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Foraging and shelter behavior of juvenile American lobster (*Homarus americanus*): the influence of a non-indigenous crab

M.A. Rossong [a,b,*], P.A. Quijon [b], P.J. Williams [c], P.V.R. Snelgrove [a]

[a] Biology Department and Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, NL, Canada A1C 5S7
[b] Biology Department, University of Prince Edward Island, Charlottetown, PE, Canada C1A 4P3
[c] Biology Department, St. Francis Xavier University, Antigonish, NS, Canada B2G 2W5

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ABSTRACT

Adult green crabs are highly aggressive predators that exhibit fast population growth in newly invaded areas and potentially compete with juvenile lobsters for limited resources. Previous studies suggest that juvenile lobsters utilize shelter to avoid predation but shelter dependence decreases as they mature and develop predator defense mechanisms. Smaller lobsters must therefore trade-off energetic needs with predation risk. In laboratory experiments we examined how the presence of an adult green crab affects foraging and shelter behavior of juvenile lobsters (25–51 mm CL) by offering juvenile lobsters protective shelter and an adjacent food patch in the presence or absence of a green crab. For each trial we monitored lobster behavior over 8 h. Our results indicate that in the presence of a green crab, small juvenile lobsters (<35 mm CL) spent significantly less time foraging and more time within the shelter. These small juveniles also spent significantly less time feeding and/or handling the food but took longer to actually locate the food source. In contrast, the presence or absence of a green crab did not have any influence on the results of trials that used juvenile lobsters over 35 mm CL. Thus, green crabs can significantly influence foraging and shelter usage of small (<35 mm CL) juvenile lobsters and re-affirm the idea that this early stage represents the most vulnerable in the benthic life cycle of lobsters.

1. Introduction

Shelter availability and use is thought to play a critical role in the recruitment dynamics of lobster. Smaller lobsters are able to bury themselves in the substrate (Berrill and Stewart, 1973; Cobb, 1971), but exhibit a strong preference for natural shelters created by rocks and crevices (Barshaw et al., 1994; Hudon and Lamarche, 1989). All size ranges of lobster utilize rocks and crevices, but dependence is greater in early benthic phases and juvenile lobsters (Cobb, 1971). Access to shelters is thought to limit lobster recruitment (Lawton and Lavalli, 1995) because shelters protect juvenile lobster from predators and thus enhance survival (Hudon, 1987; Lawton and Lavalli, 1995). Numerous observations suggest that juvenile lobsters prefer to spend the majority of their time in shallow and wide, opaque shelters (Cobb, 1971), with limited foraging excursions. As lobster increase in size, they spend more time foraging outside of the shelter (Lawton and Lavalli, 1995). Predator avoidance is therefore size specific and may result in a trade-off between safety and reduced foraging rate (Abrahams and Dill, 1989; Wahle, 1992). For example, in the presence of sculpin (*Myoxocephalus aeneus*), smaller lobsters spent less time foraging than larger lobsters (Wahle, 1992). Similarly, in the presence of caged tautogs (*Tautoga onitis*), lobsters consumed fewer mussels and often brought mussels back to the safety of the shelter before consuming them (Spanier et al., 1998).

Similar feeding responses may occur in the presence of other, potentially threatening predators such as the non-indigenous green crab (*Carcinus maenas*) (Klassen and Locke, 2007). This aggressive species has spread since the 1800s (Grosholz and Ruiz, 1995), and reached the east coast of North America in the 1850s. Over the subsequent 100 years, it expanded from New Jersey to southern Nova Scotia (Audet et al., 2003; Grosholz and Ruiz, 1995; Roman, 2006) and increasingly overlapped the geographic range of American lobster. A second introduction of genetically distinct crab populations has expedited broader expansion within eastern Nova Scotia, Prince Edward Island and, most recently, in Newfoundland (Blakeslee et al., 2010; Roman, 2006). Green crabs are highly skilled consumers of prey also consumed by lobsters, and likely compete for food with lobster and other predators at this latitude. Green crabs prey on bivalves (Palacios and Ferraro, 2003; Floyd and Williams, 2004; Klassen and Locke, 2007), juvenile fish (Taylor, 2005), other crab species (Grosholz et al., 2000; McDonald et al., 2001) and even juvenile lobsters in laboratory settings

* Corresponding author at: Biology Department and Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, NL, Canada A1C 5S7. Tel.: +1 902 566 6059; fax: +1 902 566 0740.
E-mail address: mar137@mun.ca (M.A. Rossong).

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(CL<57 mm; Rossong et al., 2006). The literature on laboratory experiments also reports that green crabs outcompete *Hemigrapsus* spp., *Cancer magister* crabs (Grosholz and Ruiz, 1995; Jensen et al., 2002; McDonald et al., 2001), and juvenile American lobster (Rossong et al., 2006; Williams et al., 2006) for limited food resources. However, studies by Bélair and Miron (2009a, 2009b) have also showed co-existence without apparent interference between green crabs and rock crabs, *Cancer irroratus*.

The current establishment and growth in green crab populations within rich lobster grounds of eastern North American shores seem harmless in some regions but increases the likelihood of interactions between these two species in others. Recent invasions of areas with juvenile lobster habitats, in particular, raise concerns for the potential detrimental effects of adult green crabs on lobster recruitment. Field studies within the Bay of Fundy, Nova Scotia, have confirmed the spatial overlap of adult green crabs and juvenile lobsters (<40 mm CL) with the highest overlap in the shallow subtidal (<1.2 m chart datum; Lynch and Rochette, 2009). Although direct interactions between green crab and juvenile lobsters have been demonstrated already, the more subtle role played by green crab-lobster indirect effects remain largely unexplored.

Here, we use a laboratory setting to determine whether the presence of a green crab influences the behavior of juvenile lobsters. Although direct green crab predation on juvenile lobsters is an obvious concern, the potential alteration of lobster behavior in the presence of increasing numbers of green crabs is expected to expand to broader scales, and potentially alter the behavior of lobsters. We examine the foraging behavior of several size ranges of juvenile lobsters exposed to the presence of a caged green crab. The specific goals of this study were to 1) document whether lobsters spend more time within a shelter in the presence of green crab; 2) document whether lobster consume prey items (mussels) in the presence of green crab; and 3) assess whether behavior is related to size of juvenile lobsters. Given that the lobsters utilized here were collected in areas not yet invaded by green crabs, and are therefore naïve to the influence of this new predator, we propose two null hypotheses: i) juvenile lobster foraging and shelter behavior are not altered in the presence of green crab, and ii) both shelter and foraging behavior in the presence or absence of green crab are both unrelated to the individual size of the juvenile lobsters.

2. Materials and methods

2.1. Collection and housing of lobsters and crabs

SCUBA divers collected juvenile lobsters (n = 17 males, n = 13 females) within a size range of 24.9–51.5 mm CL (males = 37.2 +/− 8.3 mm, 18.1–94.6 g; females = 37.9 +/− 5.4 mm, 21.4–82.7 g) on September 2, 2009 in North Rustico, Prince Edward Island, Canada. We collected male green crabs ranging in size from 65 to 76 mm ($n = 3$; CW = 70.4 +/− 4.4 mm SD; mass = 106.6 +/− 27.0 g SD) from baited traps in Pomquet Harbour, Nova Scotia on September 4, 2009. Both species were transported in coolers with ice packs and kelp to the animal care facility at St. Francis Xavier University, Antigonish, Nova Scotia. Lobsters and crabs were maintained in separate holding tanks within a temperature (10 °C) and light (12 h light/dark) controlled room. Each organism was placed in a rectangular container (25 × 45 cm) on shelves within a larger tank. Ultraviolet and bio-filtered water (salinity 31 ppt) was pumped into a storage container above the shelf, where it trickled down tubing into each container and supplied fresh, oxygenated water. Lobsters and green crabs were held in the laboratory for one week prior to experiments and fed a daily diet of mussels.

2.2. Experimental set-up and video-taping

We conducted experiments in a 90-cm diameter, cylindrical plastic tank filled with the seawater typically found in juvenile lobster habitat (10 °C, 31 ppt) to a depth of approximately 45 cm. The bottom of the tank was uniformly covered in coarse sand to a depth of 5 cm. We affixed a shelter (PVC pipe cut in half along its long axis, 15 cm length, 6 cm height) and an empty wire mesh cage (25 cm × 12 cm × 10 cm) to hold a green crab to the bottom of the experimental tank. Juvenile lobsters ranged in size from 24 to 51 mm CL and were randomly assigned to each treatment to ensure no confounding size biases. Experiments were videotaped with two CCD, low light cameras (Panasonic WV-BP334) mounted over the tank 100 cm above the sediment. Two infrared illuminators (Extreme CCTV Moonlight-IR) minimized behavioral alteration associated with bright light (Weissburg and Zimmer-Faust, 1994). Novex (NOVEX2000 V. 3.01) software interpreted signals transmitted from the cameras above the tank and recorded output to a computer located outside the room.

2.3. Foraging and shelter use

Juvenile lobsters were starved for 48 h prior to experimental trials to standardize hunger levels (Mascaro and Seed, 2001); Individuals were acclimated in the tank for 16 h, after which we introduced a covered (crushed) mussel ($x_{mussel} = 15.2 +/- 5.8$ g) as a food patch. After about 10 min, the mussel was uncovered and recording of juvenile lobster behavior commenced ($n = 15$ "control" trials). For a second type of trial ($n = 15$) we added an adult green crab, confined within the wire cage at the bottom of the tank. For these trials, we introduced the green crab immediately after the 16-h lobster acclimation period and bubbled an airstone for ten minutes to disperse the crab scent throughout the tank. After this brief period, we uncovered the crushed mussel and commenced recording each trial (controls or green crabs) for approximately 8 h ($x_{time} = 474 +/- 50$ min). Lobsters were then banded, tagged, and observed in separate holding tanks for two weeks to confirm that individuals were not aggressive pre-molt lobsters (Tamm and Cobb, 1978). Green crabs were fed and returned to the holding containers for use in later experiments. Each type of trial alternated in series of 3's (i.e. 3 control trials followed by 3 trials using green crabs) to minimize tank changes between taping and reduce number of crabs to be subsequently euthanized. All lobsters were used only once within the experiment and water changes were completed after each trial. After the trials and the two-week monitoring period, green crabs and lobsters were euthanized to comply with animal care protocols for animals held in laboratory facilities.

2.4. Video and statistical analysis

We recorded and analyzed the time spent within the shelter and time spent foraging (time feeding on the mussel), the frequency and location (near food patch or in shelter) of lobster feeding, the time spent locating food, and any other distinctive behaviors. Because trials varied in length we used proportion of time spent on different activities, which necessitated arcsine square root transformation of data. A Student's *t*-test verified that lobsters in control and green crab trials were comparable in size. Treatment differences were tested with a Mann–Whitney test. The proportion of time in the shelter and with mussel, the number of times feeding, and the time taken by the lobster to first encounter the mussel were each compared with juvenile lobster size using linear regressions. The fit of the data for time in shelter necessitated a logistic binary regression because lobsters spent less than 1% of the trial in the shelter (defined as 0) or greater than 65% of the trial in the shelter (defined as 1); no lobsters used the shelter between 1 and 65% of the time. A Pearson Chi-square Goodness of Fit test confirmed that the data fit the logistic binary regression curve (p-value ranging between 0.312 and 0.724) (Minitab 15; State College, PA).