Species–specific crab predation on the hydrozoan clinging jellyfish *Gonionemus* cf. *murbachii* Mayer, 1901 (Cnidaria, Hydrozoa), subsequent crab mortality, and possible ecological consequences (#19854)

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Species–specific crab predation on the hydrozoan clinging jellyfish *Gonionemus* cf. *murbachii* Mayer, 1901 (Cnidaria, Hydrozoa), subsequent crab mortality, and possible ecological consequences

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Here we report a unique trophic interaction between the cryptogenic and sometimes highly toxic hydrozoan clinging jellyfish *Gonionemus* cf. *murbachii*. and the spider crab *Libinia dubia*. We assessed species – specific predation on the *Gonionemus* medusae by crabs found in eelgrass meadows in Massachusetts, USA. We found that the native spider crab species *L. dubia* consumed *Gonionemus* medusae, often enthusiastically, but the invasive green crab *Carcinus maenus* avoided consumption in all trials. One out of two blue crabs (*Callinectes sapidus*) also consumed *Gonionemus*, but this species was too rare in our study system to evaluate further. *Libinia* crabs could consume up to 30 jellyfish, which was the maximum jellyfish density treatment in our experiments, over a 24-hour period. *Gonionemus* consumption was associated with *Libinia* mortality. Spider crab mortality increased with *Gonionemus* consumption, and 100% of spider crabs tested died within 24 hours of consuming jellyfish in our maximum jellyfish density containers. As the numbers of *Gonionemus* medusae used in our experiments likely underestimate the number of medusae that could be encountered by spider crabs over a 24-hour period in the field, we expect that *Gonionemus* may be having a negative effect on natural *Libinia* populations. Furthermore, given that *Libinia* overlaps in habitat and resource use with *Carcinus*, which avoids *Gonionemus* consumption, *Carcinus* populations could be indirectly benefiting from this unusual crab – jellyfish trophic relationship.

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KEYWORDS: *Libinia dubia, Carcinus maenas, Callinectes sapidus, Gonionemus*, Hydrozoa, jellyfish, invasive species, eelgrass, indirect effects

Abstract

Here we report a unique trophic interaction between the cryptogenic and sometimes highly toxic hydrozoan clinging jellyfish *Gonionemus* cf. *murbachii* and the spider crab *Libinia dubia*. We assessed species – specific predation on the *Gonionemus* medusae by crabs found in eelgrass meadows in Massachusetts, USA. We found that the native spider crab species *L. dubia* consumed *Gonionemus* medusae, often enthusiastically, but the invasive green crab *Carcinus maenus* avoided consumption in all trials. One out of two blue crabs (*Callinectes sapidus*) also consumed *Gonionemus*, but this species was too rare in our study system to evaluate further. *Libinia* crabs could consume up to 30 jellyfish, which was the maximum jellyfish density treatment in our experiments, over a 24-hour period. *Gonionemus* consumption was associated with *Libinia* mortality. Spider crab mortality increased with *Gonionemus* consumption, and 100% of spider crabs tested died within 24 hours of consuming jellyfish in our maximum jellyfish density containers. As the numbers of *Gonionemus* medusae used in our experiments likely underestimate the number of medusae that could be encountered by spider crabs over a 24-hour period in the field, we expect that *Gonionemus* may be having a negative effect on natural *Libinia* populations. Furthermore, given that *Libinia* overlaps in habitat and resource use with *Carcinus*, which avoids *Gonionemus* consumption, *Carcinus* populations could be indirectly benefiting from this unusual crab – jellyfish trophic relationship.

Introduction

Jellyfish are important and often conspicuous members of many marine communities, but blooms are often problematic as they may interfere with fisheries and aquaculture, clog power plant intake pipes, and present sting risks to humans (Purcell, Uye & Lo 2007; Graham & Bayha, 2010). Anthropogenic activities have contributed to the spread of jellyfish outside their native range (Purcell, Uye & Lo 2007; Graham & Bayha, 2010), where they can also have negative consequences to the ecosystem (Manzari et al. 2015). A likely potential impact of invasive jellyfish is through alteration of native food webs, often thought to manifest through predation and competition (Pauly et al. 2009; Graham & Bayha 2010). Jellyfish are less often thought of as prey (Arai & Jacobs 1980; Arai 2005; Ates 2017) and are sometimes assumed to be trophic dead-ends (Sommer et al. 2002; Lynam et al. 2006; Yamamato et al. 2008; Condon et al. 2011), but this paradigm is changing (Cardona et al. 2012; Diaz-Briz et al. 2017; McInnis et al. 2017).

"Jellyfish" is a general term that refers to phylogenetically diverse gelatinous zooplankton, including members of the phylum Cnidaria belonging to the Scyphozoa, Cubozoa, and Hydrozoa (collectively known as the Medusozoa), the phylum Ctenophora (ctenophores), and the phylum Chordata (salps, doliolids, and pyrosomes). Of these groups, most research has focused on a relatively small number of conspicuous scyphozoans (Purcell, Uye & Lo 2007). Despite the relative lack of attention, the Hydrozoa is by far the most speciose and diverse group with around 842 valid medusa (i.e., jellyfish) - producing species (Bouillon & Boero, 2000a). The Hydrozoa is phylogenetically well-supported (Collins et al. 2006; Kayal et al. 2013; Zapata et al. 2015) and is sometimes referred to as a superclass (Bouillon & Boero 2000b; Xu et al. 2014).

The clinging jellyfish *Gonionemus* cf. *murbachii* Mayer 1901 (Cnidaria, Hydrozoa, Limnomedusae; Fig. 1) is an increasingly conspicuous member of Northwest Atlantic eelgrass communities, and populations may be comprised of native and invasive lineages (Govindarajan et al. 2017). Like many cryptogenic species, insufficient taxonomy complicates our understanding of its biogeography (Govindarajan et al. 2017). Clinging jellyfish described as *G. murbachii* (but later synonymized with *Gonionemus vertens* Agassiz 1862) were first noted in Massachusetts and Connecticut in 1894, but nearly disappeared in the 1930s when its eelgrass habitat was decimated by a wasting disease (Govindarajan & Carman 2016). In recent years, clinging jellyfish have made a comeback in these areas (Govindarajan & Carman 2016).

Gonionemus lineages vary in their toxicity (Naumov 1960), and some Sea of Japan populations are associated with stings that can cause severe pain, respiratory difficulty, paralysis, and other neurological symptoms, while populations in other parts of the world are harmless to humans (Naumov 1960; Otsuru et al. 1974; Yakovlev & Vaskovsky 1993). Nineteenth and early 20th century *G. murbachii* populations were not associated with stings. However, painful stings similar to those associated with Sea of Japan populations began occurring in Massachusetts, USA, in 1990, suggesting an invasion of a new and highly toxic lineage (Govindarajan & Carman 2016). Since then, clinging jellyfish blooms have been occurring regularly in Massachusetts, and the jellyfish appear to be expanding their range both inside and outside of Massachusetts (Govindarajan & Carman 2016; Gaynor et al. 2016; Govindarajan et al. 2017).

Govindarajan et al. (2017) suggested that based on mitochondrial COI sequences and subtle morphological features that the Northwest Atlantic and Pacific forms (including highly toxic populations) were similar to each other, and different from *G. vertens* from the Northeast Pacific. It seems likely that the Northwest Atlantic/Northwest Pacific form will likely formally be reclassified as *G. murbachii* Mayer 1901. Thus, we refer here to this form, which is our focal species in this study, as *Gonionemus* cf. *murbachii* (or simply "*Gonionemus*") to indicate that we are referring to the Atlantic population on which this name is based, but also that further confirmation is needed.

Clinging jellyfish are found primarily in eelgrass meadows, where they "cling" to eelgrass blades using the adhesive structures on their tentacles (Naumov 1960; Fig. 1). Adult medusae typically range in size from 1 – 2.5 cm (Govindarajan et al. 2017) and feed on a variety of small zooplankton such as amphipods and isopods (Yakovlev & Vaskovsky 1993). They are not known to have any predators, although molluscs may feed on the minute polyp life cycle stage (Yakovlev & Vaskovsky 1993). The highly toxic nature of some *Gonionemus* lineages might act as a deterrent to potential predators, but it is also possible that predation on clinging jellyfish has been overlooked.

Northwest Atlantic eelgrass meadows are also home to predatory native and invasive crab species (Able et al. 2002; Garbary et al. 2014; Neckles 2015; Matheson et al. 2016). We investigated the possibility that crabs can prey on *Gonionemus*, and the potential impact of *Gonionemus* prey on crab predators. The Massachusetts, USA eelgrass beds where *Gonionemus* medusae are found are home to native spider crabs (*Libinia dubia* Milne Edwards 1834) and, occasionally, blue crabs (*Callinectes sapidus* Rathbun 1896), and the invasive green crab (*Carcinus maenus* Linnaeus 1758). Green crabs in particular are highly destructive to eelgrass ecosystems as they uproot eelgrass shoots while foraging and may graze directly on the eelgrass shoots (Malyshev & Quijón, 2011; Garbary et al. 2014). All three crab species feed on a wide variety of invertebrates (Aldrich 1974; Grosholz & Ruiz 1996; Harding 2003; Baeta et al. 2006). While predation on jellyfish is often not considered (Arai 2005), *Carcinus maenus, Callinectes* *sapidus*, and *Libinia* have been reported to feed on scyphozoan medusae (Phillips, Burke & Keener 1969; Farr 1978; Lauckner 1980; Esser, Greve & Boersma 200).

Our results demonstrated a new trophic interaction between crabs and a highly toxic hydrozoan jellyfish with consequences for invasive species impacts in ecologically sensitive eelgrass meadows. We found that the native spider and blue crabs consumed *Gonionemus*, but that the invasive green crabs did not. We further found that *Gonionemus* ingestion resulted in crab death when large numbers of jellyfish were consumed; however, blue crabs were too rare at our site to be assessed at higher jellyfish densities. Thus, we hypothesize that *Gonionemus* may potentially impact native ecosystems via differential predation by a native species (spider crabs) that may lead to a decline of that species, while avoidance of *Gonionemus* by a notoriously destructive invasive species (green crabs) may facilitate its dominance.

Material & Methods

Study area

The experimental animals in our study were obtained from Farm Pond (41.44756, -70.55694) and Lagoon Pond (41.44816, -70.59022), which are semi-enclosed coastal ponds that harbor eelgrass beds on the northeastern side of the island of Martha's Vineyard in Massachusetts, USA (Fig. 2). Lagoon Pond covers 544 acres with a mean depth of 3 m, and Farm Pond covers 33 acres, is tidally restricted, and has a mean depth of 1.5 m. Both ponds have a tidal range of < 1 m. The ponds are located in the town of Oak Bluffs, separated by about 4 km of land, and are the sites of ongoing research on invasive species (Carman Grunden & Ewart 2014; Carman et al. 2016; Colarusso et al. 2016). *Gonionemus* was first observed in Farm Pond in 2007 (Govindarajan & Carman, 2016) and has not been observed in Lagoon Pond. Permission to collect animals at our field sight was obtained through D. Grunden (Oak Bluffs, Massachusetts Shellfish Constable).

Identification of predatory crab species

We conducted 4 trials during June and July 2016 to identify which, if any, local crab species prey on *Gonionemus.* Crabs were trapped in Farm and Lagoon Ponds the week prior to each experiment using crab traps. The crabs were then kept in the cages for one week in a relatively barren area of Farm Pond that lacks *Gonionemus* habitat.

At the start of each experiment, individual crabs were transported in tubs of seawater to the laboratory at the Town of Oak Bluffs Shellfish Department in Massachusetts (Fig. 2). Crab size (carapace width) was recorded. At the same time as the crabs were removed from the crab traps, *Gonionemus* specimens were also collected from the eelgrass meadow in Farm Pond using hand held nets while wading and snorkeling, and transported along with the crabs to the laboratory.

Experiments were conducted in closed tubs (42 cm x 33 cm x 17 cm) of seawater. Five adult jellyfish (15-20 mm bell width) were placed in a tub with a single crab. Between 2 and 6 replicate tubs per crab species were set up on each sampling date, depending on the number of crabs that were caught (Table 1). Additionally, control tubs consisting of crabs only (with no jellyfish) and jellyfish only (with no crabs) were also set up for each experiment (Table 1). The number of jellyfish remaining and crab condition (dead or alive) were recorded at three time points (5 minutes, 3 hours, and 24 hours). We verified our assumption that jellyfish disappearances were due to predation by the crabs by: 1) direct observation of crabs consuming jellyfish, which we recorded by taking representative photographs and video; and 2) running jellyfish-only controls with each trial to assess jellyfish mortality independent of the crabs.

Impact of jellyfish consumption on spider crabs

As a follow-up to our first set of trials which documented predation on jellyfish by *Libinia* (as well as the relatively rare *Callinectes sapidus*) and a possible association between jellyfish consumption and mortality, we assessed *Libinia* predation at higher jellyfish densities. We ran similar predation experiments on two dates in July 2017 at four additional jellyfish densities: 10, 15, 20, and 30 jellyfish per crab. The experiments were carried out in the laboratory at the Martha's Vineyard Shellfish Group John T. Hughes Hatchery and Research Facility in Oak Bluffs (Fig. 2). As with the 2016 experiments, crabs were trapped during the week before the experiment and held in Farm Pond without supplemental food. Also as in the 2016 trials, jellyfish were obtained from Farm Pond immediately prior to the start of the experiments. Crabs were placed in tubs with a given number of jellyfish (10, 15, 20, or 30 adult jellyfish); with 6 replicates per jellyfish density. Control tubs with crabs only and jellyfish only were also set up on each experiment date. The number of jellyfish remaining and crab condition (dead or alive) after 15 minutes and 24 hours were recorded.

To confirm that the *Gonionemus* densities we used in our predation trials were realistic compared to what the crabs encounter in nature, jellyfish densities were recorded on three dates in 2017 by counting the number of jellyfish in representative 3 m x 3 m areas in the part of Farm Pond where the jellyfish are found. The jellyfish were collected by net scoops and counted. This method likely underestimates the true *Gonionemus* abundance, and so is a conservative depiction.

Results

Identification of predatory crab species

Several spider crabs (*Libinia dubia*) and green crabs (*Carcinus maenas*) were collected in our crab traps, as well as 2 blue crabs (*Callinectes sapidus*). Mean carapace width was 62 mm ± 9 S.D. in *Libinia* (n = 30), 62 mm ± 6 S.D. in *Carcinus* (n = 30), and 63 mm and 78 mm in the two *Callinectes* individuals.

Twenty-one out of 22 spider crabs and one out of the 2 blue crabs obtained consumed *Gonionemus* (Fig. 3, 4A), but none of the green crabs did. We observed *Libinia* predation on the jellyfish almost immediately at the start of our trials (Fig. 3). Often, spider crabs consumed 100% of the jellyfish, and most jellyfish consumption occurred within the first 3 hours (Fig. 4A).

At the end of the 24-hour periods, *Libinia* mortality (27.3%) was higher than in the corresponding no – jellyfish controls (12.5%), and *Carcinus* trials with (5%) and without (12.5%) jellyfish. To assess the role of crab size on mortality, the 22 *Libinia* that received the jellyfish were sorted into 3 size (carapace width) categories: 50 – 58 mm, 60 – 69 mm, and 70 – 82 mm. The percent mortality increased with size category (Fig. 5). Each size category contained individuals used on all 4 of the trial dates (suppl. data). For all trials, 100% of the jellyfish in the jellyfish-only control tubs were alive at the end of the 24-hour periods.

Impact of jellyfish consumption on spider crabs

Thirty - six *Libinia* were obtained to assess the effects of increased *Gonionemus* density on crab predation and mortality. Mean carapace width was 73 mm ± 9 S.D. Crab size differed between treatments (ANOVA, $P = 0.039$, $F = 3.36$, df = 3) and crabs in the 20 *Gonionemus* treatment were significantly smaller than in the 15 *Gonionemus* treatment (Tukey's HSD test, $P < 0.05$), but none of the other pairwise comparisons of *Gonionemus* density treatments differed significantly. As in the 2016 trials, jellyfish consumption began in the first few minutes, and was at or near 100% after 24 hours for many crabs in all *Gonionemus* density treatments (Fig. 4;

suppl. video, suppl. data) We also found that *Libinia* mortality increased as *Gonionemus* density increased, and 100% of the crabs died at the highest *Gonionemus* density treatment (Fig. 6). None of the crabs in the crab-only controls died, and none of the *Gonionemus* in the jellyfish-only controls died.

Gonionemus abundance was estimated on July 19, 2017, August 7, 2017, and August 11, 2017 and was 310 (after 60 minutes of netting), 39 (after 45 minutes of netting), and 19 (after 45 minutes of netting) medusae per 3 m x 3 m search area, respectively. These values do not represent absolute numbers of *Gonionemus* in the search areas and are based on different amounts of search efforts. Rather these values should be considered catch per unit effort estimates and represent a minimum quantity (i.e., there were likely more *Gonionemus* in the search areas, but not less). As *Gonionemus* is primarily sedentary we do not expect that there was influx into the search area from outside the search area over our search periods.

Discussion

We documented a novel trophic interaction between native crabs a cryptogenic hydrozoan jellyfish, that may indirectly facilitate dominance of a highly destructive invasive crab in ecologically sensitive eelgrass meadows. Our results are the first example that we are aware of that demonstrates predation on hydrozoan medusae by crabs. As well, the toxic effects of the jellyfish on the native crabs, coupled with avoidance of the jellyfish by the invasive crabs, provides a mechanism for an indirect, but potentially significant ecological impact on eelgrass communities. The native *Libinia* and invasive *Carcinus* co-exist in eelgrass meadows; however *Carcinus* can be very destructive to eelgrass shoots (Garbary et al. 2014; Neckles 2015; Matheson et al. 2016). Both *Libinia* and *Carcinus* have similar diets – both are generalists that prey on a wide variety of organisms (Aldrich 1974; Grosholz & Ruiz,1996). *Gonionemus* thus has the potential to promote *Carcinus* populations by inducing mortality in a native competitor.

While our study was based on laboratory observations, it is very likely that *Libinia* is preying on *Gonionemus* in the field. *Libinia* and *Gonionemus* occupy the same eelgrass microhabitat. In contrast to most jellyfish which are found in the water column, *Gonionemus* medusae spend most of their time attached to eelgrass, in particular near the bottom of the eelgrass where they would be most susceptible to crab predation. Even if the medusae were cling to the middle or upper part of the eelgrass blades, *Libinia* has the ability to climb (D. Grunden & M. Carman pers. obs.). While our field *Gonionemus* density counts do not reflect absolute densities, they do document a minimum baseline that establishes that our laboratory treatments were realistic. It is very likely that *Libinia* encounters far more than 30 *Gonionemus* individuals (as in our maximum *Gonionemus* density treatment, which resulted in 100% mortality) in a 24 hour period, especially at the height of the *Gonionemus* season in July.

It is possible that in the field, given a variety of prey options, that *Libinia* would be less likely to consume large numbers of *Gonionemus* that would have toxic effects. However, our observations showed the crabs had no reluctance in consuming the jellyfish once they were encountered (link to supplemental video), and consumption of large numbers of jellyfish may not be necessary to elicit a fatal or even a debilitating sublethal effect, as seen by the elevated mortality rate in our lower density trials.

Our results suggest conflicting observations that crab size might be a factor in *Gonionemus* – related crab mortality. In our 2016 trials where 5 *Gonionemus* were offered to each crab, crab mortality was inversely related to crab size category. We did not evaluate possible trial date effects, but note that crabs collected at all 2016 trial dates were represented in each size category. In our 2017 *Gonionemus* density trials, we found that crabs in the 20 *Gonionemus* density treatment were significantly smaller than in the 15 *Gonionemus* density treatment, but this group suffered twice the mortality rate (66.7%) than the 15 *Gonionemus* density treatment (33.3%). However, any potentially beneficial size effects were likely over-ridden by the increase in jellyfish consumption. Thus, the possible relationship between crab size and *Gonionemus* – induced mortality needs further evaluation.

Toxicity may vary between jellyfish individuals and individual crab reactions to the jellyfish toxins may also vary (as they do in humans; Otsuru et al. 1974; Yakovlev & Vaskovsky 1993). Given that in some human cases, a sting caused by a single medusa is sufficient to cause extreme pain (Otsuru et al. 1974; M. Carman and D. Grunden, pers. obs.) it seems possible that similarly, consumption of even a single medusa by a crab could have a significant negative effect. In humans, symptoms can persist for a few days (Yakovlev & Vaskovsky 1993). The type, duration, and impact of sublethal effects of *Gonionemus* consumption on crabs would be an interesting future direction. Actual predation rates on *Gonionemus* in the field are hard to assess as the jellyfish lack resistant parts that could be identified in crab gut content analyses (Arai 2005). Molecular probes, however, have great potential to identify prey items in guts that are not otherwise observable (e.g., McInnis et al. 2017), and should be considered in future work.

Cnidarian jellyfish predators include sea turtles, fish, molluscs, chaetognaths, ctenophores, and other cnidarians (Arai 2005; Ates 2017). Most of these examples involve predation on scyphozoan jellyfish, but predators of hydrozoan jellyfish (inclusive of siphonophores and *Velella* hydroids) include fish (e.g., Brodeur, Lorz & Pearcy 1987); birds (McInnis et al. 2017); hyperiid amphipods (e.g., Scheader & Evans 1975; Williams & Robins 1981); shrimp (Hefferman & Hopkins 1981; Roe 1984; Nishida, Pearcy & Nemoto 1988; Moore, Rainbow & Larson 1993); barnacles (Bieri 1966); nudibranchs and heteropods (Sentz-Braconnot & Carre 1966; Seapy 1980); scyphozoan jellyfish (Purcell 1991a; Purcell, 1997; Båmstedt, Ishii & Martlnussen 1997; Arai & Jacobs 1980); and even other hydrozoans (Arai and Jacobs 1980; Purcell 1981; Purcell 1991b). The only example of crab predation on a hydrozoan that we could find, however, is the Dungeness crab *Cancer magister* Dana 1852; who, as planktonic larvae, feed on the planktonic hydroids of *Velella* (Wickham 1979).

A small number of jellyfish – crab interactions have been reported for scyphozoan jellyfish (reviewed in Moyano et al. 2012 and Ates 2017) and ctenophores (Esser, Greve & Boersma 2014). Most of these relationships are symbiotic, where the crabs are associated with scyphomedusae and may benefit from dispersal. Intriguingly, many of the crabs involved in these associations belong to the genus *Libinia*. A small subset of these crab-jellyfish associations involves predation or partial predation on the jellyfish, as opposed to a symbiotic relationship. These include: *Libinia dubia* feeding on the sea nettle *Chrysoara quinqecirrha* Desor 1848 (Phillips, Burke & Keener 1969), the cannonball jellyfish *Stomolophus meleagris* Agassiz 1862 (Shanks & Graham 1988; Tunberg & Reed 2004), and the moon jellyfish *Aurelia aurita* Linnaeus 1758 (Jachowski 1963); and the graceful crab *Cancer gracilis* Dana 1852 feeding on the moon jellyfish *Aurelia labiata* Chamisso & Eysenhardt 1821 (Towanda & Thuesen 2006). Also, *Carcinus maenus* consumes at least some gelatinous zooplankton in its native European range. Esser, Greve & Boersma (2004) describe *C. maenus* predation on the ctenophore *Pleurobrachia pileus* Müller 1776 in the North Sea, particularly when the ctenophores approach the seafloor, and Lauckner (1980) reported observations of *Carcinus maenus* consuming tissue of the moon jelly *Aurelia aurita* in the Baltic Sea.

In addition to being unusual, the relationship between *Libinia* and *Gonionemus* may be shaped by the presence of especially toxic *Gonionemus* lineages (Govindarajan & Carman 2016; Govindarajan et al. 2017). We observed *Gonionemus*-induced mortality in *Libinia* at *Gonionemus* numbers lower than what we expect the crabs encounter in the field. The hard shells of the crabs probably provided protection from *Gonionemus* stings upon initial contact with the jellyfish. However, the soft interior tissues appear to be vulnerable. It is interesting to note that inadvertent human consumption of jellyfish on edible seaweed likely also results in toxic effects similar to external stings (Otsuru et al. 1974).

The readiness of *Libinia* to unhesitatingly consume jellyfish which may result in their death is consistent with the hypothesis of a recent introduction of a highly toxic strain (Govindarajan & Carman 2016). It seems likely that consumption of toxic jellyfish would exert a strong selection pressure on the consumers, that over time would result in the evolution of jellyfish avoidance or toxin tolerance mechanisms, or the disappearance of crabs from jellyfish habitats. Records of *Gonionemus* sightings and stings also support the hypothesis that the *Libinia* – toxic *Gonionemus* interaction may be new. Our study site, Farm Pond, is located close to Sengekontacket Pond, where a less toxic *Gonionemus* population that was regularly accessed by jellyfish collectors was known to exist for decades before the first stings were recorded (Govindarajan & Carman 2016). However, debilitating stings have occurred only in the past few years in Farm Pond (Govindarajan & Carman 2016; and directly to D. Grunden & M. Carman), suggesting the arrival of a new, highly toxic form. While we did not quantify the toxicity of the jellyfish used in our experiments, Govindarajan et al. (2017) found that Farm Pond primarily contained a mitochondrial haplotype that is found in other Northwest Atlantic locations where stings have occurred.

Our finding that in contrast to *Libinia*, *Carcinus* does not consume *Gonionemus* has significant implications for eelgrass ecosystem health. *Carcinus* is native to Europe, where a less toxic form of *Gonionemus* (*Gonionemus vertens* A. Agassiz 1862) is thought to be introduced (Edwards 1976; Bakker 1980). Thus, it may not have historically been exposed to selective pressure by the more toxic form that would explain its avoidance of *Gonionemus* consumption. Rather, the difference we observed between *Carcinus* and *Libinia* might be due to a stronger pre-existing preference of *Libinia* to consume jellyfish. As noted earlier, different species of *Libinia* are known to consume scyphozoan jellyfish (that presumably lack the extreme toxic effects of *Gonionemus*). We also observed *Gonionemus* predation by one out of the 2 blue crabs that we evaluated. While blue crabs were too rare to evaluate further, it is interesting that like *Libinia*, they have been reported to consume scyphozoan jellyfish (Farr 1980).

Our results also have implications for a broader understanding of invasive species impacts. In addition to having direct effects on native species, for example through competition or predation, invasive species can have indirect effects, but these are less explored (White, Wilson & Clarke 2006). Indirect effects occur when one species affects another via a third species (Wootton 1994), and include apparent competition, indirect mutualism/commensalism, trophic cascades, and exploitative competition (White, Wilson & Clarke 2006). We have identified a unique indirect mechanism by which a cryptogenic jellyfish can potentially increase the abundance of an aggressive and highly destructive invasive species, *Carcinus*. Both *Carcinus* and *Libinia*, overlap in habitat and as generalists, they are both known to feed on a broad array of other species, and so they are likely competing for common prey resources. Thus *Gonionemus* – induced mortality of *Libinia* could benefit *Carcinus* populations by increasing prey abundance. Given the highly negative impact of *Carcinus* to sensitive eelgrass systems, it is important to evaluate this hypothesis as well as identify other ecosystem effects of *Gonionemus* (e.g., its role as a predator, as well as prey).

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Table 1 (on next page)

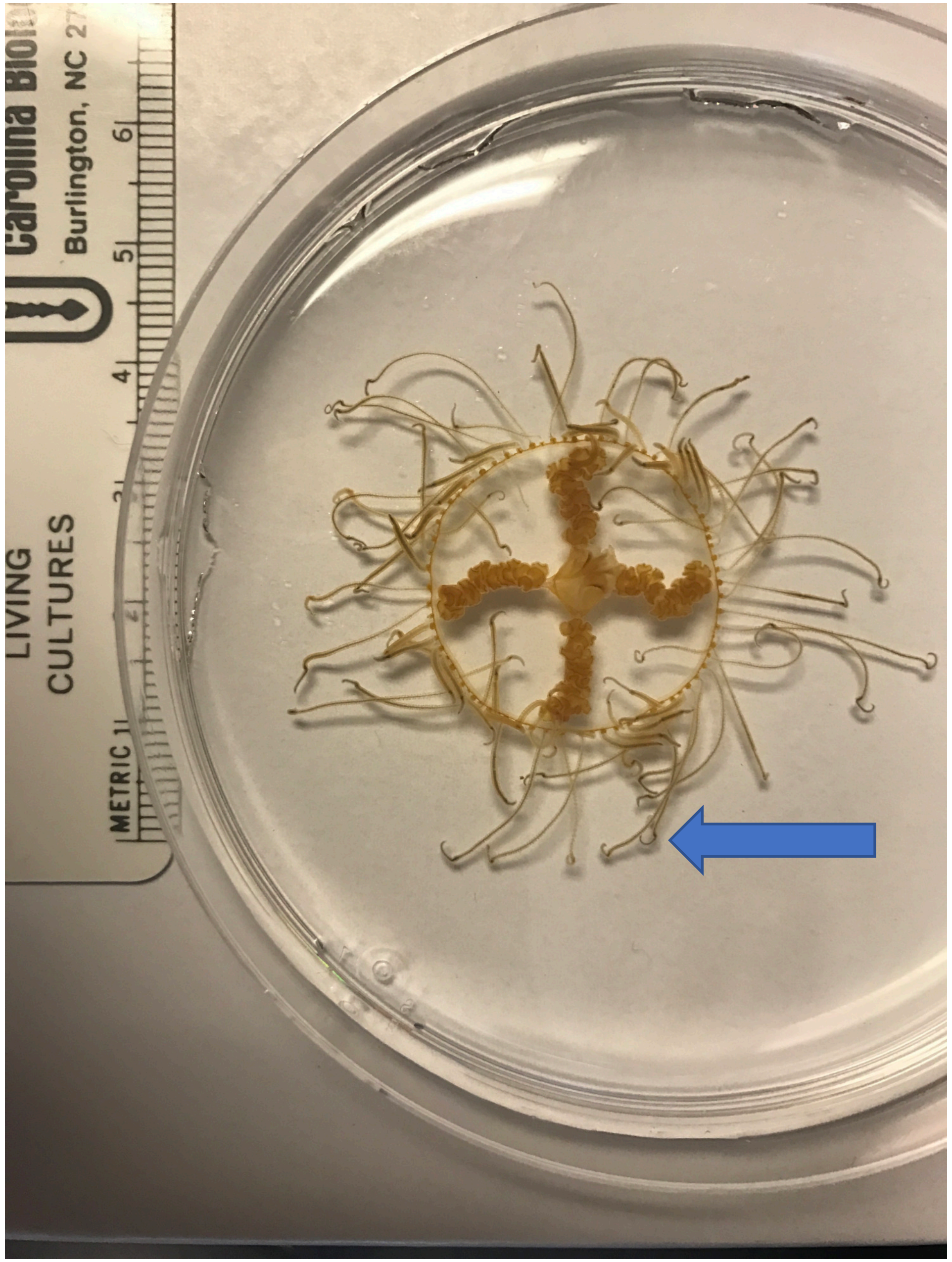
Experimental design and timeline of predation trials

Trial date	Treatment	Crabs tested and # replicates
June 30, 2016	5 jellyfish	Green crabs - 5 Spider crabs - 5 Blue crabs - 1
	0 jellyfish	Green crabs - 5 Spider crabs - 5
	5 jellyfish	No crabs – 2
June 30, 2016	5 jellyfish	Green crabs - 5 Spider crabs – 5 Blue crabs - 1
	0 jellyfish	Green crabs - 2 Spider crabs - 2
	5 jellyfish	No crabs – 2
July 21, 2016	5 jellyfish	Green crabs - 6 Spider crabs - 6
	0 jellyfish	Green crabs - 6 Spider crabs - 6
	5 jellyfish	No crabs – 2
July 28, 2016	5 jellyfish	Green crabs - 6 Spider crabs - 6
	0 jellyfish	Green crabs - 2 Spider crabs - 2
	5 jellyfish	No crabs – 2
July 7, 2017	10 jellyfish	Spider crabs - 6
	0 jellyfish	No crabs – 2
	15 jellyfish	Spider crabs - 6
	0 jellyfish	No crabs – 2
July 18, 2017	20 jellyfish	Spider crabs - 6
	0 jellyfish	No crabs – 2
	30 jellyfish	Spider crabs - 6
	0 jellyfish	No crabs – 2

Figure 1 (on next page)

The clinging jellyfish *Gonionemus* cf. *murbachii.*

The blue arrow points to the end of the tentacles where the adhesive structures are found.


Burlington, NC
LIVING
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METRIC

Figure 2(on next page)

Study locations.

Animals were collected at Lagoon Pond and Farm Pond, and experiments were conducted at the Oak Bluffs Shellfish Department and John T. Hughes Hatchery.

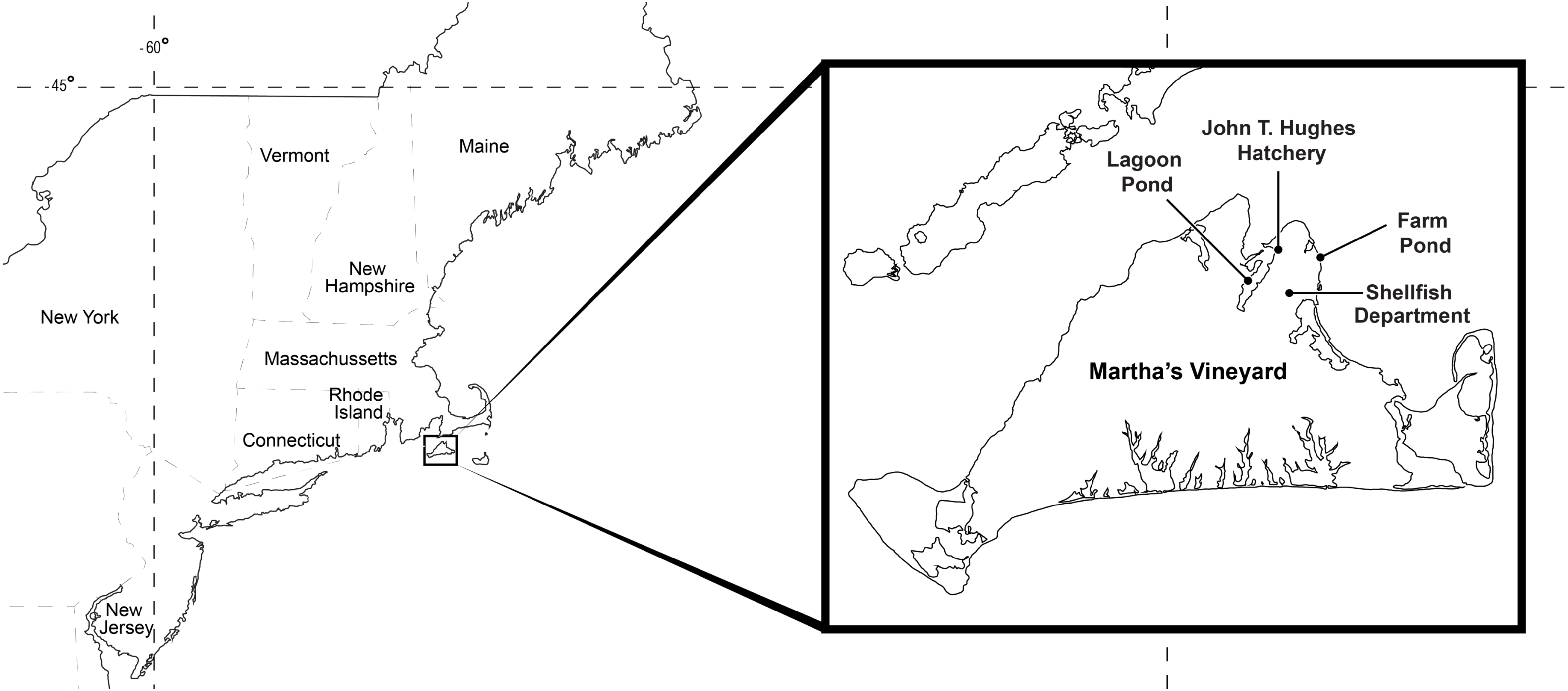

-60°
-45°
Vermont
Maine
New Hampshire
New York
Massachussetts
Rhode Island
Connecticut
New Jersey
John T. Hughes Hatchery
Lagoon Pond
Farm Pond
Shellfish Department
Martha's Vineyard

Figure 3(on next page)

Predation on *Gonionemus*.

Spider crab using its claws to capture and consume a *Gonionemus* medusa (indicated by the blue arrow).

Figure 4(on next page)

Mean number of *Gonionemus* consumed at different *Gonionemus* densities and exposure times.

Predation values are cumulative over the course of exposure. Error bars represent standard deviations. Note the differences in the y - axis scales for each graph. In each graph, the top gridline indicates the number of *Gonionemus* placed in each crab tub.

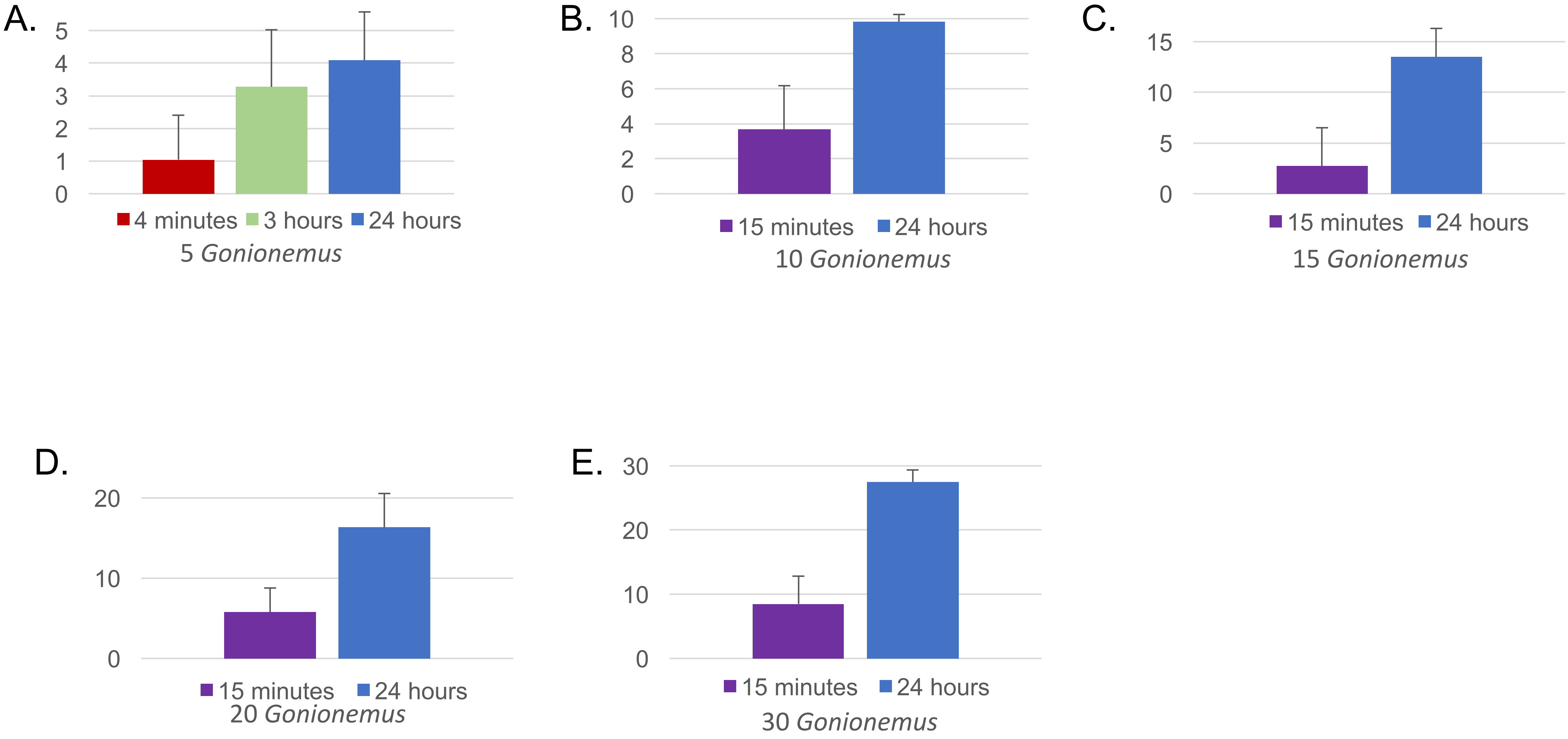

A.
5
4
3
2
1
0
4 minutes
3 hours
24 hours
5 *Gonionemus*
B.
10
8
6
4
2
0
15 minutes
24 hours
10 *Gonionemus*
C.
15
10
5
0
15 minutes
24 hours
15 *Gonionemus*
D.
20
10
0
15 minutes
24 hours
20 *Gonionemus*
E.
30
20
10
0
15 minutes
24 hours
30 *Gonionemus*

Figure 5(on next page)

Libinia mortality in each size class

Data are from the *Libinia* used in the 5 - *Gonionemus* trials.

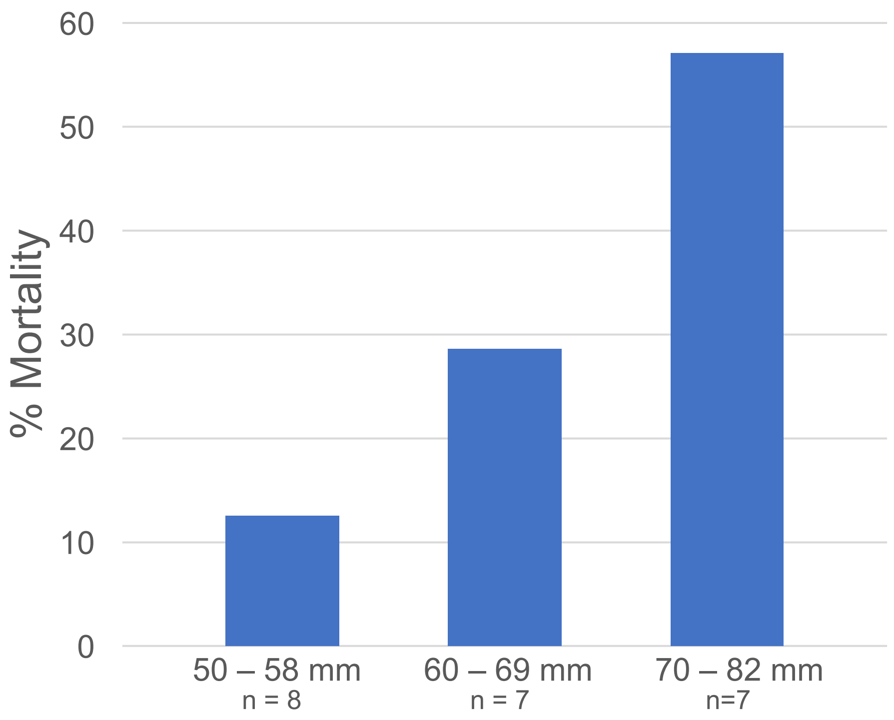
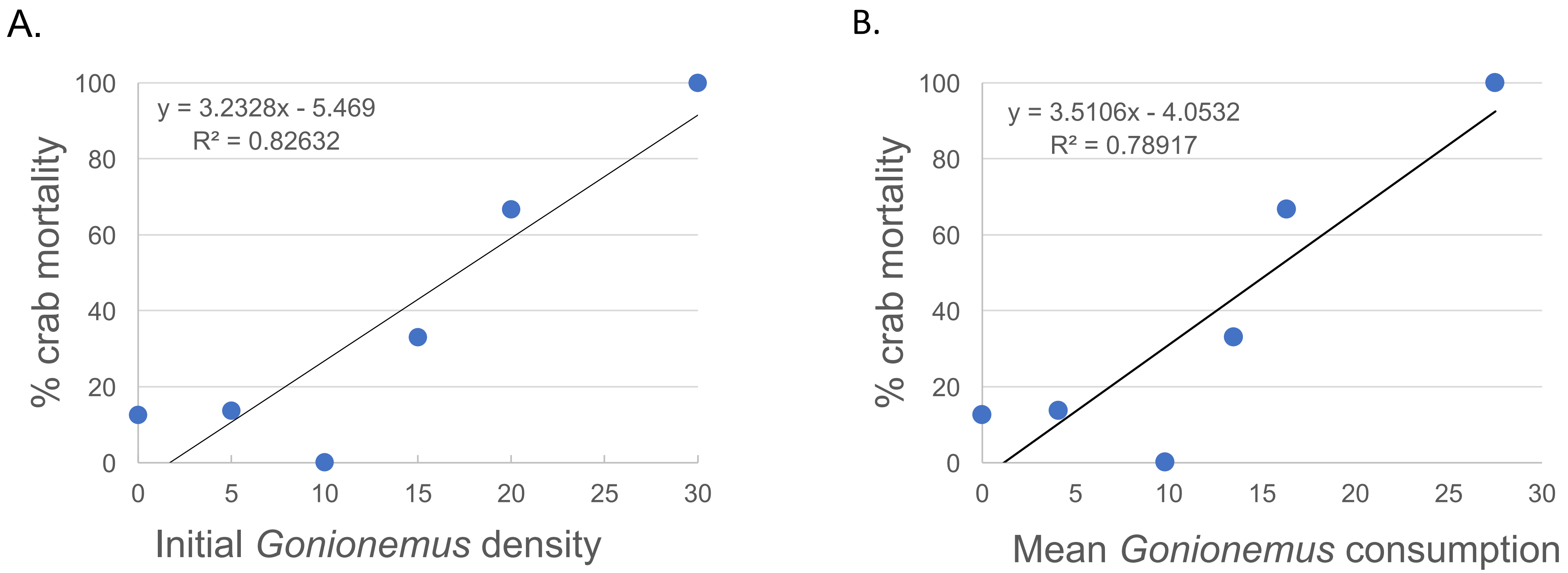

% Mortality
60
50
40
30
20
10
0
50 – 58 mm
n = 8
60 – 69 mm
n = 7
70 – 82 mm
n=7

Figure 6 (on next page)

Spider crab mortality and different *Gonionemus* densities and consumption levels.

Mean *Libinia* mortality as a function of *Gonionemus* density (number of medusae initially placed in crab containers) and *Gonionemus* predation (number of medusae consumed after 24 hours).


A.
y = 3.2328x - 5.469
R² = 0.82632
% crab mortality
100
80
60
40
20
0
0
5
10
15
20
25
30
Initial Gonionemus density
B.
y = 3.5106x - 4.0532
R² = 0.78917
% crab mortality
100
80
60
40
20
0
0
5
10
15
20
25
30
Mean Gonionemus consumption