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Effects of the parasitic dinoflagellate *Hematodinium perezi* on blue crab (*Callinectes sapidus*) behavior and predation

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ABSTRACT

Blue crabs (*Callinectes sapidus*) living in high salinity regions along the Atlantic and Gulf coasts of the United States are subject to infection by the parasitic dinoflagellate *Hematodinium perezi* with a prevalence that can exceed 50%. Infections are usually lethal, thus *H. perezi* infection represents a significant cause of mortality in many crab populations. Most studies of this host-parasite interaction have focused on epidemiology, host-pathogen dynamics, and pathogen transmission; little is known about the impact of the parasite on host behavior and population dynamics. We examined the effects of *H. perezi* on blue crab mortality from predation, activity patterns, and habitat use. Infected crabs suffered significantly higher predation than uninfected crabs when tethered in the field. Similarly, infected juvenile crabs were preyed upon significantly more often than uninfected conspecifics when exposed to a predatory adult crab in laboratory experiments. Laboratory experiments also revealed that the behavior of infected and uninfected crabs differed in ways that affected their risk of predation. Compared to infected crabs, uninfected juvenile crabs buried more frequently, moved less, and used oyster shell substrate more often when a predator was present. These differences do not appear to be driven by olfactory cues because chemosensory assays show that *H. perezi* infections do not affect detection of juvenile crabs by adult crabs, nor infected juvenile crab chemosensory responses to adult crabs. Our results indicate that *H. perezi* infection alters crab behavior in ways that enhance predatory culling of infected crabs, and this in turn may limit the spread of the parasite.

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1. Introduction

Pathogens are a ubiquitous part of the marine environment but have historically received little attention from ecologists (Keesing et al., 2008; Shields, 2012). Reports of pathogenic diseases in the wild have been steadily increasing (Daszak et al., 2000; Harvell et al., 1999), and examples from various taxa indicate that environmental stressors of anthropogenic origin often facilitate the induction and spread of marine diseases (Lesser et al., 2007; Mydlarz et al., 2006; Shields, 2013). Yet, our knowledge of the underlying causes and ecological consequences of many marine diseases remains poor, even when diseases affect species of substantial commercial and ecological value (Harvell et al., 1999).

Parasitic dinoflagellates in the genus *Hematodinium* are important pathogens of more than 35 species of marine crustaceans, including species that support important commercial and recreational fisheries (Morado, 2011; Small, 2012; Stentiford and Shields, 2005). *Hematodinium* spp. infects the hemolymph and tissues of their hosts and can cause epizootics (Shields and Overstreet, 2007), including those reported in the Tanner crab fishery in Alaska (Meyers et al., 1987), snow crab fishery in Newfoundland (Shields et al. 2005, 2007), the Norway lobster fishery in Scotland (Field et al., 1992), and the velvet crab fishery in France (Wilhelm and Mialhe, 1996). Epizootics of *Hematodinium* have also been linked to dramatic declines in blue crab (*Callinectes sapidus*) landings in the seaside bays of Maryland and Virginia (Messick and Shields, 2000). Two species of *Hematodinium* have been described: *Hematodinium perezi* in France (Chatton and Poisson, 1931) and *Hematodinium australis* in Australia (Hudson and Shields, 1994). Based on molecular evidence, *H. perezi* genotype III (closely related to the type species, *H. perezi* genotype I, from the English Channel) is responsible for infections in blue crabs along the east coast of the United States (Small et al., 2012).

The life cycle of *Hematodinium* spp. is complex and includes uni- and multi-nucleated amoeboid trophonts, arachnoid trophonts, and sporonts that occur within the host, as well as flagellated dinospores that occur in benthic sediments and the water column (Frischer et al., 2006; Hanif et al., 2013; Li et al., 2010). Transmission of the pathogen among hosts is probably via the free-living dinospores (Frischer et al., 2006; Hanif et al., 2013; Stentiford and Shields, 2005). Transmission through cannibalism or consumption of infected alternative hosts has been reported (Walker et al., 2009) but is unlikely (Li et al., 2011a; Pagenkopp et al., 2012).

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H. perezi infections in blue crabs are widespread in the high salinity areas of the eastern seaboard of the USA. In the mid-Atlantic region, where our study was conducted, infected blue crabs have been reported from the lower Chesapeake Bay and the seaside estuaries and bays of the Delmarva Peninsula of Delaware, Maryland, and Virginia (Messick, 1994; Messick and Shields, 2000; Shields, 1994). During outbreaks, the impact of *Hematodinium* spp. on fisheries is significant (Lee and Frischer, 2004; Stentiford and Shields, 2005). For example, a major decline in blue crab landings in 1992 coincided with an epizootic of *H. perezi* (Messick and Shields, 2000).

Knowledge about the host-parasite system has grown considerably since *H. perezi* was first identified in blue crabs by Newman and Johnson (1975). We now have a better understanding of spatio-temporal patterns in infection prevalence (Messick, 1994; Messick and Shields, 2000), intra-host pathogen life history (Appleton and Vickerman, 1998; Li et al., 2011b; Shields and Squyars, 2000), pathogen taxonomy (Small et al., 2012), pathology of infections (Field et al., 1992; Shields et al., 2003) and potential alternate hosts (Hamilton et al., 2009; Pagenkopp et al., 2012; Sheppard et al., 2003). However, the effect of *H. perezi* on the ecology of the blue crab host is largely unknown despite the importance of such information for blue crab population sustainability and management (Shields, 2003).

Our objective was to experimentally examine the effects of *H. perezi* on the behavior and predation of blue crabs. We quantified the relative rates of mortality of tethered infected and uninfected crabs in the field. In a laboratory experiment, we examined habitat selection, activity patterns, and mortality of infected and uninfected juvenile crabs when exposed to adult crabs, which are common predators of juveniles. Finally, the potential role of *H. perezi* infection on chemoreception by and of infected crabs was studied in a second set of laboratory experiments.

2. Methods

Crabs were collected using commercial crab pots baited with menhaden from seaside estuaries on the Eastern Shore of Virginia near the towns of Wachapreague (37° 37.494′ N, 75° 40.960′ W) and Oyster (37° 15.778′ N, 75° 50.533′ W). The sex, carapace width (CW), and number of missing appendages of each crab were recorded and each crab was screened for *H. perezi* infection by microscopic examination of a fresh hemolymph smear stained with 0.3% neutral red (see Shields and Squyars, 2000). The density of parasite cells in infected crabs was quantified by calculating the mean number of parasite cells per 40× objective field ($n = 7$ fields observed/crab as determined after preliminary sampling and power analysis). This yields a semi-quantitative measurement of the intensity of infection (Messick and Shields, 2000). Parasite life history stages were also identified as described in Li et al. (2011a, 2011b). Only naturally infected crabs were used in field mortality experiments, but some crabs used in laboratory experiments were infected by inoculation of 100 μl of infected hemolymph (50 μl for juveniles) (see Li et al., 2011b for details) when sufficient numbers of naturally infected crabs were unavailable. Inoculations of 100 μl consistently provide light to moderate infections after 14–21 days (Shields and Squyars, 2000). Crabs inoculated with a similar amount of uninfected hemolymph served as negative controls. Whether infections were natural or the result of inoculation had no effect on our laboratory results (Tiggelaar, 2012).

2.1. Effect of H. perezi infection on predation of adult blue crabs

Relative differences in predation between *H. perezi*-infected and uninfected adult crabs were examined in a field tethering experiment, a methodology that has been widely used to determine the relative mortality of portunid crabs in Chesapeake Bay (Hovel and Lipcius, 2001, 2002; Lipcius et al., 2005). The method can produce biased results if its procedural effects are not proportional among treatment groups, especially when results are compared across multiple habitat types (Peterson and Black, 1994). Despite that drawback, tethering remains one of the most widely used and best methods for estimating relative predation risk (Aronson and Heck, 1995; Aronson et al., 2001; Pile et al., 1996). To minimize possible confounding, we tethered crabs in a single, predominant bottom type in the area (mud-sand bottom), with no structure, and thus no potential for tangling of the tether.

Before deployment, infected and uninfected crabs were fitted with a harness made of 22 kg test monofilament tied around the lateral spines and affixed to the carapace using a few drops of cyanoacrylate glue. In the field, crab harnesses were attached with a snap swivel to a 3 kg brick anchor with a 1 m length, 22 kg test monofilament tether, permitting the crabs a 2 m diameter range of movement. The tethered crabs were deployed on mud bottom at shallow (1–2 m deep) or deep (3–4 m deep) sites. Crabs were placed a minimum of 10 m apart to ensure independence. After 24 h, the status of the tethered crabs was assessed. Crabs were considered victims of predation if crushed pieces of the carapace were attached to the monofilament harness or if the monofilament tether was clearly abraded; otherwise, crabs were considered to have escaped and were excluded from the analysis. We repeated this experiment approximately monthly from May 2010 through October 2010 to account for seasonal differences in predation. No data were collected in September 2010 due to poor weather. Differences in predation based on infection status, carapace width, parasite cell density, and other factors were analyzed using multi-way contingency table analyses.

2.2. Effect of H. perezi infection on predation, activity, and habitat selection of juvenile blue crabs

We designed a laboratory experiment to simultaneously examine the effect of *H. perezi* infection on juvenile crab predation, activity, and habitat selection. Each experiment with an individual, free-ranging juvenile crab proceeded through three 24-h long treatments in a repeated-measures design during which the activity, burying behavior, and habitat choice of the crab was monitored by video recording. Treatment 1 consisted of a juvenile crab alone in the experimental chamber, Treatment 2 consisted of the same crab exposed to the odor of a potential predator (i.e., adult crab), and Treatment 3 consisted of the juvenile crab exposed to a free-ranging adult crab predator.

The experiment was conducted in four rectangular (2.4 × 0.6 m) water tables in which filtered, recirculating seawater flowed the length of each table at approximately 0.25 m/s. Juvenile crabs were excluded from the upper 0.25 m of the water table near the water input by a mesh screen; this area is where the adult crab was constrained during Treatment 2 of the experiment. The remaining 2.15 m of each water table was divided into three equal substrates, or habitat sections, in random order: sand, oyster shell, and artificial seagrass (0.25 m long strands of polypropylene rope tied to plastic mesh and covered with sand). Prior to each replicate trial, the seawater in each water table was replaced and filtered through a 10 μm filter, UV light, and activated carbon for 24 h. Each 3-d experimental trial was continuously recorded; nighttime recording was done with infrared cameras and lighting because brachyuran crabs cannot see infrared light (Cronin, 1986).

To initiate an experimental trial, a juvenile crab (40–90 mm CW) was randomly placed onto one of the substrates within a water table and allowed to acclimate for 30 min. Video recording commenced after the acclimation period and the crab was allowed to roam the tank freely for 24 h with no predator present (Treatment 1). After 24 h, an uninfected adult crab (CW > 110 mm) was placed in a mesh cage at the upstream end of the water table for 24 h, and the response of the juvenile crab in the rest of the water table was again recorded (Treatment 2). At the end of the second 24-h period, the adult crab predator was released into the water table with the juvenile crab for a final 24-h period of video recording, or until the adult crab consumed the juvenile crab (Treatment 3).

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