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SURVIVAL OF EUROPEAN GREEN CRAB (*CARCINUS MAENUS* L.) EXPOSED TO SIMULATED OVERLAND AND BOATING-VECTOR TRANSPORT CONDITIONS

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ABSTRACT Juveniles and adults hitch-hiking in fishing gear, recreational vessels, and fisheries and aquaculture products are believed to be important vectors of local dispersal of invasive European green crab (*Carcinus maenus* L.). Assessing the distance green crab might spread by hitch hiking requires an estimate of survival time under typical transport conditions. An exposure experiment (stocking density 62 crabs/m^2) was conducted in fish crates containing: just crabs (no water, no cover), dry rope, damp eelgrass (*Zostera marina* L.), seawater (1.5 cm deep), rope + seawater, or eelgrass + seawater. At mean air temperature of 24°C, almost no crabs died during the first 48 h, 50% of crabs stocked alone or with dry rope survived 68 h (none survived five days), 50% of crabs in eelgrass or eelgrass + seawater survived 90–100 h, and > 80% of crabs in sea water or rope + seawater survived the full five days. The second experiment (just crabs, sea water, and rope + seawater) used three stocking levels (84, 168, and 251 crabs/m^2) and ran for seven days. Stocking density did not have a significant effect on survival. At mean air temperature of 29°C, 50% of crabs fully exposed to air survived 60 h (almost none survived seven days), whereas about 60% of crabs survived to seven days when seawater or seawater + rope were present. The survival of green crab for several days out of water under severe summer conditions would allow them to be carried on boats to any point in Atlantic Canada, or almost anywhere on the eastern seaboard on trailered boats. This could result in further northward dispersal and the introduction of "northern" genetic material into previously colonized southern portions of the range, potentially increasing over wintering survival.

KEY WORDS: invasive species, experiment, dispersal, Atlantic Canada, boat, trailer, green crab, *Carcinus maenus*

INTRODUCTION

Because of increased human travel and shipping activities, marine species invasions and range expansions are occurring at an unprecedented rate (Carlton 1989, Carlton & Geller 1993, Ricciardi 2001). The major human-mediated vectors for long-distance dispersal of marine organisms are ballast water, hull fouling, and hitch-hikers associated with bivalve introductions or commercial fisheries products (Elton 1958, Carlton 1992, Carlton & Cohen 2003). Once a nonindigenous species becomes established in a new location, secondary or local dispersal can occur by means of several human-mediated vectors, including bilge water, hull and associated structure fouling, accidental release, and the construction of canals (Carlton 1985, 1989, 1999, Ruiz et al. 1997, Vermeij 1996, Wasson et al. 2001). In marine coastal and estuarine environments, the European green crab (*Carcinus maenus* L.) is one of the more successful invasive species; it has become established in nearly all suitable habitats worldwide. Green crab arrived in Atlantic Canada in 1951 and subsequently spread throughout the Bay of Fundy and Atlantic coast of Nova Scotia (Leim 1951, Audet et al. 2003). It was absent from the Gulf of Saint Lawrence until the mid1990s where the discovery of green crab in several locations (Gillis et al. 2000, Audet et al. 2003) apparently represents a period of new introductions from populations in its northern range in Europe (Roman 2006). The green crab's distribution continues to expand into more northern waters of Atlantic Canada (Paille et al. 2006, Klassen & Locke 2007).

The potential for green crab to disrupt ecosystem structure outside its native range is well established (Cohen et al. 1995, Davis et al. 1998, Jamieson et al. 1998). For example, predation by green crab was responsible for the decline of many benthic invertebrate species in Bodega Bay Harbor, California, and was a major factor in the explosive increase in abundance of the nonindigenous eastern gem clam (*Gemma gemma* Totten), which had colonized 50 y previously (Grosholz et al. 2000, Grosholz 2005). Moreover, because green crabs are attracted to and consume large numbers of small bivalves, they are a major pest for enterprises attempting to seed benthic bivalves for stock recovery or aquaculture purposes (Walton & Walton 2001, Audet et al. 2003, Wong et al. 2005). Finally, recent work in the southern Gulf of St. Lawrence (sGSL) has implicated the green crab, because of its consumption of small predatory gastropods, in the establishment of the nonindigenous clubbed tunicate (*Styela clava* Herdman) (Locke et al. 2007). The full extent of ecosystem changes associated with the green crab in the sGSL is uncertain because green crab is still in the initial phase of the invasion process (Audet et al. 2003, Thompson & MacNair 2004, Klassen & Locke 2007).

In marine systems, many of the secondary vectors for dispersal of invading species from the initial colonization site are associated with boating, fishing, and aquaculture activities. The secondary spread of green crab along the eastern seaboard of the USA was partly caused by its hitch-hiking on fishing boats and among the catch of American lobster (*Homarus americanus* H. Milne-Edwards) and small pelagic fishes (Scattergood 1952). The areas of the sGSL with well-established populations of green crab are also the locations of many harbors, marinas, and bivalve aquaculture operations; therefore, it is likely that these invaders are being transported by vessels. In addition, some of these boats are transported overland to other locations in Atlantic Canada (Darbyson et al. in press). The overland transportation of invaders could allow them to spread even more rapidly, and to more distant

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locations, than by water-based mechanisms alone. Critical to predicting the distance susceptible to rapid secondary spread of green crab from its current distribution in the sGSL is an understanding of how long this species can survive out of water during typical summer weather. The goal of this study was to test how long green crab survive on-land exposure under normal Maritime summer conditions and with various sources of cover that simulate conditions on small boats used for recreation, commercial fishing, or bivalve aquaculture.

MATERIALS AND METHODS

Green crabs were caught in the upper portion of the Cardigan River Estuary, Prince Edward Island (PEI), on August 25, 2003 and August 20, 2004, and transported to an open backyard (no shade from the sun) in Charlottetown, PEI, for the air-exposure experiments. This location was chosen to facilitate the collection of survival data, to prevent tampering, and to ensure that green crabs were not inadvertently introduced into waters currently devoid of them.

2003 Experiment

This experiment examined the effects of a series of potential boating-related transport conditions on the survival of green crabs. Several hundred green crabs were caught with dip nets, placed in fish crates with fresh seawater, and taken to the experiment location. The time between capture of the crabs and the start of the experiment was 4–5 h. The experiment was conducted in 100 L black fish crates containing one of the following exposure treatments: no water or cover (hereafter referred to as just crabs); dry rope; damp eelgrass (*Zostera marina* L.); sea water; rope + sea water; or eelgrass + sea water. There were three replicates of each treatment. These six treatments were used because they represent conditions crabs would likely encounter on deck, in the bilge, or in equipment of boats steaming between harbors or being transported overland on trailers. The amount of rope and eelgrass used was 0.5 kg (9.1 m $\times$ 1.6 cm diameter, yellow nylon) and 1 kg, respectively, for each crate. The eelgrass was collected from the Hillsborough River just before the beginning of the experiment. The amount of seawater used for treatments containing seawater was 4 L, resulting in water 1.5-cm deep in the crates. This water was not changed or replaced during the experiment. The six treatments were placed in three blocks arranged in a single row.

Twenty-three haphazardly chosen green crabs (both sexes combined) were placed into each crate, which represented a density of 62.2 crabs/m^2. The average carapace width of the crabs was 37.4 mm (range 17–70 mm). The experiment began at 20:00 on 25 August 2003. Crates were examined for dead crabs 1, 2 and 4 h after the experiments began and then every 6 h except at 24:00 h on subsequent days. The experiments ended after five days (120 h). A crab was considered to be dead based on lack of movement of the crab's papillae or by the absence of reflexive retraction of legs when tugged gently. Dead crabs were immediately removed.

The weather conditions were recorded each time the crates were checked for dead crabs. The maximum and minimum temperature and relative humidity were measured with a Springfield Precise Temperature Digital Thermometer and Humidity Meter, model #90856-TG. This device was set near the crates and reset after each examination for crab mortalities.

2004 Experiment

The second exposure experiment considered the effect of varying crab density in addition to three exposure treatments. Green crabs were caught in the same location and maintained in the same manner as in the 2003 experiments. For this experiment 20-L white plastic buckets were used as the experimental unit. Experimental treatments consisted of 3 exposure treatments (just crabs, sea water, and rope + sea water) and three crab densities representing 83.8 crabs/m^2 (5 crabs), 167.5 crabs/m^2 (10 crabs), or 251.3 crabs/m^2 (15 crabs). Treatments with water contained 1.25 L of seawater (water depth ~2.5 cm). The sea water + rope treatment used 9.1 m (0.5 kg) of yellow nylon rope. There were three replicates for every treatment/density combination arrayed in three blocks. Crabs were randomly assigned to treatment buckets. The mean carapace width of the crabs was 47.3 mm (range 22–69 mm).

The experiment began at 21:00 h on August 20, 2004. Buckets were examined for dead crabs at 7:30, 13:30, and 19:30 for seven days. As in 2003, weather conditions were recorded each time the buckets were checked. Mortality was determined as in 2003, and dead crabs were immediately removed.

Statistical Analysis

A randomized block design was used for these experiments so that the data could be analyzed using either ANOVA or the nonparametric Kruskal-Wallis test. Statistical analyses were carried out using SPSS v.13 statistical package (SPSS 2004). Based on Levene test, the variance of the survival data for the 2003 green crab exposure experiment was heterogeneous even after transformation; therefore, the Kruskal-Wallis test was used to test for the effect of treatment on the percentage of crabs alive at the end of the experiment and *a posteriori* comparisons were done using the Mann-Whitney test (Zar 1999). The variances were homogeneous for the 2004 experiment; therefore, an ANOVA was performed to test for the effects of both treatment factors on survival after seven days, and *a posteriori* comparisons were carried out using Tukey's test.

RESULTS

2003 Experiments

During the 2003 experiment, the weather was mainly clear with a trace of rain at hour 35 and two brief rain showers during the last 24 h of the experiment (Fig. 1). The average daytime high was 24.4°C and the average nighttime low was 11.2°C. The average daytime relative humidity was 87% compared with 68% at night. These are typical summer weather conditions for the Atlantic Maritime Provinces.

There were no live crabs left in either of the just crab or rope-only treatments by the end of the experiment (Fig. 2). The time to 50% mortality for the rope-only and just crab treatments was 67 h and 69 h, respectively. A small (mean ± SE) but variable percentage of crabs remained alive in the eelgrass (1.5 ± 2.5%) and eelgrass + seawater (8.7 ± 11.5%) treatments at the end of the experiment. The time to 50% mortality was 91 h for the eelgrass-only treatment compared with 101 h for the eelgrass + seawater treatment. In the case of the sea water (89.9 ± 9.1%) and rope + sea water (91.3 ± 7.5%) treatments, most of the crabs

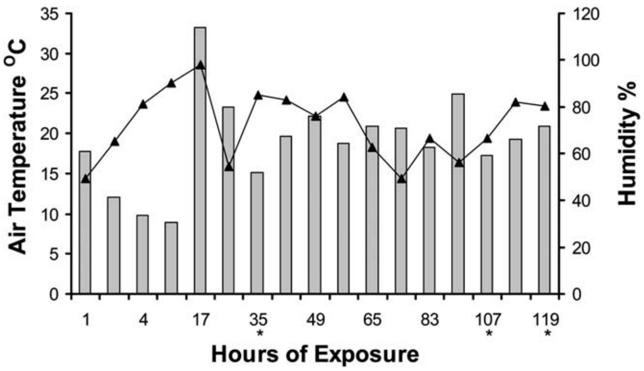

Figure 1. Air temperature (bars) and relative humidity (line) for each time interval between mortality checks for 2003 green crab exposure experiment. An asterisk under the hour of exposure indicates a rain event.

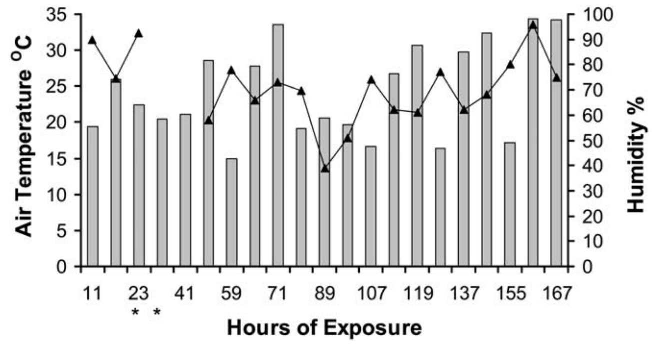

Figure 3. Air temperature (bars) and relative humidity (line) for each time interval between mortality checks for the 2004 experiment. An asterisk under the hour of exposure indicates a rain event.

survived the five day exposure period; consequently, the time to 50% mortality could not be determined.

At the end of the experiment, a significant difference in percent survival was found among treatments (Mann-Whitney test; $\chi^2 = 14.435$; DF = 5; $P = 0.013$). Significantly fewer crabs survived in the just crab, rope-only, and eelgrass-only treatments compared with the seawater and rope + sea water treatments (Fig. 2). No significant differences were found between the other treatments.

2004 Experiments

The weather conditions during the 2004 experiment (Fig. 3) were more extreme than those recorded in 2003. The mean daytime high was 29.4°C and mean nighttime low was 10.3°C. The daytime humidity averaged 71.2% compared with 55.6% at night. There were few brief showers during the second night of exposure.

No crabs survived to the end of the experiment (seven days) in the just crab treatment with densities of 10 or 15 animals, whereas a small percentage ($6.7 \pm 11.5\%$) survived in the crates with a density of five animals (Fig. 4). For each of the just crab treatments, the average times to 50% mortality were 71 h, 105 h, and 59 h for crab densities of 5, 10, and 15 individuals, respectively. In the case of the seawater and rope + sea water treatments more than half the crabs survived the full 7 d in all the crates regardless of the density.

Exposure treatment had a strong effect on the percentage of crabs surviving for seven days (ANOVA, $F_{2,8} = 98.1$, $P < 0.001$) but the density and interaction terms were not significant ($P > 0.05$). Significantly fewer crabs survived the just crabs treatment compared with either seawater ($P < 0.001$) or rope + sea water ($P < 0.001$) treatments. There was no significant difference in crab survival between the seawater and rope + sea water treatments.

DISCUSSION

Green crabs kept in dry treatments (just crabs, rope, and eelgrass) did not survive as well as those with seawater present. Green crabs are known to tolerate exposure to air at high temperatures for short periods. Under natural conditions, green crabs can inhabit burrows dug above the low water mark that, during neap tides, are not covered by water for several days (Crothers 1968). These burrows are cooler than the outside air and provide a damp substrate; hence, the principal stress appears to be a lack of opportunity to feed. At water temperatures of 34°C to 36°C, green crabs have been observed to move out of the water onto the exposed substrate of salt marshes and mudflats; laboratory studies indicate that green crabs leave the water once the temperature reaches about 30°C, and become moribund if water temperatures exceed 34°C (Ahsanullah &

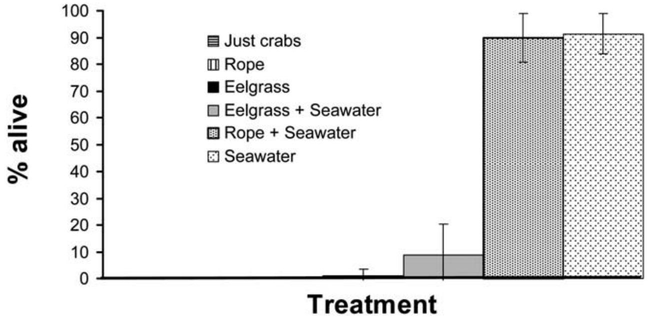

Figure 2. Mean (±SE) percentage of green crab surviving to the end of the aerial exposure experiment (5 days) under different overland transportation scenarios, September 2003. Just crabs refers to the treatment where cover and water were absent.

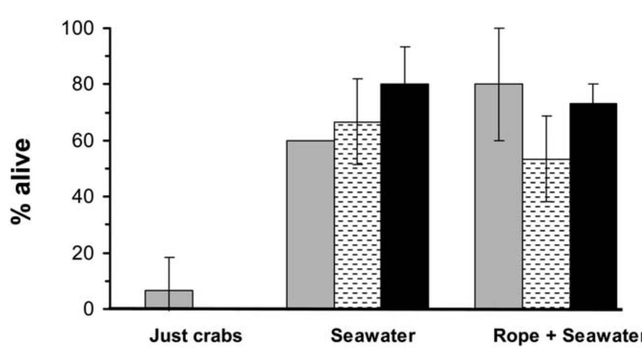

Figure 4. Mean (±SE) percent survival of green crab (three densities, three exposure conditions) at the end of seven days (2004 experiment). Just crabs refers to the treatment where cover and water were absent. Grey bars 84 crabs/m^2; stippled bar 10 crabs m^2; black bar 15 crabs/m^{2}t.

Newell 1977). Green crab can survive in dry air, using aerobic metabolism for at least 5.5 h at 15°C (Ahsanullah & Newell 1971, Newell et al. 1972), as long as the gill surface is kept moist. In addition, this species can survive up to two days in anoxic conditions by means of anaerobic metabolism (Spaargaren 1977, Hill et al. 1991). The present study is consistent with these earlier findings, showing that the survival time for green crabs exposed to air was longer than seven days when traveling in little (>50% survival) seawater. As pointed out by Crothers (1968), one of the critical factors is that the green crabs can keep their gills wet although a small percentage (6.7%) of crabs maintained with no cover or sea water survived the full 7 day experiment at an average daytime high of >29°C .

The survival rates for green crabs with no cover or water may decrease if they are exposed to higher amounts of wind, higher temperatures or drier conditions than those occurring in our study. Conversely, under more benign conditions (mainly lower air temperature and higher humidity), green crabs could survive longer out of water. We did notice that the crabs tended to form dense aggregations at either end of the crate or bucket, with crabs of all sizes piled one on top of the other. There was no evidence, however, that this behavior improved survival because the density effect in the ANOVA was nonsignificant. These aggregations may improve survival in some organisms; for example, zebra mussels survived exposure to air for longer periods when occurring in clumps compared with solitary individuals presumably because clumping reduces the exposed surface area of the individuals, helps retain water, and provides shelter from wind (Ricciardi et al. 1995).

The presence of damp eelgrass slightly extended (by about 23 h) the length of time crabs could survive without water. This is likely caused by the eelgrass providing cover for the crabs and/or slowing water loss through evaporation. These factors are consistent with the distribution of green crab during periods of emersion at low tide when they are most commonly found in areas with an algal canopy, under wrack, or in rock crevices (Crothers 1968, Janke 1990). The presence of dry rope did not, however, extend survival suggesting it was the moisture in the eelgrass rather than cover that contributed to the extended survival in the eelgrass treatment. Zebra mussels (*Dreissena polymorpha* Pallas) that are surrounded by vegetation also survive aerial exposure better because they are protected from the effects of sun and wind (Ricciardi et al. 1995).

The presence of eelgrass was not always beneficial. Survival was reduced in the eelgrass + seawater treatment relative to seawater alone. The eelgrass began to decay, which apparently created unfavorable conditions. We did not attempt to determine what byproduct of the decay of eelgrass became toxic to green crabs.

Lack of food is unlikely to limit the ability of green crab to disperse by overland or boating vectors and starvation likely was not a cause of death of crabs in our experiments. The crabs in the present study fasted for a week whereas Wallace (1973) starved green crabs for three months before 50% died.

One factor that we did not test was whether body size affects survival time for green crabs exposed to air. A separate, controlled, experiment would be needed to test for potential differences in survival for crabs of different body size. Given the very high survival for all crabs when a small amount of water was accessible to the crabs, this factor seems most likely only to be relevant for the most extreme treatments in which there would be no cover present or only dry rope.

Knowledge of aquatic species' abilities to withstand emersion is an important aspect of invasive species research. Organisms' survival during transport is a key element for the creation of dispersal models that can predict the spread of organisms from infested to uninfested areas. We found that at least 50% of green crabs could survive >2–3 days out of water—and at least 7 days if a small amount of water was present. Assuming a modest 200 km per day travel distance, this is enough time for this species to be transported to any marine or brackish water in Atlantic Canada by boats steaming between ports. If the boat is being carried on a trailer, and assuming a conservative travel distance of 500 km per day, the crabs could be transported almost anywhere along the eastern seaboard of North America even if cover or water were minimal. The present study was conducted under severe summertime conditions for Atlantic Canada and even greater survival would be expected under the cool and damp conditions of spring and fall. This likely is irrelevant given the long distances possible as calculated for the present study. Even though green crabs likely will spread to most parts of the sGSL during the next couple of decades by natural means, human activities will most likely increase the rate of spread of these organisms by moving the adults to uninfested areas on boats or in gear associated with boating, fishing, or bivalve aquaculture. Based on a study of boater movements in 2003–2004 (Darbyson et al. in press), the Magdalen Islands were predicted to be one of the next locations to be colonized by green crab. Subsequently, green crabs were collected in the lagoons of the Magdalen Islands (Paille et al. 2006). An even more recent expansion to Placentia Bay on the south shore of Newfoundland (Klassen & Locke 2007) may be caused by hitch-hiking of adults from a variety of locations but transfer of larvae in ballast water from North American or northern Europe sources cannot be ruled out until genetic studies are completed. In the case of waters where green crab have existed for many years (i.e., East-Coast of the USA), green crab arriving from the sGSL could change the genetic makeup of the extant green crab populations and reduce the apparent vulnerability of more southern populations to the effects of unusually cold winters that, in the past, may have caused large fluctuations in green crab numbers (Berrill 1982, Roman 2006, Klassen & Locke 2007).

Clearly, green crab can survive several days out of water under severe summer conditions, which would allow them to be carried by water throughout Atlantic Canada, or almost anywhere on the eastern seaboard with trailered boats. These results can be used to predict how current invaders or newly arrived alien species with similar biological characteristics could survive overland transport and spread throughout Atlantic Canada. For example, in 2004 another notoriously invasive crab, the Chinese mitten crab (*Eriocheir sinensis* H. Milne Edwards), was found in the St. Lawrence River (de Lafontaine 2005) for the first time and models indicate it has the potential to spread over much of Atlantic North America (Herborg et al. 2007). The type of information gathered in the present study is critical to determining how long invaders may survive overland transport under typical summer conditions. Specifically, this study provides an estimate of survival time for green crab during summer-time activities related to marine boating— providing one of the fundamental pieces of information needed to predict invasion patterns (e.g., Buchan & Padilla 1999, MacIsaac et al. 2004). Moreover, this information can be used with the appropriate models to predict the potential rate and extent of geographic spread of any potential new invaders once the suite of environmental conditions required for successful colonization is better identified (e.g., Bossenbroek et al. 2001, MacIsaac et al. 2004, Herborg et al. 2007).

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