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Structured habitat provides a refuge from blue crab, *Callinectes sapidus*, predation for the bay scallop, *Argopecten irradians concentricus* (Say 1822)☆

Ana L. Hernández Cordero, Rochelle D. Seitz *

Virginia Institute of Marine Science, College of William & Mary, P.O. Box 1346, Gloucester Point, VA 23062, USA

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ABSTRACT

Predation in estuarine systems is an important source of mortality for benthic organisms. In laboratory mesocosm experiments, we assessed the survival of bay scallops (*Argopecten irradians concentricus*) of various sizes (10–19 mm, 20–29 mm, 30–39 mm, and 40–50 mm shell height; SH) as a function of female blue crab, *Callinectes sapidus*, predation as it varied with habitat (oyster shell, sand, *Gracilaria* spp.) and predator size (>140 mm, ≤140 mm carapace width; CW) in a balanced two-by-three factorial design. Scallops of all sizes were afforded higher proportional survival with small female crabs (0.61, SE = 0.05) compared to that with large female crabs (0.36, SE = 0.05), and the proportion of scallops surviving was highest in oyster shell (0.61, SE = 0.08), as compared to the *Gracilaria* spp. and sand treatments, at 0.41 (SE = 0.06) and 0.42 (SE = 0.07), respectively. Subsequent field-tethering experiments conducted in the Lynnhaven River sub-estuary of the lower Chesapeake Bay further illustrated the effect of habitat on the survival of juvenile bay scallops (<30 mm SH); survival after 48 h differed significantly by habitat and location, but not size, and there were no interactions. Proportional survival was significantly higher in *Gracilaria* spp. treatment (0.60, SE = 0.07) as compared to other habitats, and it was higher at Alanton's Cove (0.60, SE = 0.10) compared to other locations. Overall, scallop survival was low; however, transplanting scallops in structured substrates with protection against predation, such as oyster shell and *Gracilaria* spp., will likely increase the success of restoration efforts.

1. Introduction

Predation by crabs in estuarine systems is an important source of natural mortality for a variety of benthic organisms, particularly during the juvenile phase (Jensen and Jensen, 1985; Juanes, 1992; Strieb et al., 1995). Numerous studies have demonstrated the crab's ability to regulate bivalve population dynamics and community structure (Arnold, 1984; Holland et al., 1980; Virnstein, 1977). Bivalve prey can coexist alongside their predators with a reduced risk of mortality if (1) they reach a partial or total size refuge at adult sizes (Eggleston, 1990a,b; García-Esquivel and Bricelj, 1993), (2) exist in a habitat inaccessible to predators (Byers, 2002; Grabowski, 2004), (3) develop heavy shell morphology (Blundon and Kennedy, 1982a,b), and/or (4) employ behavioral mechanisms to avoid predation (i.e., ability to swim), as in the case of bay scallops (Peterson et al., 1982). Increased habitat complexity provides spatial refuge from predators, particularly during the early stages of bivalve development (Arnold, 1984; Talman et al., 2004), and can decrease predator foraging efficiency and trophic transfer (Grabowski and Powers, 2004).

The blue crab, *Callinectes sapidus* (Rathbun), is an ecologically and commercially important large epibenthic predator found along the eastern seaboard of North America (Eggleston et al., 1992). In Chesapeake Bay, blue crabs are dominant predators, reaching high abundances with vigorous foraging activity from late spring through autumn (Eggleston et al., 1992; Lipcius and Hines, 1986; Moody, 1994), though as temperatures approach 10 °C they become sluggish (Churchill, 1919). Blue crabs consume fish, crabs, detritus, shrimp, aquatic plants, conspecifics, and mollusks (Lipcius et al., 2007; Seitz et al., 2011); however, bivalve mollusks form a major fraction of their diet (Hines et al., 1990; Laughlin, 1982; Seitz et al., 2001, 2011). In some environments, bay scallops, *Argopecten irradians*, may also be an important component of the blue crab diet; juvenile scallops are particularly vulnerable to crab predation because of their thin shells, inability to maintain prolonged valve closure, and limited mobility (Bishop and Wear, 2005). In addition to blue crabs, other potential predators of juvenile scallops include other species of crabs (*Dyspanopeus sayi*, *Libinia* spp., *Cancer irroratus*, *Ovalipes ocellatus*, *Pagurus longicarpus*, *Pagurus pollicaris*, *Pagurus annulipes*) (Morgan et al., 1980; Tettelbach, 1986), cownose rays (*Rhinoptera bonasus*) (Bishop et al., 2005; Peterson et al., 2001), sea stars (*Asterias forbesi*) (Belding, 1910), oyster drills (*Urosalpinx cinerea*) (Ordzie and Garofalo, 1980), and seagulls (Gutsell, 1930; Peterson et al., 1989; Prescott, 1990; Tettelbach, 1986), only some of which (mud crabs,

☆ Blue crab predation on bay scallops.
* Corresponding author.
E-mail address: seitz@vims.edu (R.D. Seitz).

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cownose rays, oyster drills, and seagulls) are commonly found in our study area, lower Chesapeake Bay (Rodney and Paynter, 2006; Seitz and Lawless, 2008; Smith and Merriner, 1985).

Beginning in the 1930s, bay scallop populations declined considerably along the Western Atlantic and Gulf coasts following the decimation of eelgrass (*Zostera marina* L.) beds, the preferred habitat for bay scallops, by eelgrass wasting disease (Dreyer and Castle, 1941; Orth et al., 2006). In more recent decades, populations have continued to decline (Tettelbach and Wenczel, 1993), which may be attributed to harmful algal blooms (Tettelbach et al., 2002), recruitment limitation (Peterson and Summerson, 1992; Peterson et al., 1996), trophic cascades (Myers et al., 2007), and habitat loss associated with increased nutrient loading (Serveiss et al., 2004). Bay scallop restoration efforts implemented throughout the country have been met with variable success (Arnold et al., 2005; Goldberg et al., 2000; Leverone et al., 2010; Peterson et al., 1996; Tettelbach and Smith, 2009). In Chesapeake Bay and its vicinity, bay scallop population demise was primarily a result of habitat loss due to anthropogenic effects, eelgrass wasting disease, and damage from the “Storm King” hurricane (Castagna and Chanley, 1973; Orth and Moore, 1983). Since the mid-1990s, attempts to establish bay scallop populations have been moderately successful in the seaside lagoons (i.e., South Bay) adjacent to Chesapeake Bay (M. Luckenbach, personal communication), where the recovery of eelgrass has allowed more intensive scallop introduction efforts (Orth et al., 2010). Concerns that environmental conditions would preclude the survival of reproducing individuals have thwarted any attempts to establish bay scallops in the lower Chesapeake Bay. However, Hernández Cordero et al. (2012) demonstrated that, in the absence of predation, bay scallops are able to survive in areas of the lower Chesapeake Bay.

Habitat complexity affects the ecological interactions of species, including the abundance and distribution of structure-dependent invertebrates and fish (Hovel and Lipcius, 2002). Seagrasses, specifically eelgrass, are recognized as the bay scallop's preferred habitat (Belding, 1910; Gutsell, 1930; Thayer and Stuart, 1974) because this habitat offers larvae a favorable substrate for attachment (Eckman, 1987), and because it provides a spatial refuge for larvae and juveniles from epibenthic and avian predators (Ambrose and Irlandi, 1992; García-Esquivel and Bricelj, 1993; Pohle et al., 1991), as well as from siltation associated with the bottom (Castagna, 1975; Thayer and Stuart, 1974). However, bay scallops can also occur at high abundances in natural habitats devoid of eelgrass (Marshall, 1947) by attaching to other substrates, such as small branching algal species, shells, rocks, or sessile animals (Carroll and Peterson, 2013; Carroll et al., 2010; Smith et al., 1988; Thayer and Stuart, 1974). Preference for complex habitats is likely a function of size. Young bay scallops (<15 mm shell height; SH) in mesocosms equally selected cobble, algal, and eelgrass habitats, all of which were selected over sand; older bay scallops (>25 mm SH) exhibited no difference in settlement among cobble, algae, eelgrass, and sand (Chintala et al., 2005). Survival of planted bay scallops was higher in eelgrass compared to bare sand (Tettelbach et al., 2011), and in field experiments conducted by Hernández Cordero et al. (2012) using eelgrass, macroalgae, oyster shell, and rubble, caged scallops (>27 mm SH) had increased survival in eelgrass and macroalgal habitats. The use of structured habitats aside from seagrass by bay scallops (*Argopecten irradians concentricus*) in Chesapeake Bay is unknown, but this information has utility for restoration efforts, particularly in degraded systems.

Through mesocosm and field experiments, we assessed predation on southern bay scallops (*Argopecten irradians concentricus*). In mesocosm experiments, we quantified the impacts of female blue crab predation on juvenile and adult bay scallops (10–19 mm, 20–29 mm, 30–39 mm, 40–49 mm SH) as it varied among habitats (oyster shell, sand, *Gracilaria* spp.) and with differing predator sizes (>140 mm, ≤140 mm carapace width; CW). In the field, we examined predation by tethering scallops at various locations and in different habitats within the Lynnhaven River sub-estuary of the Chesapeake Bay, Virginia. We hypothesized that the structured habitats, oyster shell, and *Gracilaria* spp., would provide the scallops refuge from predation.

2. Methods

2.1. Mesocosm experiments

2.1.1. Experimental design and technical approach

On 12 January 2009, scallops ranging from 12.3 to 44.7 mm SH were collected from an 18 m × 29 m shore-side mesocosm pond at the UNC Institute of Marine Sciences (IMS) in Morehead City, North Carolina, USA (34°43.354 N, 76°45.146 W). The scallops were transported in coolers with moist burlap sacks and ice packs to the Virginia Institute of Marine Science's (VIMS) Eastern Shore Laboratory (ESL), in Wachapreague, Virginia, USA (37°36.313 N, 75°41.265 W). This method of transport greatly reduces handling mortality (Peterson et al., 1996), and few scallops died in transport. Scallops were held in quarantined conditions and fed a diet of mixed cultured phytoplankton. All macroepibionts were removed, and a subset of the scallops was selected for use in subsequent experiments. On 25 February 2009 scallops were obtained from the ESL and transported to the VIMS Seawater Research Laboratory (SRL), in Gloucester Point, Virginia, USA (37°14.886 N, 76°30.100 W) using the same transport methods previously described; transport mortality was negligible.

2.1.2. Predation mortality

On 9 March 2009, intermolt or adult female blue crabs ranging from 112.0 to 167.7 mm CW were obtained from the annual VIMS Blue Crab winter dredge survey. Only female crabs were used in this experiment to compare relative predation rates among treatments and to avoid sex-related biases in feeding behavior and cheliped morphology (Barbeau and Scheibling, 1994; Eggleston, 1990b; Nadeau and Cliche, 1998). Crabs were fed frozen fish while held in captivity, so as not to increase their ability to feed on bivalves (Cunningham and Hughes, 1984). Subsequently, they were starved for 48 h prior to the commencement of each trial to standardize hunger levels – a common technique that has been used successfully in previous blue crab predation experiments (Hovel and Lipcius, 2001; Lipcius and Hines, 1986; Seitz et al., 2003) – and allowed to acclimate to their new environment. Each crab was used only once per trial, and the water temperature of the tanks was maintained near 20 °C to ensure normal blue crab feeding activity, as established through pilot experiments conducted prior to the commencement of our predation experiments. We also determined the predation duration that would allow approximately 50% mortality across treatments, which is a common method for detecting treatment effects in predator-prey experiments. This allowed for a similar number of bivalves consumed per trial, as in previous successful predator-prey studies (Lipcius and Hines, 1986).

To examine the effect of predator size, prey size, and habitat on the survivorship of bay scallops, 11 feeding and control trials were performed from 2 April 2009 to 5 June 2009. Six experimental circular tanks measuring 56 cm diam × 59 cm height (145.3 L) were randomly assigned one of the three habitat treatments (oyster shell, sand, *Gracilaria* spp.; only the sand treatment had bare sand on the bottom of the mesocosm), one of the two predator sizes (large: >140 mm CW; small: ≤140 mm CW—similar to size breaks used in previous blue crab predation experiments conducted by Eggleston (1990a,b)), and populated with a total of eight scallops (two from each size class: 10–19 mm, 20–29 mm, 30–39 mm, 40–49 mm SH). This equated to 32 scallops m^{-2}, approximating natural field densities that range 0-44 m^{-2} and average 24.8 m^{-2} before the harvest season opens (Hernández Cordero et al., 2012; Peterson et al., 1996; Thayer and Stuart, 1974). Though crab chela size was not measured, crusher chela size is directly positively related to crab size (Eggleston, 1990b), and crushing strength is related to chela size in other crabs (Elner, 1980). Approximately 3 gallons of oyster shell and *Gracilaria* spp., with no