



Black gill increases the susceptibility of white shrimp, *Penaeus setiferus* (Linnaeus, 1767), to common estuarine predators

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ABSTRACT

Parasites can kill hosts directly, but also indirectly, by enhancing susceptibility to environmental factors and biotic interactions. In the United States South Atlantic Bight region of the northwest Atlantic Ocean, white shrimp (*Penaeus setiferus*) support a substantial commercial fishery and are also valuable prey for many marine and estuarine species. Since the late 1990s, a condition known as black gill has been observed in penaeid shrimp in the South Atlantic Bight. In this region, black gill has been linked to an apicomplexan ciliate that elicits an innate immune response in shrimp, manifested through the melanization of gill tissues, which impedes respiratory functions and hemolymph ion regulation. The objective of this study was to determine if black gill subjects shrimp to higher rates of predation by red drum (*Sciaenops ocellatus*), spotted seatrout (*Cynoscion nebulosus*), and blue crab (*Callinectes sapidus*). A series of simultaneous prey choice mesocosm experiments was conducted, during which single-species predators were able to consume shrimp that were both symptomatic and asymptomatic of black gill over a four-hour period. Predator species were 1.4 to 3.0 times more likely to consume symptomatic shrimp than asymptomatic shrimp. The hinderance of shrimp physiology and escape responses due to gill melanization likely increases the vulnerability of shrimp to predation. This study emphasizes that mortality from parasitic infections is not always direct and that black gill may have a significant impact on penaeid shrimp through secondary, or indirect, mortality.

1. Introduction

Parasites can directly affect host fitness by altering growth rates (Fernandez and Esch, 1991), hindering reproductive development (Astete-Espinoza and Caceres, 2000), or transmitting diseases (Dobson and Hudson, 1986). Parasites can also impact their hosts indirectly by causing behavioral modifications in prey species that increase their susceptibility to predation (Lafferty and Morris, 1996; Kunz and Pung, 2004; Brinton and Curran, 2015). For example, the cestode *Polydora pocephalus* sp. increases shrimp activity upon infection and thus susceptibility to predation by the ultimate host of the cestode, likely a skate or ray (Carreon and Faulkes, 2014). Other parasites affect the physiological functions of their hosts, which can also ultimately lead to increased host vulnerability (Hudson et al., 1992). Because indirect effects of parasites and disease must be considered in a multispecies,

community context, they can be more difficult to discern than direct effects (Wood et al., 2007; Dunn et al., 2012). These types of interactions are known to have negative effects on commercially important species (Shirakashi et al., 2008).

White shrimp (*Penaeus setiferus*; Linnaeus, 1767) are both economically and ecologically important in estuarine and coastal environments of the United States (U.S.) South Atlantic Bight region of the northwest Atlantic Ocean. In addition to supporting an extensive commercial fishery in the southeastern U.S. (Gillet, 2008; NMFS, 2017), white shrimp, in their migrations between salt marsh and offshore habitats, contribute substantially to the diets of many vertebrate and invertebrate species (Overstreet and Heard, 1978; Hettler Jr., 1989; Scharf and Schlight, 2000). In South Carolina and Georgia, U.S., white shrimp landings have decreased in recent years (NMFS, 2017), and the decline may be attributed partially to a parasitic infection directly

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affecting shrimp gills (Gambill et al., 2015; Frischer et al., 2017, 2018).

Over the past few decades, a condition known as black gill has been observed at high prevalence levels in white shrimp in the South Atlantic Bight (Gambill et al., 2015; Fowler et al., 2018), peaking in the fall with an average peak prevalence of 48% (SCDNR, unpubl.). This condition can manifest as the melanization of gill tissues as an innate immune response to gill irritants elicited across the subphylum Crustacea (Burnett and Burnett, 2015) due to a variety of pathogens, parasites, contaminants, and nutrient deficiencies (Lightner, 1985; Cerenius et al., 2010; Frischer et al., 2017). In South Carolina and Georgia, black gill is specifically linked to an immune response caused by an apistome ciliate (Frischer et al., 2017). While black gill has been hypothesized to have contributed to the decline of the shrimp fishery in Georgia (Frischer et al., 2018), the effects of black gill on shrimp populations have yet to be mechanistically determined.

Impaired physiological functions in shrimp that are symptomatic of black gill suggest that these shrimp may experience increased rates of mortality due to predation (Frischer et al., 2018). Melanized nodules, which can be associated with black gill, can form on the gills of shrimp and obstruct respiratory function and ion regulation (White et al., 1985; Martin et al., 2000; Burnett and Burnett, 2015). Limited respiratory function can increase direct mortality of shrimp, particularly under hypoxic or anoxic conditions and at higher temperatures (Lightner et al., 1975; Delves-Broughton and Poupard, 1976). The impairment of respiratory functions due to nodules has been previously reported in Pacific white shrimp (*Penaeus vannamei*; Boone, 1931; Scholnick et al., 2006), and blue crabs (*Callinectes sapidus*; Rathbun, 1896; Burnett et al., 2006; Thibodeaux et al., 2009). Burnett and Burnett (2015) also demonstrated that nodules on the gills can negatively affect cardiovascular activity and metabolism in several crustacean species. These physiological responses can potentially lead to increased vulnerability to predation.

In the wild, shrimp are important prey for many predator species in estuarine environments (Pearson, 1929; Bass and Avault Jr., 1975; Overstreet and Heard, 1978; Laughlin, 1982). The objective of this study was to test the hypothesis that shrimp that are symptomatic of black gill are more susceptible than asymptomatic shrimp to predation by three abundant predator species in estuarine environments of the southeastern U.S. The selected predators, each representing different feeding modes, included two recreationally valued finfish species, red drum (*Sciaenops ocellatus*; Linnaeus, 1766), and spotted seatrout (*Cynoscion nebulosus*; Cuvier, 1830), as well as the commercially and recreationally important blue crab. While red drum and blue crabs are both benthic feeders, red drum typically hunt in groups and blue crabs tend to be more solitary. Spotted seatrout, also schooling fish, generally forage in the pelagic zone (Llansó et al., 1998). Each of these species, while using various feeding methods, consume penaeid shrimp (Pearson, 1929; Bass and Avault Jr., 1975; Alexander, 1986; Fujiwara et al., 2016). Black gill may induce high secondary mortality, potentially leading to broad ecological and fishery implications, even if the parasite exerts low direct mortality on its host. By determining if black gill increases the susceptibility of shrimp to predation, this study expands knowledge of black gill effects in a community context, which is an important step toward understanding larger scale impacts of black

gill on shrimp populations.

2. Materials and methods

2.1. Experimental mesocosm system

To quantify whether predators differentially consumed shrimp with and without black gill, a simultaneous prey choice mesocosm experiment was conducted, utilizing four outdoor mesocosms (3.7 m diameter, 0.6 m water depth) at the South Carolina Department of Natural Resources (SCDNR) Marine Resources Research Institute in Charleston, South Carolina. The mesocosms were supplied with raw, flow-through water from Charleston Harbor and were continuously aerated. All standpipes were surrounded by taller mesh-covered pipes to prevent predator or prey escape. Every three to four days, excess waste material and sediment were siphoned from the mesocosms. Water temperature in each mesocosm was monitored throughout the experiment using HOBO Pendant Data Loggers (model: UA-001-08, Bourne, Massachusetts). Dissolved oxygen, salinity, and temperature were measured once in each mesocosm during all trials using a YSI Pro 2030 water quality meter.

2.2. Collection and holding of experimental animals

All trials were conducted during August, September, or October 2017 and 2018, periods when black gill is generally most prevalent in the natural environment (Fowler et al., 2018). White shrimp were collected from the Ashley River and Charleston Harbor throughout the study by towing a 4.6- or 6.1-m otter trawl for five to 10 min. Shrimp ranged from 80 to 100 mm total length (TL), a size consumed by all three predator species used in this study. Prior to each trial, all shrimp were acclimated for one to two days in a holding tank (1.8 m diameter) with flow-through water and aeration as described for experimental mesocosms above. All predator species were also collected in and around Charleston Harbor (Table 1). Predator size was selected to reflect the size class most likely to encounter and feed on shrimp during the fall (Anweiler, personal communication, February 26, 2018). Finfish predators were collected by hook-and-line and during trammel net surveys conducted by the SCDNR Inshore Fisheries Section. All blue crabs were collected using crab pots baited with Atlantic menhaden (*Brevoortia tyrannus*; Latrobe, 1802). Upon collection, all finfish were placed into oxygenated containers immediately and remained there for transport. Blue crabs were transported in crab baskets under damp burlap, which effectively kept them calm and prevented them from desiccating.

For each species, predators were stocked into mesocosms based on the total length of each individual to ensure that each mesocosm contained a relatively equal biomass of predators. Predators were then allowed time to acclimate to holding conditions. Acclimation time was determined based on the robustness of the predator (e.g., spotted seatrout required more time to settle and begin feeding than red drum or blue crab). Prior to beginning the trials, red drum were acclimated for four days, spotted seatrout were acclimated for 34 days, and blue crabs were acclimated for two days.

Table 1

Collection dates, collection locations, experimental dates, number of replicates, and size ranges for each predator species used in this study.

Predator species	Collection dates	Collection locations ^a	Trial dates	Number of replicates	Size ^b (mm)
Red drum	21 Jul - 25 Jul 2017	Wando River, Charleston Harbor	28 Sep - 11 Oct 2017	9	265–355
Spotted seatrout	27 Jun - 3 Jul 2018	Ashley River, Wando River, Charleston Harbor	28 Aug - 28 Sep 2018	10	283–458
Blue crab	21 Sep - 1 Oct 2018	Ashley River	3 Oct - 8 Oct 2018	12	> 127

^a Wando River: 32.87°N, 79.87°W; Charleston Harbor: 32.76°N, 79.89°W; Ashley River: 32.82°N, 79.97°W.

^b Size ranges for the two finfish species are total length, measured from the mouth to the longest lobe of the caudal fin; crab size refers to the carapace width, measured point-to-point along the lateral spine.

2.3. Experimental design

Each predator species was tested separately. For the purposes of this study, individual mesocosm tanks were considered replicates of each predator species evaluated. Trials, defined as a set of two to four concurrent replicates, were conducted on three separate dates for each of the predator species, resulting in a total of nine replicates for red drum, 10 replicates for spotted seatrout, and 12 replicates for blue crabs. During periods of acclimation and time between trials, predators were fed mummichogs (*Fundulus heteroclitus*; Linnaeus, 1766) or white shrimp with clipped pleopods to ensure that these food items were not mistaken for experimental shrimp. Prior to each trial, predators were starved for approximately three days. The number of predators introduced to each mesocosm in all but one case was > 1 to allow for possible group hunting techniques, but low (< 10), to minimize interference among them (Griffen and Byers, 2006; Table A1).

The same predator individuals were used throughout the experiment, apart from replacing a small number of deceased animals between trials (five spotted seatrout and five blue crabs). No predator mortalities occurred during the trials. Each mesocosm with red drum contained three predators. Of the 10 mesocosms with spotted seatrout, six mesocosms contained three predators each. The other four mesocosms contained a lower number of predators ($n = 1-2$) due to predator mortalities between successive trials. Over the course of the blue crab trials, the number of crabs per mesocosm was reduced from nine ($n = 4$ replicates) to eight ($n = 4$ replicates) to five ($n = 4$ replicates) to minimize the confounding effects of intraspecific agonistic behaviors among crabs on shrimp consumption (Table A1). Only blue crabs with both claws and all legs intact were introduced into mesocosms. There was also some variation in predator number due to crab mortalities that occurred between trials in four mesocosms.

Before beginning each trial, white shrimp were removed from the holding tank and placed in mesh baskets inside each mesocosm at the surface. Each basket was stocked with 32 shrimp, 16 each of symptomatic (i.e., highly melanized gills) and asymptomatic (i.e., showing no visual signs of gill melanization) shrimp, which were categorized under natural light conditions by the naked eye. This number of shrimp provided predators with sufficient opportunities to encounter prey without any confounding effects of overcrowding. Shrimp were acclimated for 30 min in the baskets, after which any dead, moribund, or lethargic shrimp were replaced. Baskets were then slowly lowered into the tanks, allowing shrimp to swim into the water column simultaneously, and the trial commenced. After four hours, all mesocosms were drained, predators were removed and placed into aerated holding bins, and all remaining shrimp were collected and categorized as either symptomatic or asymptomatic of black gill. Missing shrimp were assumed to have been consumed by the predators. Shrimp molts and unconsumed shrimp carcasses were counted and recorded.

2.4. Stomach content analysis

To verify the assumption that shrimp that were not recaptured at the end of the four-hour trials had been consumed by the predators in the mesocosms, stomach content analyses were conducted after one of the experimental trials. Following the end of the last spotted seatrout trial, each fish was sacrificed, and stomach contents were removed and immediately frozen. Upon thawing days later, stomachs were opened, and shrimp were removed. The shrimp were undigested enough to easily determine the number of shrimp in each stomach and to characterize each shrimp as symptomatic or asymptomatic of black gill.

2.5. Statistical analyses

To standardize data and to account for differences in the numbers of live predators between replicates, predation rates were calculated as the number of white shrimp consumed per predator per hour. Predation

rates were compared across predator species to assess variability in rates using non-parametric Kruskal-Wallis tests where Shapiro-Wilk tests indicated non-normal distribution of data. To test for differences in the probabilities and odds of each of the three predator species consuming symptomatic shrimp and asymptomatic shrimp, generalized linear mixed effects models of shrimp mortality with binomial distributions, logit link functions, and associated likelihood ratio tests were used. Individual shrimp within each replicate were designated as symptomatic or asymptomatic of black gill (predictor variable) and as consumed or unconsumed (response variable). To account for the experimental design, replicate was nested within trial and used as a random effect in each of the models. Probabilities represent shrimp consumed from each group (i.e., symptomatic and asymptomatic) compared to all shrimp available within each group. The relative risk of symptomatic shrimp being eaten was calculated as the ratio of symptomatic to asymptomatic probabilities. Odds represent the number of shrimp consumed compared to the number of shrimp left unconsumed within each group (i.e., symptomatic and asymptomatic). The odds ratio is the odds of symptomatic shrimp being consumed compared to asymptomatic shrimp for each predator species and can be interpreted as an effect size. These analyses were conducted in the 'lme4' package in R version 3.5.1 (Bates et al., 2015; R Core Team, 2018).

3. Results

3.1. Water quality

The temperature records collected continuously throughout the study by the HOBO Pendant Data Loggers did not differ substantially between mesocosms. Additional water quality measurements (i.e., temperature, salinity, and dissolved oxygen) taken with the YSI Pro 2030 during each trial changed slightly over time throughout the study but did not differ considerably between mesocosms and remained well within tolerance ranges for predator and prey species (Table A1). Temperature ranged from 26.0 °C to 29.9 °C (mean = 27.8 °C). Salinity ranged from 21.8 to 29.0 (mean = 25.9). Dissolved oxygen ranged from 4.9 mg/L to 5.9 mg/L (mean = 5.5 mg/L). Calculated percent oxygen saturation (which incorporated salinity, temperature, dissolved oxygen, and barometric pressure) ranged from 73.3% to 87.78% (mean = 79.9%).

3.2. Predation rates

All three predator species used in this study were more likely to consume symptomatic shrimp than asymptomatic shrimp. Throughout the study, red drum consumed 40.6% of shrimp available ($n = 288$), spotted seatrout consumed 36.6% of shrimp available ($n = 320$), and blue crabs consumed 11.2% of shrimp available ($n = 384$). Red drum consumed greater numbers of symptomatic shrimp than asymptomatic shrimp in eight of the nine replicates. In total, red drum consumed 71 symptomatic shrimp and 46 asymptomatic shrimp. Spotted seatrout consumed greater numbers of symptomatic shrimp than asymptomatic shrimp in five of 10 replicates, ultimately consuming a total of 68 symptomatic shrimp and 49 asymptomatic shrimp. Blue crabs consumed more symptomatic shrimp than asymptomatic shrimp in nine of 12 replicates, consuming a total of 32 symptomatic shrimp and 11 asymptomatic shrimp. Throughout the experiment, there were only two instances when predator species consumed more asymptomatic shrimp than symptomatic shrimp in the mesocosms. In one mesocosm, spotted sea trout consumed seven symptomatic shrimp and eight asymptomatic shrimp, and in another mesocosm, blue crab consumed zero symptomatic shrimp and one asymptomatic shrimp.

The predation rate on shrimp by blue crabs was significantly lower (0.13 shrimp predator⁻¹ h⁻¹) than red drum (1.03 shrimp predator⁻¹ h⁻¹) and spotted seatrout (1.2 shrimp predator⁻¹ h⁻¹; p -values < .001). Mean predation rates were greater for symptomatic

Table 2

Total numbers of symptomatic and asymptomatic white shrimp consumed by each predator species and the average predation rates (shrimp predator⁻¹ hour⁻¹) of prey of each condition for each predator species (\pm SE).

Predator species	Number of white shrimp offered (symptomatic/asymptomatic)	Number of white shrimp consumed (symptomatic/asymptomatic)	Symptomatic white shrimp consumed predator ⁻¹ h ⁻¹	Asymptomatic white shrimp consumed predator ⁻¹ h ⁻¹
Red drum	288 (144/144)	117 (71/46)	0.63 (\pm 0.09)	0.40 (\pm 0.07)
Spotted seatrout	320 (160/160)	117 (68/49)	0.68 (\pm 0.08)	0.49 (\pm 0.04)
Blue crab	384 (192/192)	43 (32/11)	0.10 (\pm 0.01)	0.03 (\pm 0.01)

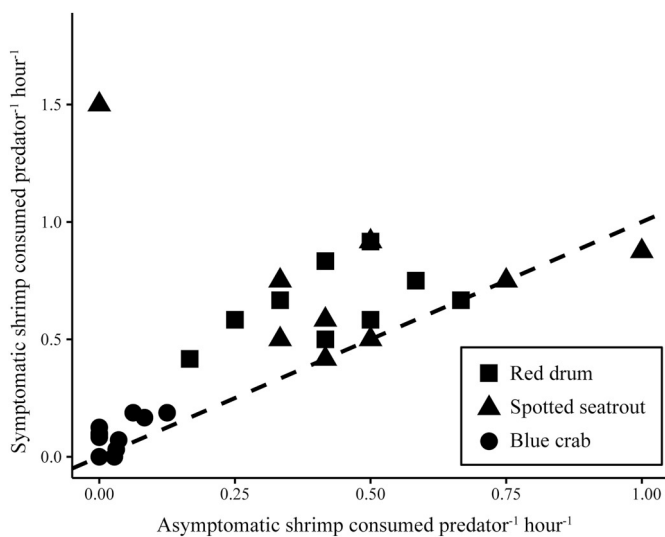


Fig. 1. Comparison of predation rates (calculated as number of shrimp consumed predator⁻¹ hour⁻¹) of symptomatic and asymptomatic shrimp for red drum (*Sciaenops ocellatus*), spotted seatrout (*Cynoscion nebulosus*), and blue crab (*Callinectes sapidus*). Each point represents the predation rate calculated for each predator species within a single mesocosm over the four-hour trial period. The dashed line indicates equal consumption of both shrimp conditions.

shrimp than asymptomatic shrimp (Table 2). Across all predator species, symptomatic shrimp were more likely to be consumed than asymptomatic shrimp (Fig. 1) with the minimum odds ratio for each species consistently > 1 (Table 3). Based on these data, relative risks suggested that a symptomatic shrimp was 1.5 and 1.4 times more likely to be consumed over a shrimp asymptomatic of black gill by red drum and spotted seatrout, respectively. In the blue crab trials, a symptomatic shrimp was 3.0 times more likely to be consumed over an asymptomatic shrimp. Across all predator species, symptomatic shrimp were an average of 2.0 times more likely to be consumed than asymptomatic shrimp. Of the total number of shrimp consumed ($n = 277$) by all predators throughout the study, 61.7% were symptomatic of black gill and 38.3% showed no visible symptoms of black gill.

3.3. Stomach content analysis

All shrimp that had been released into the mesocosms during the last of the spotted seatrout trials were either recovered unconsumed at the end of the trial or found in the stomachs of the eight spotted

Table 3

Results from generalized linear mixed effects models assessing the probability of an individual white shrimp being consumed by respective predators if symptomatic or asymptomatic of black gill. Odds ratio reports the odds of symptomatic shrimp being consumed compared to asymptomatic shrimp for each species. Confidence intervals (95%) are provided in parentheses.

Species	Symptomatic consumption probability	Asymptomatic consumption probability	Odds ratio	p-Value
Red drum	0.49 (0.29–0.70)	0.32 (0.24–0.41)	2.09 (1.29–3.40)	0.004
Spotted seatrout	0.42 (0.22–0.64)	0.30 (0.21–0.40)	1.70 (1.07–2.73)	0.025
Blue crab	0.15 (0.04–0.43)	0.05 (0.02–0.09)	3.42 (1.70–7.40)	< 0.001

seatrout. Additionally, the total number of symptomatic and asymptomatic shrimp found in the stomachs matched the number of shrimp that were expected to have been consumed based on the recoveries of live shrimp. Together, these results support the assumptions that 1) all shrimp that were not recovered at the end of the experiment were consumed by predators in the mesocosms, and 2) shrimp classified as symptomatic before the experiment were also classified as symptomatic at the end of the experiment.

4. Discussion

The effects of parasites on host behavior and endurance are important to consider when examining predator-prey interactions. Parasites can alter or slow the locomotion of their hosts, which can lead to decreased feeding behaviors and movement (Belgrad and Griffen, 2015) and increased susceptibility to predation (Hoogenboom and Dijkstra, 1987; Poulin, 2010; Gehman and Byers, 2017). It can be advantageous for parasites to increase host susceptibility to predation by the parasite's definitive host, but there is also evidence of non-trophically linked parasites changing the behavior of their hosts (Poulin, 2010). For example, Shirakashi et al. (2008) found that the invasive monogenean *Neoheterobothrium hirame* (Ogawa, 1999), a parasite of olive flounder (*Paralichthys olivaceus*; Temminck and Schlegel, 1846), caused no direct mortality to the host, but rather altered flounder behavior by increasing activity level, hindering burrowing success, and decreasing swimming endurance that ultimately led to increased host susceptibility to predation. The decline of flounder populations in Japan has been partially attributed to the predation-enhancing effects of this monogenean (Shirakashi et al., 2008). Some predators may be indifferent to infections carried by prey (Hulscher, 1973), especially if the predator feeds indiscriminately or if the prey is already easily caught or exhibits minimal reaction to the parasite. This study suggests that in a community context, a non-trophically linked parasite might increase prey mortality by increasing susceptibility to predation.

In this study, white shrimp symptomatic of black gill were 1.4 to 3.0 times more likely to be consumed than asymptomatic shrimp by three common and abundant predator species within estuarine and coastal marine habitats in the southeastern U.S. The mechanism for the increased susceptibility to predation of symptomatic shrimp may be due to the physiological limitations associated with the immune response during infection, including restricted respiration and cardiovascular functions, as documented in other crustaceans symptomatic of black gill (Burnett and Burnett, 2015). Frischer et al. (2018) demonstrated reduced escape responses and physical endurance in white shrimp with melanized gills. Additionally, these researchers found that

asymptomatic shrimp spent more time moving forward on a treadmill apparatus, while symptomatic shrimp displayed exhaustion behaviors more quickly and more frequently. Burnett et al. (2006) found similar results in blue crabs with damaged gills. Aggregated hemocyte nodules on blue crab gills led to reduced capacity to perform actions demanding a higher oxygen supply, including predator evasion (Burnett et al., 2006). Similarly, Thibodeaux et al. (2009) reported that blue crabs with impaired gill function consumed oxygen at a lower rate during and after periods of increased activity. Therefore, it is possible that behavioral differences attributable to lower stamina between symptomatic and asymptomatic shrimp contribute to differential mortality. Although mortality rates of shrimp were not evaluated in control tanks (i.e., those lacking predators) during this study, consumption rates of symptomatic and asymptomatic shrimp should sufficiently reflect comparative susceptibility of predation, rather than any differential mortality of symptomatic shrimp following handling, due to the short duration of the trials, the stable survivorship of shrimp in holding tanks before initiating the trials, and equal handling of symptomatic and asymptomatic shrimp.

Poor water quality, specifically hypoxic conditions, may exacerbate stressors on shrimp symptomatic of black gill. Under natural conditions in southeastern U.S. estuaries, oxygen levels can be reduced, particularly in warmer months at the benthic boundary layer, producing conditions that can introduce oxygen-related stress in biota (Lenihan et al., 2001; Wenner et al., 2004), possibly accentuating the propensity for black gill to compromise anti-predator responses in infected shrimp hosts. Even in healthy shrimp, hypoxia may cause energy constraints or restrictions on growth and activity, as well as lead to changes in behavior or a decreased tolerance to other stressors (Burnett and Stickle, 2001). Fowler et al. (2018), in an analysis of long-term white shrimp fisheries independent data collected by the SCDNR, suggested that high salinities and low dissolved oxygen concentrations over at least a month act synergistically to lower the resistance of shrimp to black gill. The presence of melanized hemocytic nodules in gill tissues associated with increased immune responses have reduced respiratory function in other decapods (Burnett et al., 2006), so low-oxygen conditions could be especially challenging for symptomatic shrimp. Oxygen-related stress was likely minimized during this study, during which dissolved oxygen remained relatively high (~5 mg/L) and above levels that would generally induce oxygen-related stress in shrimp (Renaud, 1986).

Predation on parasitized prey can vary by predator species, which may be partially driven by the different feeding strategies used by various predators. In this study, although all predators used different methods of feeding, they all exhibited predation bias toward shrimp with black gill. Both red drum and spotted seatrout are schooling fish (Wilson and Nieland, 1994; Handegard et al., 2012). When schooling fish encounter prey, feeding activity can signal to other fish that prey are in the area (Keenleyside, 1955). Additionally, schooling fish, such as spotted seatrout, often strike together, placing more pressure on prey and increasing the likelihood for prey consumption (Handegard et al., 2012). In contrast, blue crabs in this study appeared to be more territorial and aggressive towards other crabs, and when in proximity to one another, seemed more focused on other crabs rather than on shrimp prey (Gooding, personal observation). Additionally, in the natural environment, blue crabs typically target slow or sessile prey, such as gastropods and bivalves (Laughlin, 1982; Alexander, 1986; Hines et al., 1990). The finding that all three predator species, which utilize a variety of feeding methods, preferred symptomatic shrimp over asymptomatic shrimp suggests that shrimp with black gill are more vulnerable regardless of predator species.

The predators used in this study typically consume prey species that are the most abundant in their environment (Llansó et al., 1998; Rosas et al., 1994), including shrimp during the summer and fall (Laughlin, 1982; Overstreet and Heard, 1982; Scharf and Schlicht, 2000). In the South Atlantic Bight, black gill prevalence generally peaks during the fall (Gambill et al., 2015; Fowler et al., 2018), and high black gill

prevalence could lead these and other predators to consume more shrimp than would be consumed in the absence of black gill. Such a subsidy to predators could boost their population sizes over time, while also influencing food web structure, possibly leading to further increased pressure on shrimp and other prey populations (Noonburg and Byers, 2005).

If black gill leads to an overall increase in shrimp consumption by predators, this increased top-down pressure on shrimp populations may be contributing to reduced landings of shrimp in the commercial trawl industry in the South Atlantic Bight region. A number of other factors may also be contributing to the decline in shrimp landings over the past few decades, including reductions in fishing effort, both in terms of the number of vessels shrimping and the number of hours fished (SEDAR, 2014), and climate (Fowler et al., 2018; Lopes et al., 2018; Oxenford and Monnereau, 2018; SCDNR, unpubl.). This study suggests secondary mortality resulting from black gill as another possible factor.

4.1. Conclusion

This study demonstrates that shrimp symptomatic of black gill are more susceptible to predation by three different common predator species. Secondary mortality resulting from physiological limitations may exacerbate the effect of black gill on shrimp populations, potentially contributing to the observed regional decline in landings. The effects of a parasite on a host may not fully manifest until the host is placed in a community context that includes the complexity of other biotic and abiotic interactions. To fully understand the impact of black gill or any other infections that may influence additional predator-prey interactions, it is critical to consider both the direct and indirect effects resulting from these species interactions.

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Declaration of Competing Interest

None.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jembe.2019.151284>.

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