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Non-indigenous predators threaten ecosystem engineers: Interactive effects of green crab and oyster size on American oyster mortality

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A B S T R A C T

Non-indigenous green crabs (*Carcinus maenas*) are emerging as important predators of autogenic engineers like American oysters (*Crassostrea virginica*) throughout the eastern seaboard of Canada and the United States. To document the spreading distribution of green crabs, we carried out surveys in seven sites of Prince Edward Island during three fall seasons. To assess the potential impact of green crabs on oyster mortality in relation to predator and prey size, we conducted multiple predator-prey manipulations in the field and laboratory. The surveys confirmed an ongoing green crab spread into new productive oyster habitats while rapidly increasing in numbers in areas where crabs had established already. The experiments measured mortality rates on four sizes of oysters exposed to three sizes of crab, and lasted 3–5 days. The outcomes of experiments conducted in Vexar® bags, laboratory tanks and field cages were consistent and were heavily dependent on both crab size and oyster size: while little predation occurred on large oysters, large and medium green crabs preyed heavily on small sizes. Oysters reached a refuge within the 35–55 mm shell length range; below that range, oysters suffered high mortality due to green crab predation and thus require management measures to enhance their survival. These results are most directly applicable to aquaculture operations and restoration initiatives but have implications for oyster sustainability.

1. Introduction

One of the most pressing issues in coastal ecosystems is the decline and loss of ecosystem engineers (Wilberg et al., 2013). Biogenic habitats like oyster beds and reefs maintain and improve water quality, provide valuable resources to inshore fishermen (Grabowski and Peterson, 2007) and have been declining from a variety of causes (Kennedy et al., 2011). Among these causes, predation by non-indigenous species is emerging as a major source of oyster mortality (Kimbro et al., 2009; Grason and Buhle, 2016). Predation influences oyster abundance, productivity and long-term sustainability (e.g. Bisker and Castagna, 1987; Flimlin and Beal, 1993). However, the arrival of non-indigenous predators like the European green crab (*Carcinus maenas*) entails an additional level of concern and uncertainty for ecologists and managers (Rindone and Eggleston, 2011). Wild beds of American oysters (*Cassostrea virginica*) are prominent features and sustain one of the most traditional industries along the eastern seaboard of the United States and Canada (e.g. Glude, 1955; Elner and Lavoie, 1983). Although in recent years there has been a trend towards off-bottom oyster aquaculture, in many areas this industry still relies on the harvesting of wild beds and on benthic grow-out conditions for at least part of the oyster life cycle (PEI DFARD, 2007). In these instances, an unknown fraction of oysters remains, or is intentionally placed on the bottom and becomes vulnerable to predation.

Coastal predator-prey interactions have been studied in the past (Elner and Lavoie, 1983; Harding et al., 2007; Kennedy et al., 2009; Wong et al., 2010; Rindone and Eggleston, 2011). However, our ability to predict the outcome of green crab-oyster interactions, and therefore the impact of this invader on oyster beds, remains limited. This is partly due to the lack of integrative studies exploring these interactions at different life stages of both predators and prey.

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Green crabs are voracious predators of bivalves (Cohen et al., 1995; Mascaro and Seed, 2000a; Baeta et al., 2006). In their European home range, green crabs forage on blue mussels (*Mytilus edulis*) (Dare and Edwards, 1976), Pacific oysters (*Crassostrea gigas*) (Walne and Davies, 1977), and hard clams (*Mercenaria mercenaria*) (Walne and Dean, 1972). Meanwhile, in their expanded range green crabs forage on species like venerid clams (*Katelysia scalarina)* in Tasmania (Walton et al., 2002), native clams (*Nutricola tantilla* and *N. confuse*) in the west coast of North America (Grosholz et al., 2000), and blue mussels, soft-shell clams (*Mya arenaria*), and American oysters in eastern North America (Glude, 1955; Miron et al., 2005).

Green crabs were first confirmed in Prince Edward Island (hereafter PEI) in the late 1990s (Audet et al., 2003) and since then have gradually spread until reaching some of the most productive oyster habitats in the region (Audet et al., 2008): PEI bottoms account for ~80% of the oyster production in Atlantic Canada (PEI DFARD, 2007). Concerns among biologists, government and industry have prompted us to document green crab abundances and to assess the vulnerability of wild oyster beds. The outcome of size preference experiments varies and is often dependent on a variety of factors (e.g. Wong et al., 2010). However, we focused on two alternative hypotheses: First, large predators have the ability to prey on a wider range of prey sizes than small predators; second, large predators avoid small prey due to their low profitability. Our first hypothesis is based on studies showing that small crabs endure physical limitations to break or open large bivalve shells (e.g. Boulding, 1984; Behrens Yamada and Boulding, 1998). Our second hypothesis is based on profitability studies (e.g. Hughes, 1980; Juanes and Hartwick, 1990; Aronhime and Brown, 2009) showing that small prey do not necessarily offer a nutritive return high enough to compensate for the time used by predators to handle their prey.

2. Materials and methods

2.1. Study area and green crab abundance

Bedeque Bay (46°22′30″N, 63°46′38″W) and North River (46°15′11″N, 63°10′48″W) are shallow estuarine systems located along the southern shoreline of PEI (Fig. 1). Bedeque Bay includes the estuarine portions of Wilmot River and Dunk River, whereas North River is embedded within the Hillsborough River system that drains into the Hillsborough Bay. Both systems are characterized by extensive oyster beds and by sandy and muddy bottoms surrounded by extensive eelgrass beds (*Zostera marina*) and salt marsh vegetation. Both systems also have relatively small tide ranges and fairly similar temperatures and salinities (Poirier et al., 2016).

To characterize green crab relative abundances, trapping surveys were conducted at seven representative sites during the fall seasons of 2008–2010: three sites were located in North River and four in Bedeque Bay (two in Wilmot River and two in Dunk River; Fig. 1). Abundances were estimated by 24 h deployments of 8–12 multispecies Fukui traps (60 cm × 45 cm x 20 cm high, with a 40 cm opening at each end) per site. Each trap was baited with ~100 g of Atlantic mackerel (*Scomber scombus*) and cleaned after use to avoid unintentional transfer of invasive species between systems. Field experiments reported below were conducted in Stewart Cove, Stratford, located nearby (~2 km away) the Lower reach site in North River (Fig. 1). Relative abundances reported here correspond to crabs $trap^{-1}day^{-1}$.

2.2. Collection of experimental animals: green crabs and oysters

Green crabs were collected from the seven sites identified above and two other sites located ~60 km away: Basin Head and Souris River (Fig. 1). To minimize variability associated with gender and condition, only intact male green crabs were kept for experiments (see Smallegange and van der Meer, 2003). Males were classified into three size categories hereafter called small (35–45 mm carapace width; CW), medium (45–55 mm CW), and large green crabs (55–75 mm CW). The crabs used in the experiments were starved for 48 h prior to the beginning of the trials to standardize hunger levels (e.g. Mascaro and Seed, 2001), and used only once to avoid potential learning after repetitive trials (Cunningham and Hughes, 1984). Oysters were obtained from a private PEI oyster lease (wild seed oysters sorted and grown on off-bottom bags) in Malpeque Bay (Fig. 1), and were classified into four size ranges hereafter referred as spat (5–15 mm shell length; SL), small (15–25 mm SL), medium (25–35 mm SL), and large oysters (35–50 mm SL).

2.3. Vexar® bags, laboratory tanks and cage inclusion experiments

Oyster mortality rates were measured in three distinct settings (see Electronic Appendix - Fig. 1). First, field trials were conducted off-bottom in individual Vexar® floating bags (44 cm × 88 cm × 12 cm high) similar to those used in the region for culturing oysters. These bags were made with a 1 cm coated mesh and before their use were carefully cleaned to ensure they were free of sediment, seaweeds, and fouling organisms. Bags were placed in the shallow subtidal with thirty oysters of a given size (spat, small, medium or large oysters) in each Vexar® bag and a single green crab of a given size (small, medium or large) added afterwards.

A second set of experiments was conducted in laboratory tanks (21.6 cm × 41 cm × 25 cm high) filled with prepared seawater (18–22 ppt; 18–20 °C) fitted with an air stone. Tanks had a hood to avoid crab escapement and were covered to maintain darkness and avoid external visual stimuli that could alter crab behavior (e.g. Palacios and Ferraro, 2003). These trials were intended to match field trials but under more controlled conditions and to facilitate observations of crab feeding. Due to time and feasibility constraints, only two oyster sizes were used in these and the experiments described below. Because the outcome of trials conducted in Vexar® bags consistently showed near 0% mortality of large oyster and near 100% mortality of spat (see Results), we chose to conduct these experiments with those size ranges exhibiting the most variation: small and medium oysters. Thirty oysters of a given size were added into each tank before a crab of a given size was added.

A third set of experiments was held directly on the shoreline bottom using inclusion cages (50 cm × 50 cm × 75 cm high) constructed of 1 cm mesh plastic coated wire. Cages had open bottoms and were inserted 5–10 cm into the sediments of the lower intertidal zone to avoid crab escape. These trials were conducted in close proximity to where Vexar® bag experiments were conducted, over sandy sediments with scattered mussel and oyster clumps and near the edge of eelgrass beds (see Pickering and Quijón, 2011). In comparison to Vexar® bags and laboratory experiments, cage experiments aimed to measure oyster mortality rates in a larger area and under less controlled conditions: green crabs were in contact with the seafloor and therefore had access to other potential prey. At the time the cages were placed, large (visible) epibenthic organisms were removed by hand. However, to avoid unnecessary disruption, sediments were not excavated and/or sieved to remove smaller infauna (see Lutz-Collins et al., 2016). Thirty oysters (either small or medium) were placed in each cage before a single crab was added.

2.4. Experimental procedure and size-choice experiments

Oysters placed in Vexar® bags, laboratory tanks and field cages