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Agonistic interactions between invasive green crabs, *Carcinus maenas* (Linnaeus), and sub-adult American lobsters, *Homarus americanus* (Milne Edwards)

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Abstract

The invasive green crab, *Carcinus maenas*, has recently expanded its range into the Southern Gulf of St. Lawrence, where there is potential for substantial niche overlap with juvenile American lobsters, *Homarus americanus*. We used two experiments to elicit, record and analyze the agonistic interactions of adult green crabs (carapace width of 63–75 mm) and sub-adult (carapace length of 55–70 mm) lobsters. The first experiment gave each animal equal access to a limited food resource. The green crabs were first to the food in significantly more trials, spent a significantly greater proportion of time with the food, and were able to successfully defend the food from attacks by the heavier lobsters. In the second experiment, we allowed the lobsters to gain possession and initiate feeding on the food before releasing the green crabs. In these trials, the lobsters spent significantly more time with the food, and were able to defend the food from the green crabs. The results of both experiments are discussed in the context of game theory. The different behaviour of the crustaceans in the two experiments is consistent with the "bourgeois" strategy in a hawk and dove game simulation. With this strategy, an animal acts like a hawk if in possession of a resource, but acts like a dove if the other animal is in possession of the resource. The fact that the green crabs were able to physically compete with, and in many cases dominate the larger, heavier lobsters supports the potential for competitive impacts of green crabs on sub-adult lobsters.

Keywords: Agonistic interactions; *Carcinus maenas*; Competition; Crustaceans; *Homarus americanus*; Invasive species

1. Introduction

The European green crab, *Carcinus maenas* (Linnaeus), has established populations in many estuarine and coastal regions outside of its native distribution in the eastern Atlantic. The majority of research exploring the impact of green crabs has focused on the prey of this omnivorous crustacean, and significant changes at the individual, population and community level of prey species have been attributed to the establishment of green crab populations (Hughes and Elner, 1979; Vermeij, 1982; Grosholz et al., 2000; Trussell and Smith, 2000; Walton et al., 2002; Floyd and Williams, 2004). However, recent studies have begun to concentrate on the potential of green crabs as a competitor with native crustaceans.

The southern Gulf of St. Lawrence is a relatively shallow body of water on the eastern coast of Canada. Green crabs are a recent addition to this area, with the

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first confirmed sightings in 1994 in the eastern part of the Gulf (Audet et al., 2003). Green crabs have since spread westward along the coast, and reached the western part of the Gulf in 2002 (Audet et al., 2003). Typically, green crabs first become established in estuaries and bays, where the resultant population serves as a source of larvae and emigrants for further range expansion (Cohen et al., 1995). The intervening coastal regions eventually also become populated with green crabs. The southern Gulf, with its abundant estuaries and warm summer temperatures, offer ideal conditions for green crabs (Gillis et al., 2000; Audet et al., 2003). As green crab populations increase, the potential exists for competition between them and native crustaceans, such as the rock crab, *Cancer irroratus*, and the American lobster, *Homarus americanus*. The present study examines agonistic behaviour between adult green crabs and sub-adult American lobsters.

Conflicts between animals are resolved by agonistic behaviour, a term that encompasses a spectrum of behaviour ranging from escape at one extreme to physical combat that may result in injury or death of the combatants. Game theory (Maynard Smith, 1974) has provided a conceptual framework for the analysis of animal conflicts and agonistic behaviour. With this approach, the conflict becomes an optimization game, in which the potential benefits (food, shelter, access to mates) are balanced against the potential costs (injury or death, exposure to predators, increased metabolic output) of conflict. Game theory predicts that if fighting is costly (due to risk of injury, etc.), then conflicts should be resolved at an early stage, based on some indicator of fighting ability (Glass and Huntingford, 1988). In addition, agonistic interactions should escalate from non-injuring displays to behaviour that has the potential to cause injury (Huntingford et al., 1995).

Most of the described agonistic behaviour of lobsters pertains to intraspecific interactions. Lobsters are solitary animals (Karavanich and Atema, 1998) and will fight each other if placed in close proximity (Zeitlin-Hale and Sastry, 1978; Atema and Voigt, 1995; Huber and Kravitz, 1995). These fights seem to fit the general predictions for game theory, beginning with threatening displays, progressing to some pushing with claws, followed by unrestrained combat (Atema and Voigt, 1995). The threat displays, which involve conspicuous posturing with the chelae, are often sufficient to resolve conflicts (Atema and Voigt, 1995; Karavanich and Atema, 1998). In the laboratory, lobsters quickly establish dominant–subordinate relationships, and subsequent encounters between these animals do not involve combat, but are resolved by retreats and avoidance by the subordinate, thereby minimizing risk and injury to the combatants (Karavanich and Atema, 1998; Spanier et al., 1998). In general, size is the determining factor affecting the outcome of intraspecific interactions.

Little is known about agonistic behaviour of lobsters in interspecific interactions, although Miller et al. (1971) suggests that interspecific competition for food in kelp beds is intense. Experimental work by Cobb et al. (1986) explored habitat use and shelter occupancy with lobsters and two species of crab, the rock crab, *Cancer irroratus*, and the jonah crab, *Cancer borealis*. Regardless of relative size, lobsters dominated competition for the limited resource, shelter. Richards and Cobb (1986) found similar results with lobsters and jonah crabs and suggest that the high cost of not obtaining a shelter provides the motivation for the lobsters to win the battles for shelter, even against a larger opponent.

Agonistic behaviour of the green crab appears quite different than that of lobster. Whereas lobsters tend to be solitary, green crabs can be found at relatively high densities (up to 5/m^2; Young et al., 1999). Over 200 crabs were captured in one cylindrical trap (60 cm × 30 cm) in a 2-h set in Pomquet Harbour, Nova Scotia (Campbell, 2001), so the presence of con-specifics is not a deterrent to green crab foraging. While lobsters make extensive use of displays and show an escalation of aggression before actual combat, green crab battles do not begin with displays, but rather go directly to intense physical fighting (Sneddon et al., 1997a,b). This study investigates the interspecific interactions of the American lobster and the invasive green crab.

We set up two experiments that used competition for a limited food resource to elicit agonistic interactions between relatively large, sub-adult lobsters and adult green crabs. The first experiment was designed to test the following hypotheses: 1) the larger lobsters will spend significantly more time with the food; and 2) the lobsters will "win" a significantly greater proportion of agonistic interactions. The results of the first experiment suggested the need for another experiment, in which the lobsters were permitted to gain possession of the food before the green crabs. In this experiment, we tested the following hypotheses: 3) if allowed to feed first, lobsters would spend significantly more time with the food; and 4) the lobsters will "win" a significantly greater proportion of agonistic interactions. In addition to the specific hypotheses, we wished to describe the agonistic behaviour of the two species when paired together, and compare that be-