SHORT COMMUNICATION

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Effects of habitat complexity on cannibalism rates in European green crabs (*Carcinus maenas* Linnaeus, 1758)

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Abstract

The habitat in which predator–prey interactions take place may have a profound influence on the outcome of those interactions. Cannibalism is an intriguing form of predation whereby foraging by predators may contribute to the regulation of their own populations. This is particularly interesting in the case of invasive species, like the widely distributed European green crab (*Carcinus maenas*). This study explores how habitat complexity influences cannibalism rates in green crab populations of Prince Edward Island, Atlantic Canada. Both laboratory and field experiments were conducted to measure feeding rates by individual adult green crabs on a standard number of smaller conspecifics. In the laboratory, experimental treatments mimicked unstructured to increasingly structured habitats: water, sandy bottom, oyster shells, mussel shells, oyster shells with sandy bottom and mussel shells with sandy bottom. In those trials, adult green crabs consumed several times more juveniles on unstructured habitats than on the most structured ones, with a gradual decrease in predation rates across increasingly complex habitats. Field inclusion experiments used the same approach and were conducted in sandy bottoms, sandy bottoms with a layer of oyster shells and sandy bottoms with a layer of mussel shells. These trials showed similar patterns of decreasing feeding rates across increasingly complex habitats, but differences among treatments were not significant. These results support the idea that complex habitats have the potential to mediate predator–prey interactions, including adult–juvenile cannibalism in green crabs.

KEYWORDS
experiments, green crab cannibalism, habitat complexity, predator–prey interactions

1 | INTRODUCTION

Predation is an important determinant of the abundance and size of prey (Orth, Heck, & van Montfrans, 1984), particularly in sedimentary bottoms (see reviews by Peterson, 1979; Wilson, 1991; Thrush, 1999). It has also been demonstrated that the habitat in which predation takes place can influence its outcome (*e.g.* Diehl, 1992; Ebersole & Kennedy, 1995; Hill & Weissburg, 2013): for instance, prey may seek refuge from predators more easily in complex habitats compared to structurally simple habitats, reducing encounter rates or making predators less efficient at foraging for prey (Crowder & Cooper, 1982). One intriguing

form of predation is cannibalism, whereby under certain conditions predators may regulate their own populations (Cushing, 1991; Lloyd, 1968). Unfortunately, the influence of cannibalism in aquatic invertebrates is complex and not well understood (*e.g.* Dick, 2005; MacNeil, Dick, & Elwood, 1999) and considerably less documented than the influence of inter-specific predation (Claessen, deRoos, & Persoon, 2003). This knowledge gap also applies to the shortage of studies addressing the influence of habitat on cannibalism rates.

Cannibalism in relation to habitat is particularly interesting in the case of invasive species. If we accept that this self-regulation mechanism has the potential to control an invader's population growth

(Govindarajulu, Altwegg, & Anholt, 2005), we should assume that it may also indirectly affect the invader's potential impact on native prey or biodiversity. The European green crab (*Carcinus maenas* Linnaeus, 1758) is an interesting model species given its foraging abilities (Cunningham & Hughes, 1984) and its use of a broad range of coastal habitats (Grosholz et al., 2000). In their invaded range, green crabs have been associated with declines of several commercially important bivalve species (Grosholz et al., 2000; Poirier et al., 2017) and negative interactions with native crustaceans (Gehrels et al., 2016; Gregory & Quijón, 2011; Rossong et al., 2011; Rossong, Williams, Comeau, Mitchell, & Apaloo, 2006). However, despite the common occurrence of cannibalism in green crabs, studies of green crab cannibalism in relation to habitat properties have lagged behind.

From the handful of available studies, stomach content analyses have estimated that cannibalism accounts for 2%–4% (Chaves, Horta, Chainho, Costa, & Costa, 2010) or 6.7% (Baeta, Cabral, Neto, Marques, & Pardal, 2005) of the diet of adult green crabs. Experimental studies have focused mostly on green crab cannibalism on newly settled crabs (*e.g.* Almeida, González-Gordillo, Flores, & Queiroga, 2011; Moksnes, 2004; Moksnes, Pihl, & van Montfrans, 1998) and suggest self-regulation during high seasonal settlement (Moksnes, 2004). Other experiments have also shown that adult green crabs are able to cannibalize juveniles but prefer to prey on a native species of similar size (Gehrels et al., 2016). Green crab cannibalism has also been observed, suggested or confirmed but not quantified by other studies (*e.g.* Elner, 1981; Ropes, 1968) without explicit consideration of habitat influence. Poirier et al. (2016) and our own preliminary observations suggest that cannibalism occurs often in a variety of habitats available in Atlantic Canada.

In this study, we investigated the influence of habitat on adult green crab cannibalism rates on juveniles crabs. Our null hypothesis was that prey mortality rates are similar regardless of habitat mimic. However, based on prior studies examining the effects of habitat complexity on various predator–prey interactions, we expected prey mortality to be the highest in the structurally simplest habitats (*e.g.* Crowder & Cooper, 1982; Fernández, 1999; Fernandez, Iribarne, & Armstrong, 1993; Hernández Cordero & Seitz, 2014; Hill & Weissburg, 2013).

2 | MATERIAL AND METHODS

2.1 | Crab collection

Large adult (predators, 70–80 mm carapace width, CW) and small green crabs (prey, 25–35 mm CW) were collected in North River, a shallow, soft-bottom estuary embedded in the larger Hillsborough estuarine system on the southern shore of Prince Edward Island (PEI), Canada. The physical characteristics of this and similar PEI estuaries have been summarized in Pickering and Quijón (2011), Pickering et al. (2017) and Gehrels et al. (2016). We used folding Fukui traps to target adult crabs (63 × 46 × 23 cm; 1.6 cm mesh; with wide, slit-like openings) and minnow traps to target smaller crabs (21 × 37 cm; 2.5 cm diameter openings; 0.5 cm mesh). All traps were baited with frozen mackerel (*Scomber scombrus*). To prevent unnecessary biases, only

intact (uninjured) male green crabs were used (see Tummon Flynn, Mellish, Pickering, & Quijón, 2015), which were always starved for 48 hr prior to experiments to standardize hunger levels (Mascaró & Seed, 2001). In addition, new individuals were used for each replicate to prevent biases associated with potential learning (*e.g.* Cunningham & Hughes, 1984).

2.2 | Laboratory experiments

Experiments were run in glass tanks with dimensions 21.6 × 41 × 25 cm, filled with prepared seawater (~25 ppt, 18–20°C). Each tank had an oxygen stone, the sides were covered and a lid placed on top to minimize external visual stimuli (Palacios & Ferraro, 2003) and prevent crab escape. Six distinct habitat mimics representing increasing habitat complexity were prepared: no substrate (tanks with water only), sandy sediments (tanks fitted with a 3-cm layer of sandy sediments), mussel bed (tanks fitted with a 3-cm layer of mussel shells), oyster bed (tanks fitted with a 3-cm layer of oyster shells), mussel bed with sandy sediments, and oyster bed with sandy sediments. Sandy sediments (fine to medium sands, ~0.5-1.0 mm grain size) and oyster shells (5.0-6.8 cm SL) were collected from North River. Mussel shells (~3.5–4.5 cm) were collected from Primrose Point; both shorelines were located within the same estuarine system in which the field experiments were conducted (Figure 1). Before their use in any experiment, sandy sediments, mussel and oyster shells were repeatedly washed and filtered in order to remove any live organisms that may act as an alternative prey. As with predators, water and habitat mimics were replaced after each individual trial.

Once habitat mimics were prepared, five juvenile green crabs (prey) and one large green crab (predator) were added to each tank. Our choice of number of prey was driven by a trade-off between having the highest possible number of prey available to measure mortality rates and field observations indicating that five is approximately the highest number of juveniles to aggregate in such a small area (Geherels et al., 2016; P. A. Quijón, personal observations). Due to logistic and time constraints, replicates per habitat mimic were conducted in different years but at approximately the same time during the summer season (Table 1). Mussels with sand and oyster with sand trials were run in the summer of 2016, mussel shell trials were run in 2015, and oyster shell, sand and no substrate trials were run in 2014–15. In each individual trial, prey mortality (*i.e.* the number of small crabs that died after a given number of hours) was recorded after 0.5, 1, 2, 3, 4, 5 and 24 hr in order to identify potential differences in timing of foraging and detect cases in which crabs die for unknown reasons or exhibited signs of molting (*e.g.* Pickering & Quijón, 2011). Given that no consistent short-term trends were observed (most predation took place during the night hours) statistical analyses were only applied to the data recorded after 24 hr (*i.e.* at the end of the experiments). The duration of these laboratory trials (24 hr) was dictated by previous experience working on this species.

2.3 | Field experiments

Experiments were run in cylindrical wire cages (40 cm diameter, 26 cm height) arranged in parallel to the low inter-tidal area of Stewart Cove,
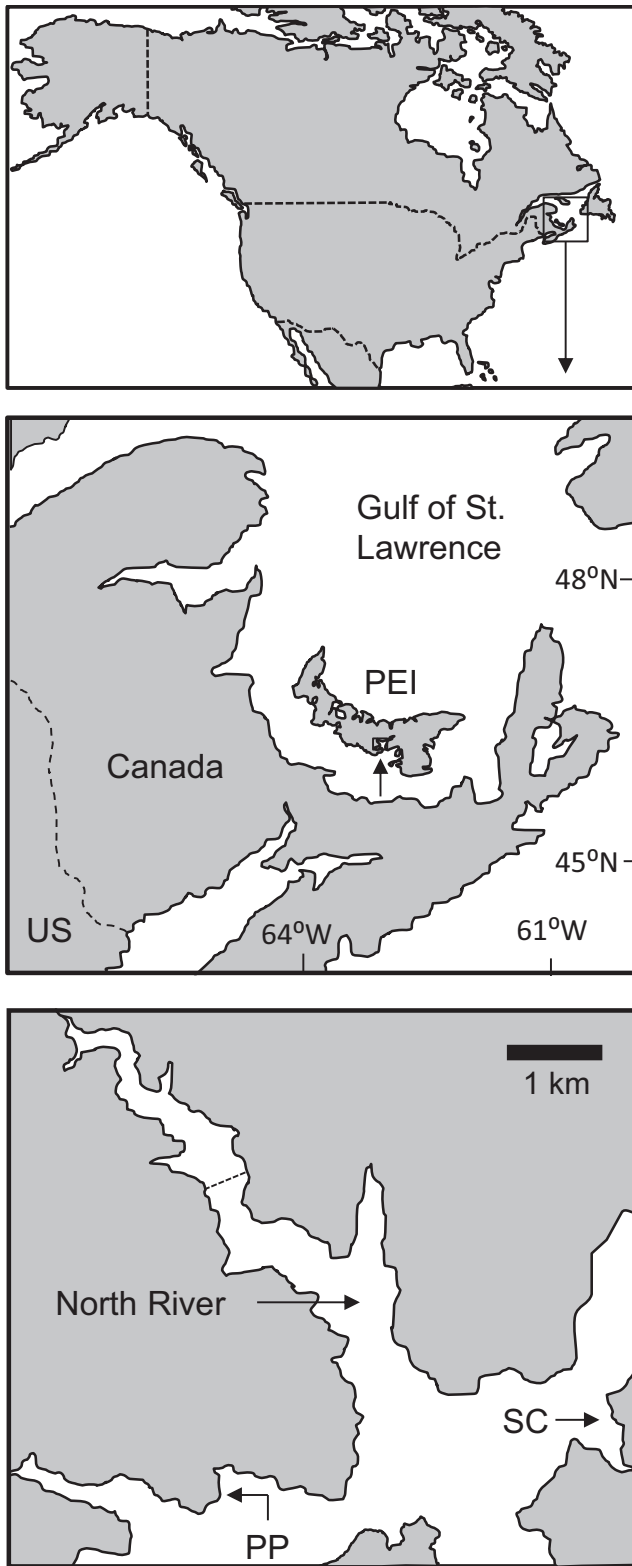
FIGURE 1 Outline of the study area, identifying the location of Prince Edward Island (PEI) within Atlantic Canada, and North River, Stewart Cove (SC) and Primrose Point (PP) within Southern PEI

PEI (Figure 1; 46°13′06′′N, 63°06′30′′W). The area is embedded into a microtidal system characterized by sandy sediments and scattered mussel and oyster clumps, in addition to eelgrass beds (see Pickering &

Quijón, 2011 for a detailed habitat description). Three distinct habitat mimics representing increasing habitat complexity were prepared: bare sediment (sand), mussel bed (75% of the bottom of the cage was covered by mussel shells) and oyster bed (75% of the bottom of the cage was covered by oyster shells). As in the laboratory experiments, mussel and oyster shells were repeatedly washed and filtered before use in any experiment. The same number of prey was added to each cage (five small green crabs exposed to one adult green crab). Prey mortality (*i.e.* the number of small crabs that died as a result of predation) was measured after 36 hr. Our initial intention was to measure mortality after 24 hr but due to feasibility issues during the first set of field trials, we were unable to check the cages until the following low tide (at 36 hr). For consistency, all the subsequent field experiments were checked after 36 hr.

2.4 | Statistical analysis

We analysed the laboratory and field data separately. Data from a few replicates were not included in the analyses when experiments had either a predator or prey that showed signs of molting or died for unknown reasons. Data were analysed using the Kruskal–Wallis non-parametric model in MINITAB 17 (2010) because the data violated one of the assumptions of the parametric one-way analysis of variance: normality. When significant differences among habitat mimics were found, we tested post-hoc pair-wise differences using Dunn's method. Statistical significant difference was defined as $p \leq .05$.

3 | RESULTS

3.1 | Laboratory experiments

Crab mortality rates gradually decreased with an increase in habitat complexity (no habitat, sandy sediments, oyster shells, mussel shells, sand + oyster shells, and sand + mussel shells; Table 1). On average, mortality rates ranged between zero and three crabs per day. A few significant differences among individual treatments were detected: mortality rates were significantly higher in the least complex habitats (first three treatments) than in the most complex ($H_{(5)} = 43.623$, $p < .001$, Table 1; Figure 2).

3.2 | Field experiments

A similar pattern was observed in the field experiments (cannibalism rates decreased with an increase in habitat complexity; Table 2). Prey mortality rates ranged between one and two crabs per day. Despite the differences, the Kruskal–Wallis non-parametric model indicated that mortality rates were not significantly different across habitat mimics ($H_{(2)} = 2.04$, $p = .360$, Figure 3).

4 | DISCUSSION

Our experiments provide quantitative evidence of green crab cannibalism and suggest that cannibalism rates may be affected by habitat

| Habitat mimic	*n*	Mean mortality (± *SE*)	Median mortality	Mean rank	*Z*
No sediment	13	2.80 (0.28)	3	54.5	3.43
Sandy sediments	15	2.47 (0.13)	3	51.3	3.08
Oyster shells	11	2.09 (0.27)	2	43.0	1.13
Mussel shells	11	1.18 (0.36)	1	28.9	−1.31
Sand + oyster shells	11	0.63 (0.15)	1	20.7	−2.72
Sand + mussel shells	11	0.09 (0.09)	0	12.0	−4.23
Overall	72			36.5	

$H = 43.62$; *df* = 5; *p* < .0001.

complexity. Adult green crabs consumed between 1.8% and 56% of the prey items available in the laboratory experiments, and between 26% and 36% in the field experiments. Such mortality rates are considerably higher than those previously reported for green crabs (*e.g.* Baeta et al., 2005; Chaves et al., 2010) and other species of decapods (*e.g.* Amaral, Paula, Hawkins, & Jenkins, 2009). With the exception of a prior study that focused primarily on inter-specific interactions

(Gehrels et al., 2016), this is the first report on habitat complexity influencing adult–juvenile green crab cannibalism at this size range. To date, most other studies examining cannibalism in green crabs have focused on the predation of juveniles by conspecific juveniles (*e.g.* Almeida et al., 2011; Moksnes, 2004; Moksnes et al., 1998) or have collected evidence from stomach contents (Baeta, Cabral, Marques, & Pardal, 2006; Hughes & Elner, 1979; Ropes, 1968).

The laboratory experiments showed that adult green crabs consumed more juvenile green crabs when habitats were structurally simple compared to the habitats that were more structurally complex. These results are in agreement with a growing body of evidence that suggests that increasing habitat complexity decreases prey mortality (*e.g.* Fernandez et al., 1993; Dittel, Epifanio, & Natunewicz, 1996; Fernández, 1999; Langellotto & Denno, 2006; Stoner, Ottmar, & Haines, 2010; Hill & Weissburg, 2013; Hernández Cordero & Seitz, 2014). The most likely mechanism to explain the influence of habitat complexity is a decrease in the rate of predator–prey encounters. In complex habitats, small crabs seek refuge or hide from predators more easily. In addition, predators may become less mobile or less efficient at catching prey in these more structurally complex habitats compared to less structured habitats (Crowder & Cooper, 1982; Grabowski, 2004). Regardless of the specific mechanism in place, a reduction in a predator's foraging efficiency in structurally complex habitats would likely translate in lower predation and injury rates (*e.g.* Gehrels et al., 2016), as our results show.

We found a similar pattern but weaker differences between habitat mimics in the field experiments compared to the laboratory. This may be related to the less striking structural differences among the three habitat treatments (*e.g.* Hill & Weissburg, 2013). Shells of oysters and mussels were expected to reflect increased habitat complexity in comparison to less structured sandy sediments (see Hernández Cordero & Seitz, 2014; Gehrels et al., 2016). However, our mimics were set on sandy sediments, which were an integral part of the habitats as well and may have removed some of the distinctiveness among habitats. Visual observations suggest that juvenile green crabs did hide under oyster and mussel shells and therefore actively used this layer in an attempt to avoid predation, as they did in the laboratory. However, they also buried themselves within the sediment apparently gaining some degree of additional refuge. This limitation in our field design
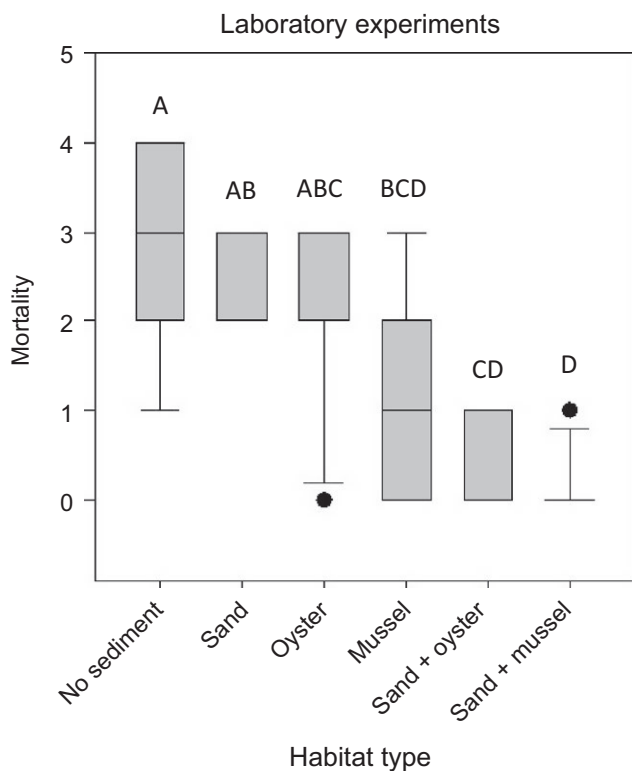

FIGURE 2 Box plots showing the results of the laboratory experiments: juvenile green crab mortality in six different habitat mimics. Boxplots show upper quartile (Q3), median and lower quartile (Q1), bars show the range of the data, and dots represent individual data points that are 3/2 above and below the Q1 and Q3, respectively. Different letters at the top of the boxplots indicate significant differences among individual treatments. Mean values (±*SE*) for the same data are presented in Table 1

TABLE 2 Field habitat mimics, number of replicates (*n*) and juvenile green crab mean mortality (±*SE*), in addition to median, mean rank and *Z* values from Kruskal–Wallis comparisons. The *H*-value is presented at the bottom

Habitat mimic	n	Mean mortality (± *SE*)	Median mortality	Mean rank	Z
Bare sediment	14	1.86 (0.26)	2	23.9	1.35
Oyster shells	13	1.31 (0.37)	1	17.9	−0.97
Mussel shells	13	1.46 (0.35)	1	19.4	−0.40
Overall	40			15	

$H = 2.04$; $df = 2$; $p < .360$.
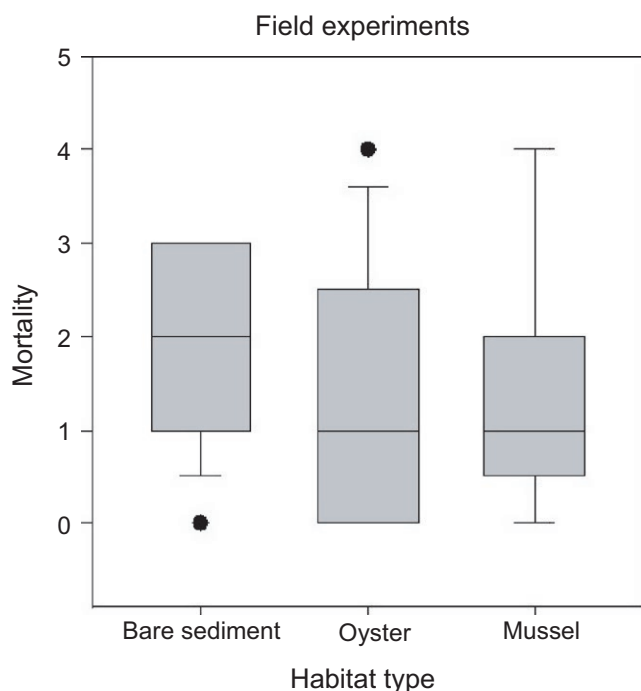
FIGURE 3 Box plots results from the field experiments, showing juvenile green crab mortality in three different habitat mimics. Boxplots show Q3, median and Q1, bars show the range of the data, and dots represent individual data points that are 3/2 above and below the Q1 and Q3, respectively. Mean values (±SE) for the same data are presented in Table 2

likely reduced among-treatment differences but we cannot ignore that cannibalism rates still showed a gradual decrease with increasing habitat complexity as they did in the laboratory. We are, however, cautious in our interpretation. Additional factors like the presence of alternative (infaunal) prey (*e.g.* Gregory & Quijón, 2011; Lutz-Collins, Cox, & Quijón, 2016) or the increased size of the arenas (cages were ~40% bigger than tanks) may have reduced predator–prey encounters (Crowder & Cooper, 1982) and therefore contributed to diminishing the differences among treatments.

Our results, in particular the high rates of cannibalism detected, may direct further research about cannibalism in this and other decapods. In addition to prey mortality rates quantified here, predator and prey movements are part of the complex behavioral patterns that this type of species can display (*e.g.* Wong, Bibeau, Bishop, & Rosenthal, 2005). Such further studies may provide evidence about how visible a mobile prey is to the predator in the different habitat mimics, and about how predator search behavior is affected by habitat type. In addition, given that green crabs are not solely visual predators (*e.g.* Rittschof, 1992; Robinson, Smee, & Trussell, 2011), visual stimuli are clearly not the only mechanism by which they forage or, in the case of small crabs, by which they potentially avoid predators. For instance, there have been cases in which prey burying themselves in the sand may have masked the odor plume on which predators rely for foraging (*e.g.* Kats & Dill, 1998). Visual and chemical cues are a likely research venue for the study of intraspecific predator–prey direct and indirect interactions (Mathis, 2003; Mirza & Chivers, 2001) and a logical follow up for the experiments documented here.

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