test the prediction that tiger shrimp are preferentially feeding on some species but not others and control for any natural mortality or intraguild predation under these statistical limitations, we assumed that the average control mortality (and intraguild predation) was also occurring in tiger shrimp treatments, and we added the average number of animal mortalities for each species prey type in control groups to the percent survival in tiger shrimp trials. The corrected percent survival across species was then compared using a Friedman's test. This statistical approach represented the most conservative approach to test our predictions, while accounting for the non-independence of the data (diet choice) for a small experiment.

Table 1. Average (± SE) number of individuals of each species that survived in control (n = 4) and tiger shrimp (n = 5) treatments.

Species	Number added to tank	Average number of individuals surviving	
		Control	Tiger Shrimp
Tonguefish	1	1.00 ± 0.00	0.80 ± 0.20
Penaeid shrimp	3	2.25 ± 0.48	1.60 ± 0.60
Grass shrimp	3	2.75 ± 0.25	2.60 ± 0.25
Blue crabs	3	3.00 ± 0.00	0.40 ± 0.40
Polychaetes	6	4.50 ± 0.65	0.00 ± 0.00

Feeding observations

We also filmed tiger shrimp feeding on juvenile blue crabs to gain qualitative insights into tiger shrimp feeding behaviors. Feeding behavior was recorded using a Sony video camera over short (one to two minute) intervals on various dates and times. Shrimp were video-taped while in holding tanks with other individuals several days after use in predation experiments. Four to six juvenile blue crabs were added to these holding tanks. After a brief acclimation period, tiger shrimp (which normally are nocturnal predators FAO 2016a) were enticed to feed by adding their food, dead grass shrimp, to tanks during daytime hours where they could be filmed. As with many crustaceans, chemosensory food cues often elicited searching behaviors.

Results

Mesocosm diet-choice experiment

In control trials, survival was species dependent likely due to intraguild predation (Table 1), but survival was usually above 75% for each species. When survival rates in tiger shrimp treatments were conservatively corrected for intraguild predation from control trials (see Methods), polychaete worms and blue crabs were the only prey to suffer significant predation (>75%; Figure 1; Friedman's test, X^2=12.653, df = 4, p = 0.013).

Video feeding observations

We filmed several successful and unsuccessful predation attempts on juvenile blue crabs on at least four occasions with at least three different tiger shrimp. In all predation attempts, tiger shrimp searched for prey by probing the sediment with their chelae, which often resulted in locating buried juvenile blue crabs. These crabs were quickly attacked and after a short struggle were successfully consumed (Supplementary video material A, B). On occasion, naïve juvenile blue crabs would approach and pinch

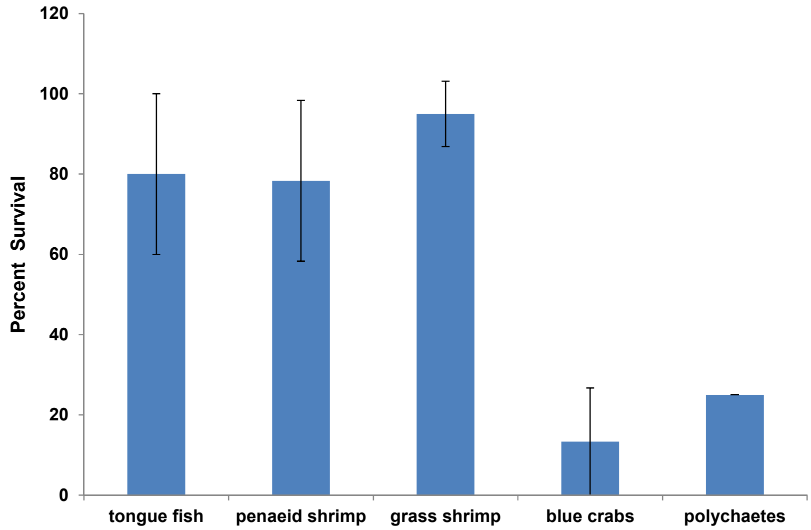

Figure 1. Tiger shrimp diet choice depicted as the average ± S.E. percentage of organisms surviving after 24 hours (n = 5). The survivorship of each species in tiger shrimp treatments was increased by adding the average number of each species missing in control trials to survivorship totals in tiger shrimp treatments (Table 1).

tiger shrimp and/or perform a meral spread which typically resulted in their death. Some blue crabs, especially larger individuals (>25 mm CW), were able to successfully ward off predation attempts by aggressively fighting the shrimp (Supplementary video material C).

Discussion

Our predation experiments and feeding observations demonstrated that Asian tiger shrimp can attack and consume juvenile blue crabs and polychaetes found in eastern US estuaries. The low survival of juvenile blue crabs and polychaetes suggest that tiger shrimp may prefer these organisms as prey over grass shrimp, juvenile penaeid shrimp, and black-cheeked tonguefish. Consumption of polychaetes is common in many shrimp species (McTigue and Zimmerman 1998; Beseres and Feller 2007), and the consumption of blue crabs is consistent with tiger shrimp diets in their native range, where they primarily consume small crabs, shrimp, and mollusks (Thomas 1972; Marte 1980; Motoh 1985). Surprisingly, although the tiger shrimp's native diet indicates that shrimp may be preferred prey (Thomas 1972), juvenile penaeid and grass shrimp in our trials were often able to evade predation and their survivorship was high. High survivorship of adult and juvenile brown and white shrimp species has also been confirmed in other single species mesocosm predation experiments (JM Hill, unpublished data), further suggesting that tiger shrimp are unlikely to pose a predation threat to native shrimp populations.

Tiger shrimp consumption of juvenile blue crabs in our experiments suggests that they have the potential to negatively impact blue crab populations in the field. The rapid and large scale invasion of other predators, such as lionfish (*Pterois* spp.) and the green crab, have had serious implications for invaded ecosystems. Lionfishes, for example, feed upon many juvenile reef fishes, including commercially important species such as snapper and nassau grouper, resulting in decreased recruitment rates on coral reefs (Albins and Hixon 2008; Morris and Akins 2009; Morris and Whitfield 2009; Dahl and Patterson 2014). Similarly, the introduced green crab caused significant declines in infaunal bivalve species (Grosholz and Ruiz 1996) and also facilitated the spread of another invasive bivalve (*Gemma gemma* Lea, 1842) on the US west coast (Grosholz 2005). However, our preliminary results are not enough to put tiger shrimp on the same invasion scale as lionfish and green crabs.

Due to experimental limitations, we only tested a limited variety of prey species that may not fully represent the wide variety of prey available in nature. The availability of alternate prey species may affect predation rates (Křivan 1996) and ongoing analyses of gut contents of tiger shrimp (Amy Fowler, South Carolina Department of Natural Resources and the Marine Resources Research Institute, Charleston, personal communication) will supplement the findings from our diet experiment. In addition, it is too early to determine how often tiger shrimp and juvenile blue crabs will interact. Tiger shrimp currently are uncommon in the Gulf of Mexico, and most adults are caught on commercial shrimping grounds (NAS 2016), which are often located in estuarine bays at depths of two to six meters or in offshore habitats. Tiger shrimp in these areas are less likely to encounter juvenile blue crabs that reside in shallow nursery habitats, such as salt marshes and seagrasses (Heck and Orth 1980; Heck and Thoman 1984; Thomas et al. 1990; Lipcius et al. 2005; Ralph et al. 2013). The high occurrence of tiger shrimp in subtidal habitats may simply reflect the greater sampling efforts of commercial shrimpers in these locations. Some tiger shrimp have also been caught within and adjacent to marshes and seagrass beds on the Gulf and eastern US coast (NAS 2016) where overlap with juvenile blue crabs is more likely. However, tiger shrimp may have to become more common and easy to collect to fully document their distribution and impacts on blue crab populations. Tiger shrimp will occupy estuarine nursery habitats as juveniles (Motoh 1985) suggesting this exotic species will have additional impacts on juvenile crustaceans and other estuarine species and further research investigating the impacts of juvenile tiger shrimp on estuarine communities is necessary and recommended.

Tiger shrimp vigorously attacked juvenile blue crabs in experiments and in video observations. In our experiments, 100% of blue crabs were consumed by tiger shrimp with the exception of the smallest male tiger shrimp, which only consumed one of three crabs. The voracity of predation on juvenile blue crabs does not appear to be a function of the relatively small size of experimental mesocosms. These same mesocosms yielded much higher survivorship (60–80%) of shrimp, for example, suggesting that tiger shrimp foraging behavior affects blue crab predation rates more than the size of the mesocosm.

Low juvenile blue crab survivorship was likely exacerbated by blue crab antipredator behavior. Our video observations show that tiger shrimp probe sediments for prey and buried blue crabs were quickly located. Other native prey have shown similar ineffective antipredator strategies or naïveté towards invasive predators (Cox and Lima 2006; Paolucci et al. 2013; Lönnstedt and McCormick 2013). In our experiments, prey that were not primarily infaunal or epibenthic (i.e. shrimp and tonguefish) were able to escape tiger shrimp predation by retreating to higher water depths where tiger shrimp predation attempts were often unsuccessful. Therefore, slower moving macrobenthic prey are likely to be more common prey items for tiger shrimp in their newly established range.

In conclusion, we have provided laboratory evidence that tiger shrimp prefer juvenile blue crabs and polychaetes over other estuarine species; however, further experiments are needed to determine if, when, and to what extent tiger shrimp could affect commercially important blue crabs, brown and white shrimp, and other organisms in the newly invaded range on the east coast of the USA. Although the impacts of their invasion are uncertain, we advocate increased efforts to understand how tiger shrimp interact with native species.

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Supplementary material

The following supplementary material is available for this article:

Video material A. Tiger shrimp consumes blue crab.
This material is available as part of online article from:
http://www.reabic.net/journals/bir/2017/Supplements/BIR_2017_Hill_etal_Video_A.wmv

Video material B. Tiger shrimp consumes another blue crab.
This material is available as part of online article from:
http://www.reabic.net/journals/bir/2017/Supplements/BIR_2017_Hill_etal_Video_B.wmv

Video material C. Unsuccessful predation attempt on a blue crab.
This material is available as part of online article from:
http://www.reabic.net/journals/bir/2017/Supplements/BIR_2017_Hill_etal_Video_C.wmv