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ORIGINAL PAPER

# Localized invasion of the North American Harris mud crab, *Rhithropanopeus harrisii*, in the Panama Canal: implications for eradication and spread

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**Abstract** As the rate of biological invasions continues to increase, a growing number of aquatic introduced species are becoming globally widespread. Despite this ubiquitous phenomenon, rarely do we discover aquatic invaders early enough to allow the possibility of eradication. Recently, the North American Harris mud crab (*Rhithropanopeus harrisii*) was found in the waters adjacent to the Panama Canal and herein we provide an assessment of the crab's distribution in Panama to evaluate the possibility of eradication. Using salinity tolerance experiments, we also evaluate the potential for further spread of this crab within the Canal. Our results suggest that populations of *R. harrisii* are currently limited to two manmade lagoons which are adjacent to the Panama Canal. Our experiments suggest that both juvenile and adult *R. harrisii* can survive in salinities found outside its current range in Panama. Although it is difficult to predict the potential for future spread and impacts in Panama, current management strategies could reduce the probability for spread locally as well as elsewhere in the world given the intensity of shipping in this region. The current containment of this invader suggests that a localized eradication may be possible.

**Keywords** Introduced species · Biological invasions · Shipping · Global invader · Salinity tolerance

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## Introduction

Globalization of the world's economies has substantially increased the rate of biological invasions worldwide (Mack et al. 2000; Meyerson and Mooney 2007). While the study of factors driving biological invasions has a much longer record on land than in the water, coastal estuarine and marine habitats are among the most heavily invaded systems on Earth (Grosholz 2002). Indeed, aquatic invasions appear to be increasing at an accelerating pace (Cohen and Carlton 1998; Ruiz et al. 2000), and several non-native species have become global invaders, rapidly expanding their distribution across the world (Roman and Palumbi 2004; Robinson et al. 2005). In marine and coastal environments shipping is a major mechanism of species transfer to new biogeographic regions (Carlton and Geller 1993; Ruiz et al. 1997; Cohen and Carlton 1998; Lodge et al. 2006).

Once established, exotic species often become abundant, spread locally, and cause ecological and economic damage. These invasive species threaten world-wide biodiversity and cause billions of dollars in economic damage each year (Wilcove et al. 1998; Pimentel et al. 2005). Eradication of established exotic species is a challenging endeavor, but several examples of successful removals exist (Myers et al. 2000; Simberloff 2003). Eradication in aquatic systems may be even more challenging relative to terrestrial systems, but recent examples of successful removals in marine and brackish water provide hope (Kuris and Culver 1999; Bax et al. 2002; Anderson 2005). In all of these instances eradication was facilitated by limited, localized invasions (Myers et al. 2000).

Recently, we discovered an established population of the North American Harris mud crab, *Rhithropanopeus harrisii*, in the Panama Canal area (Roche and Torchin 2007). Given the imminent expansion of the Canal and the current magnitude of shipping in Panama, there is considerable potential for this species to spread at the regional and the global scale. However, this discovery could provide an unusual and timely opportunity for eradication if the established population is localized.

*Rhithropanopeus harrisii* is a small estuarine crab native to the Atlantic coast of North America. It first invaded Europe in the late 1800s and is now established in 21 different countries on the European and the American continents (Roche and Torchin 2007) and recently it has been reported from Japan (Iseda et al. 2007). The broad tolerance of *R. harrisii* to environmental variation has likely facilitated its success as a global invader. To date, this species has successfully colonized several different habitats ranging from freshwater lakes in Texas, bays and estuaries on the eastern and western Pacific, ports and estuaries in the Mediterranean and in Europe, and now a tropical lagoon system. It currently has an introduced range of over 45° of latitude and has the potential for further spread (Roche and Torchin 2007; DL Felder pers. comm.). Notably, *R. harrisii* has been identified as one of the top 30 species of concern from a list of 851 marine pests likely to invade Australia (Hayes and Sliwa 2003). Although the impacts of the crab in its introduced range remain largely unquantified, anecdotal reports suggest that it competes with native species and causes economic damage by fouling pipe systems and spoiling fish catches in gill nets in the US and in the Caspian Sea, where it has reached very high abundances (GISD 2007; Roche and Torchin 2007).

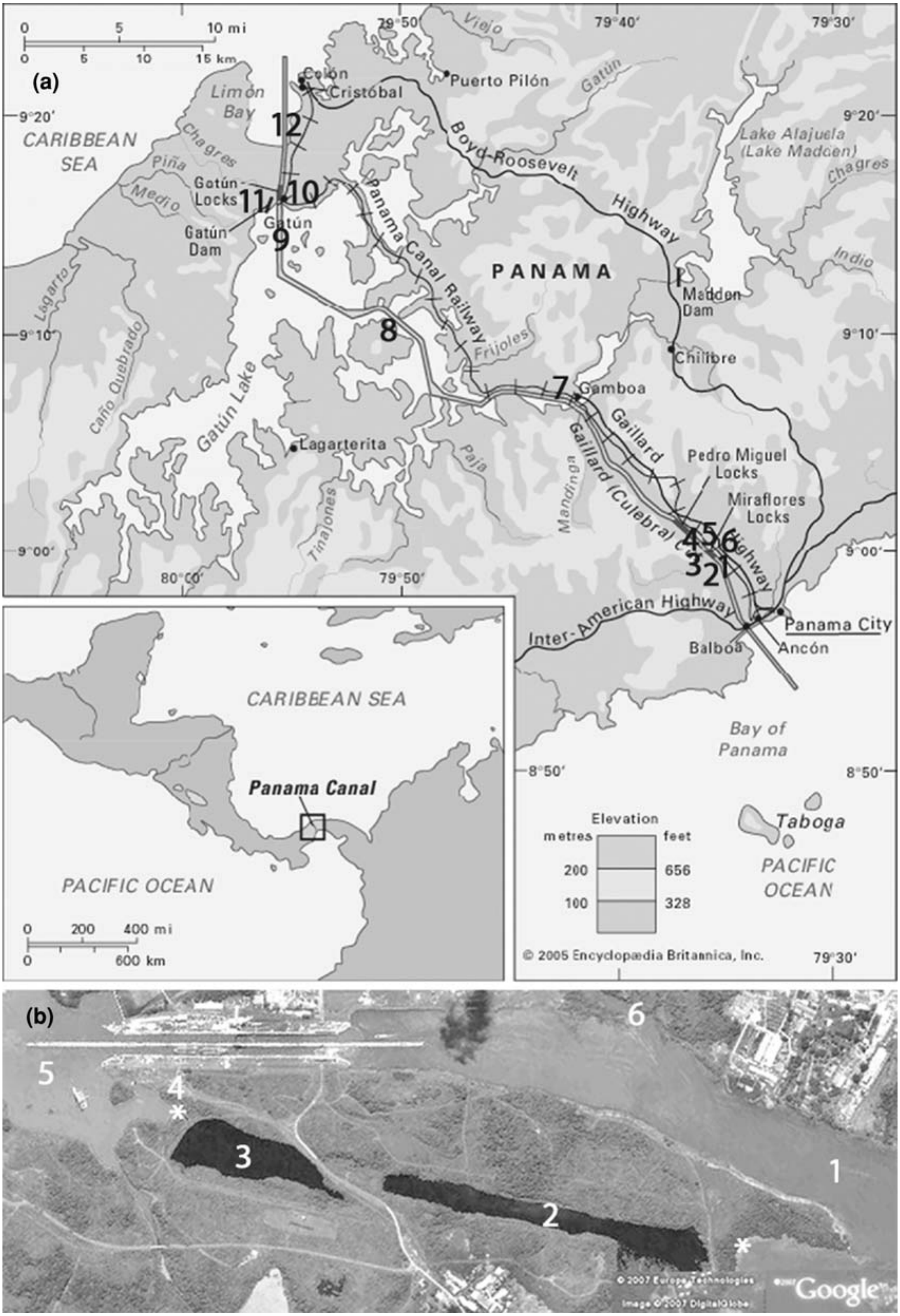
The Panama Canal is one of the busiest maritime routes in the Americas, with over 12,000 commercial ship transits annually, which is more than twice the number of ship arrivals in the largest ports in the U.S. (Ruiz et al. 2006). In addition to canal transits connecting the Atlantic and Pacific Ocean basins, Panama's bi-coastal ports serve as major hubs for international shipping, elevating the potential for ship mediated species transfers. Thus, the presence of *R. harrisii* in Panama merits consideration given the likelihood that the Canal may serve as a source of secondary introductions worldwide. To evaluate the potential for eradicating *R. harrisii* in Panama, we used a standardized quantitative approach to assess the geographic distribution, abundance, and demographics of the crab in the Canal. In addition, since salinity is the most important factor limiting this species distribution at the local scale (Costlow et al. 1966; Turoboyski 1973; Cronin 1982), we conducted salinity tolerance experiments to evaluate the potential for further spread within the Panama Canal and elsewhere in the world.

## Methods

### Study site

The Panama Canal joins the Pacific and the Atlantic Oceans and functions by allowing ships to transit the Isthmus of Panama, via three sets of locks (Fig. 1a). Located adjacent to the Miraflores Locks, on the west side of the Canal, are two manmade lagoons, remnants of a project to expand the Canal which was abandoned in the 1940s (Fig. 1b; Rubinoff and Rubinoff 1968; Roche and Torchin 2007). During the course of this study, the salinity in the Southern

**Fig. 1** (**a**) Map of the Panama Canal with sites surveyed for ▶ *R. harrisii*: 1. Pacific approach; 2. Soutern Lagoon; 3. Northern Lagoon; 4. Culverts at the Miraflores Lake; 5. Miraflores Lake; 6. Miraflores Spillway; 7. Gatun Lake; Gamboa; 8. Gatun Lake; Barro Colorado Island; 9. Gatun Lake; Gatun Locks; 10. Gatun Third Lock Lagoon; 11. Gatun spillway and French Canal; 12. Atlantic approach. By courtesy of Encyclopaedia Britannica, Inc., copyright 2005; used with permission. (**b**) Inset of the Miraflores Third Lock Lagoons adjacent to the Miraflores Locks (modified from Roche and Torchin 2007)—asterisks indicate sites where water will be drained out of the lagoons


(a)
CARIBBEAN SEA
Limón Bay
Colón
Cristóbal
Puerto Pilón
Boyd-Roosevelt Highway
Lake Alajuela (Lake Madden)
Gatún Locks
Gatún Dam
Gatún
Gatún Lake
Panama Canal Railway
PANAMA
Madden Dam
Chilibre
Gamboa
Lagarterita
Gaillard
Gaillard (Culebra) Cut
Pedro Miguel Locks
Miraflores Locks
Inter-American Highway
Balboa
Ancón
Panama City
Bay of Panama
Taboga
PACIFIC OCEAN
CARIBBEAN SEA
Panama Canal
PACIFIC OCEAN
Elevation
metres feet
200 656
100 328
© 2005 Encyclopædia Britannica, Inc.
1 2 3 4 5 6 7 8 9 10 11 12
(b)
1 2 3 4 5 6
Google

Lagoon (initially termed the Miraflores Third Lock Lake by Rubinoff and Rubinoff 1968) varied between 2.1‰ and 4.3‰ whereas the salinity in the Northern Lagoon varied between 0.4‰ and 0.6‰ (Appendix). These two excavations, hereafter referred to as the Miraflores Third Lock Lagoons, were built separately and are not connected (USPCSED 1944). The Southern Lagoon is currently isolated since the culverts connecting it to the Pacific entrance of the Canal were blocked by the Panama Canal Authority in 2006 (FO Guardia pers. comm.). In contrast, the Northern Lagoon remains connected to a small inlet in the Miraflores Lake by a single underground culvert (pers. obs.). However, despite the current containment of the Miraflores Third Lock Lagoons, plans to expand the Panama Canal will significantly alter these habitats. Water from these lagoons will be pumped into the Miraflores Lake and into the Pacific approach, eventually draining these habitats (ACP 2006a; Fig. 1b). Already, the Southern Lagoon was partially drained into the Pacific Ocean February 2006 and in February 2008.

## Canal wide survey & monthly samplings

To evaluate the distribution and abundance of *Rhithropanopeus harrisii* across the Panama Canal, we used plastic mini-crates (approx. 8 l) filled with bivalve shells. These standardized collecting units were not baited but rather provided crabs with substrate for colonization. The collecting units were deployed in the field for a period of four weeks and returned to the lab for subsequent analysis. We recorded the number of crabs (catch per unit effort), crab size (carapace width—cw) and sex. All specimens were subsequently preserved in 95% alcohol. Between July 2007 and April 2008, a total of 179 collecting units were deployed at 12 sites transecting the Canal (Fig. 1, Table 1). We chose the sites based on our assessment of habitat suitability for *R. harrisii* and we measured environmental parameters (habitat type, depth, salinity, temperature, pH, conductivity, DO) using a YSI 85. Using the same techniques, we sampled the two lagoons where *R. harrisii* were known to occur on a monthly basis from November

**Table 1** Sites surveyed and number of collecting units analyzed to assess the presence of *R. harrisii* in the Panama Canal (excluding monthly samplings in the Miraflores Third Lock Lagoons)

| Site | General coordinates | Collection date | Coll units | *R.h.* pres |
|---|---|---|---|---|
| 1. Pacific approach | 08°58′37″ N 79°35′02″ W | 05-Jun-07 | 2 | N |
| | | 10-Sept-07 | 4 | N |
| | | 21-Feb-08 | 8 | N |
| 2. Southern Lagoon | 08°59′03″ N 79°35′18″ W | 05-Jun-07 | 2 | Y |
| | | 01-Aug-07 | 8 | Y |
| 3. Northern Lagoon | 08°59′38″ N 79°35′41″ W | 05-Jun-07 | 1 | Y |
| | | 01-Aug-07 | 6 | Y |
| 4. Culvert Miraflores Lake | 08°59′45″ N 79°35′42″ W | 14_Jan-08 | 3 | Y |
| | | 21-Feb-08 | 2 | Y |
| | | 24-Mar-08 | 2 | Y |
| | | 28-Apr-08 | 2 | Y |
| 5. Miraflores Lake | 09°00′28″ N 79°36′05″ W | 05-Jun-07 | 4 | N |
| | | 11-Sept-07 | 6 | N |
| | | 07-Dec-07 | 18 | N |
| 6. Miraflores Spillway | 08°59′41″ N 79°35′06″ W | 10-Oct-07 | 12 | N |
| 7. Gatun Lake—Gamboa | 09°07′12″ N 79°42′58″ W | 7-Nov-07 | 5 | N |
| 8. Gatun Lake—BCI | 09°09′55″ N 79°50′03″ W | 7-Nov-07 | 10 | N |
| 9. Gatun Lake at Gatun Locks | 09°15′43″ N 79°55′24″ W | 08-Jan-08 | 21 | N |
| 10. Gatun Third Lock Lagoon | 09°16′52″ N 79°54′49″ W | 20-Jan-08 | 6 | N |
| 11. Gatun Spillway/French Canal | 09°15′51″ N 79°56′01″ W | 20-Jan-08 | 7 | N |
| 12. Atlantic Approach | 09°17′30″ N 79°54′54″ W | 20-Feb-08 | 5 | N |

2007 to April 2008 using 5 collecting units at each site.

### Salinity tolerance experiments

We evaluated the salinity tolerance of *R. harrisii* with two experiments. The first tested a wide range of salinities, from freshwater to marine, using water prepared by adding Coralife scientific grade marine salt to distilled water. The water was buffered with CombiSan$^{TM}$ Marine Supplement to add trace elements naturally found in sea and brackish water. The second experiment attempted to account for natural water chemistry by using water collected in the field from different sites within the Canal. We used adult crabs with a carapace width ≥5.5 mm and juvenile crabs with a carapace width ≤4.5 mm (Turoboyski 1973) from the Miraflores Third Lock Lagoons for both experiments.

The first experiment tested both juvenile and adult crab survival in a total of 12 different salinities ranging from 0‰ to 35‰. Water from the Southern Lagoon served as a control. Ten juveniles and ten adults were randomly assigned a treatment group, and individually placed in a plastic cup containing 100 ml of water. A total of 260 crabs were used for the experiment. Each cup was covered with a plastic lid with breathing holes to minimize evaporation (Ruscoe et al. 2004). Prior to the beginning of the experiment, crabs in high salinity treatments were gradually acclimated to their experimental treatments by increasing salinity by 5‰ per day until the desired salinity was reached. Treatments were randomly divided between four water baths at 28.5°C (the prevailing water temperature in the Canal) and the temperature was stabilized with water heaters. Each crab was fed a pellet of freeze-dried brine shrimp twice a week, before the water was changed. Survivorship was recorded daily between 10 am and 12 pm for a total of 30 days during November and December 2007.

In the second experiment, conducted between January and February 2008, we used the same methodology, with different individuals, except that the water for the salinity treatments was collected from the field. We used rainwater (0‰), water from Gatun Lake (0.1‰), Miraflores Lake (0.4‰), the Pacific approach to the Canal (18.5‰), the Atlantic approach to the Canal near Gatun Lake (23.6‰), and the Bay of Panama (29.0‰) (see Fig. 1). A total of 140 crabs were used and they were not gradually acclimated.

### Statistical analysis

We used a two-way ANOVA to test for differences in the relative abundance of crabs between the Southern Lagoon and the Northern Lagoon, through time. Abundances were square root transformed to meet the assumptions of the model. We also used a *t*-test to compare the size of adult crabs (log transformed) between the two lagoons. Analyses were carried out in R (R Development Core Team 2007).

## Results

### Canal wide survey & monthly samplings

We successfully retrieved 134 of the 179 collecting units deployed. *R. harrisii* was only found in the two lagoon sites adjacent to the Canal (sites 2 and 3, Fig. 1). While most collecting units recovered from other sites contained organisms, including other crab species, none contained *R. harrisii* (Table 1). Although *R. harrisii* was not recovered from the Miraflores Lake, which was sampled twice throughout this study since it is the closest potentially suitable habitat for the crab, several specimens, including ovigerous females, were found at the mouth of a single culvert connection between the Northern lagoon and a small inlet to the Miraflores Lake (site 4, Fig. 1). Further sampling following this discovery indicated that *R. harrisii* was restricted to the vicinity of this culvert. The average catch per unit effort of *R. harrisii* was almost two times higher in the Northern Lagoon (44 crabs/collecting unit) compared to the Southern Lagoon (26 crabs/collecting unit) ($F_{1,52} = 5.85$, $P < 0.05$), although this difference was dependent on the collection date ($F_{6,52} = 3.81$, $P < 0.01$) (Fig. 2). In both lagoons, there appeared to be a pulse of reproduction during the middle of the year, with a subsequent decrease in the abundance of juveniles over time (Fig. 2). While statistically significant, the average size of adult crabs was only 3% greater in the Northern Lagoon (8.41 mm, range 4.58–18.89 mm) compared to the Southern Lagoon (8.16 mm, range 4.53–17.96 mm) ($t_{1459} = -2.28$, $P < 0.05$).

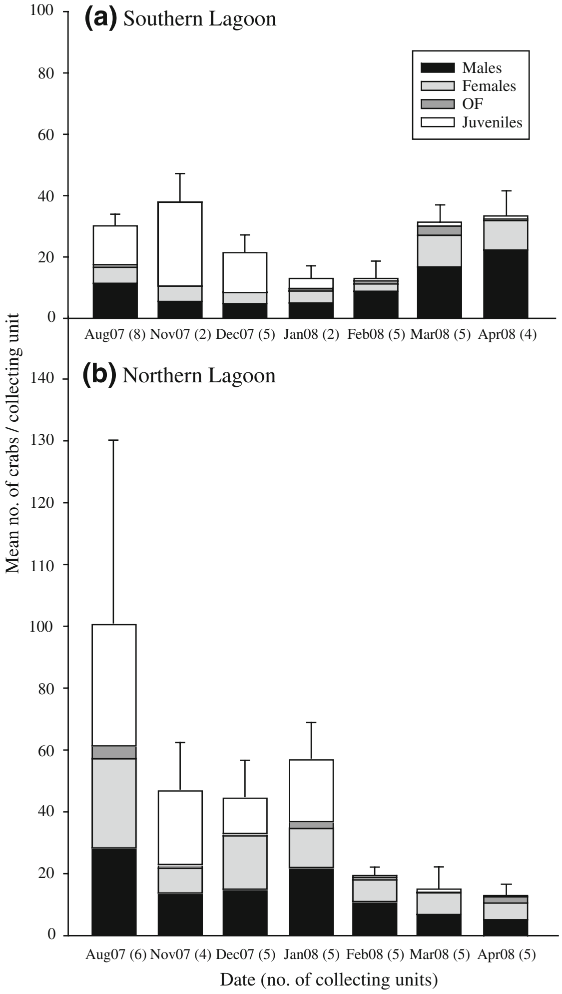



**Fig. 2** Mean number of *R. harrisii* per life-stage per collecting unit in (**a**) the Southern Lagoon and (**b**) the Northern Lagoon, between August 2007 and April 2008. The number of collecting units analyzed per month is indicated in parenthesis; error bars are SE for the mean total crabs per collecting unit

Salinity measurements recorded throughout the Canal in our study, along with values reported by previous studies (see Cohen 2006), are presented in the Appendix. Salinity and other environmental variables measured during our study suggest the existence of suitable habitat for *R. harrisii* at sites adjacent to the Miraflores Third Lock Lagoons, based on similarities with these environments (Table 2). Analysis of monthly data on surface water quality in the Miraflores Lake between 2003 and 2005 (ACP 2006b) indicated a decreasing salinity gradient from the section of the lake closest to the northern lagoon (avg = 0.7‰, range = 0.4–1.4‰) toward the section farthest away (avg = 0.6‰, range = 0.1–1.0‰). Despite temporal variability, the salinity at sampling stations closest to the Northern Lagoon never reached levels below 0.4‰, the prevailing salinity recorded in this lagoon throughout the study.

## Salinity tolerance experiments

The survival of juvenile and adult *R. harrisii* increased with increasing salinity in both salinity tolerance experiments (Fig. 3). Overall, adults appeared to tolerate low salinities better than juveniles in both trials. Although no crabs survived the freshwater treatment in either of the experiments, all juveniles died within 5 h whereas adults survived up to 6 days. Interestingly, the survivorship of both life stages was higher at low salinities in the experiment with field water compared to the experiment with prepared water. One hundred percent of the adult and fifty percent of the juvenile crabs survived in water from the Gatun Lake (0.1‰) during the 30 day trial. Similarly, adults and juveniles survived as well in water from the Miraflores Lake (0.4‰) as they did in the controls (Fig. 3). The anomalously high mortality of juvenile crabs in water from the Pacific approach (18.5‰) (Fig. 3c) could be due to the filamentous algae we found growing on the crabs and in the cups exclusively in treatments with water from this

**Table 2** Mean surface environmental characteristics of the Miraflores Third Lock Lagoons and adjacent habitats

| Site (*n* = measurements) | Date | Salinity (‰) | Temp. (°C) | pH | Adj cond (µS/cm) | DO (%) |
|---|---|---|---|---|---|---|
| Southern Lagoon (5) | 14-Jan-08 | 2.1 | 28.1 | 6.9 | 3939.8 | 89.3 |
| Northern Lagoon (5) | 14-Jan-08 | 0.4 | 28.0 | 6.2 | 866.8 | 79.6 |
| Miraflores Culvert (4) | 14-Jan-08 | 0.4 | 28.1 | 6.5 | 870.3 | 83.7 |
| Miraflores Lake (18) | 7-Dec-07 | 0.38 | 27.8 | 7.8 | 763.4 | 94.1 |
| Pacific Approach (4) | 9-Aug-07 | 19.9 | 30.3 | 5.4 | $32.1e10^3$ | 79.7 |

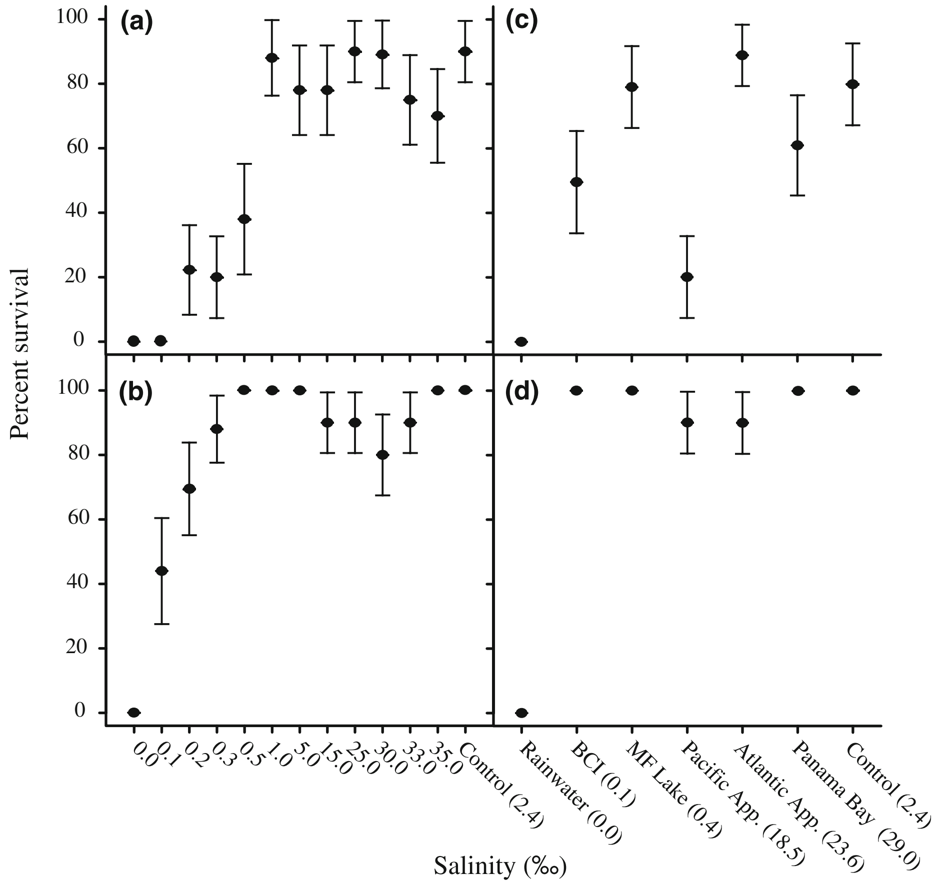



**Fig. 3** Survival of juvenile (top) and adult (bottom) *R. harrisii* subjected to 30 days of treatments of different salinities in water (**a**, **b**) artificially prepared and (**c**, **d**) collected in the field. Error bars are SE for a binomial distribution

location. This may have affected the availability of oxygen in this treatment.

## Discussion

Our results suggest that the invasion of *Rhithropanopeus harrisii* in Panama is localized in two man-made lagoons adjacent to the Panama Canal. This may provide an unusual opportunity for eradication of the crab since the established populations are relatively contained. While our data indicate that these two populations are well established and reproducing, their spatial isolation from the Canal proper suggests that timely management will be key in reducing the potential for their spread within Panama and possibly elsewhere in the world.

Shipping activity probably led to the introduction of *R. harrisii* to Panama (Roche and Torchin 2007), but ships do not transit the Miraflores Third Lock Lagoons. Given the previous and current connection between these lagoons and the Canal proper, it is puzzling that *R. harrisii* only occurs at these sites and no where else in the Canal. It is possible that the combination of sufficient propagule pressure and suitable habitat (Leung and Mandrak 2007) may have allowed nascent foci to form in the Miraflores Third Lock Lagoons, whereas other isolated and low density introductions may have failed elsewhere in the Canal, perhaps even repeatedly. For instance, *R. harrisii* was first reported in the Pedro Miguel Locks in 1969 (Abele and Kim 1989) but subsequent surveys suggest that it did not establish (Cohen 2006; this study). In the future, however, a sufficient number of crabs displaced from the Third Lock

Lagoons could elevate the probability that *R. harrisii* will establish in adjacent areas.

Our salinity tolerance experiments suggest that both juvenile and adult *R. harrisii* can survive in areas adjacent to the crab's current distribution in the Canal, namely in the Miraflores Lake and the Pacific approach. However, although the Southern Lagoon was partially drained into the Pacific approach in February 2006 and in January 2008, we did not recover any crabs in our collecting units at this site. Perhaps this is because the drainage occurred from the bottom layers of the lagoon, which are anoxic and highly sulfurous (McCosker and Dawson 1975; pers. obs.), and likely do not support *R. harrisii*. Interestingly, the crab is also not currently established in the Miraflores Lake beyond the mouth of the culvert which connects it to the Northern Lagoon. Several non-exclusive hypotheses may explain *R. harrisii*'s absence from the Miraflores Lake: (a) physical conditions in the lake preclude its establishment, (b) propagule pressure (dispersal) is insufficient for establishment, and (c) biotic interactions limit the distribution of the crab.

While our salinity tolerance experiments indicate that juvenile and adult crabs can persist 30 days at very low salinities, Costlow et al. (1966) found that *R. harrisii* larvae did not survive at salinities below 1‰. The salinity tolerance of the larvae may therefore be the limiting factor impeding the establishment of *R. harrisii* in the Miraflores Lake. However, our data indicate that *R. harrisii* is well established and successfully reproducing in the Northern Lagoon, where we constantly recorded salinities between 0.4‰ and 0.6‰ (Appendix). In fact, at times, the catch per unit effort of crabs at this site was more than twice that of the more saline Southern Lagoon, however the abundance of crabs appeared to decrease over time (Fig. 2). Although adult and juvenile crabs survived as well as the controls in water from the Miraflores Lake at 0.4‰ (Fig. 3c, d), salinity may not be the only factor limiting the establishment of *R. harrisii* in the lake. Perhaps other, unmeasured environmental variables may also influence survival. An alternative explanation for the crab's absence from this site may be the limited dispersal (propagule pressure) originating from the adjacent Northern Lagoon. Restricted dispersal of crabs (Cronin 1982) through a single culvert may not be sufficient to allow successful colonization of the Miraflores Lake since propagule pressure has been identified as a consistent predictor of invasion success (Colautti et al. 2006). The greater the propagule pressure, the more likely an invader is to successfully establish (Williamson 1996; Hutchinson and Vankat 1997; Lonsdale 1999; Kolar and Lodge 2001). Alternatively, biotic interactions in the Miraflores Lake may limit the spread of *R. harissii*. While we found few potential benthic predators or competitors in the collecting units recovered from this site, we did not evaluate the presence of larger predators which may also be important. However, if dispersal (i.e., propagule pressure) from the Northern Lagoon were high enough, we would expect to have encountered at least a few *R. harrisii* in our collecting units since biotic interactions would likely impact demographics rather than establishment per se (Drake 2003).

Regardless of which factors currently limit the spread of *R. harrisii*, our results demonstrate that this crab is well established in the Miraflores Third Lock Lagoons and suggest that it could potentially spread further. Given the current intensity of global shipping through the Canal and the impending expansion of the Canal to include a third set of locks in the region where *R. harrisii* is established, current management strategies could reduce the potential future spread of this crab in Panama and elsewhere in the world. Our evaluation of the distribution and abundance of *R. harrisii* in Panama suggests that this invasion provides an unusual and timely opportunity for eradication since the established populations are currently localized.

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## Appendix

Measurements of surface salinity (parts per thousand) at different sites along the Panama Canal (modified from Cohen 2006)

| Date | Pacific Approach | SL | NL | MF Spillway | MF Lower Locks | MF Upper Locks | MF Lake | Pedro Miguel Locks | Gatun Lake | Gatun Upper Locks | Gatun Lower Locks | Gatun TLL | Gatun Spillway | Atlantic Approach | Ref. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Jun 1935 | | | | | | | | | | 0 | 10–16 | | | 18–20 | 1 |
| <1939 | 16–20 | | | | | | 0.1–3.0 | | ≤0.02 | | | | | 18–20 | 1 |
| ≤1968 | 30[a] | | | | 26[a] | | 1.0[a] | 0.0[a] | 0.0[a] | | 24[a] | | | 28.5[a] | 2 |
| Feb 1969 | | | | | | | | 0.0–0.4 | | | | | | | 3 |
| Jan 1972 | | | | | | 20[b] | | | | | | | | | 4 |
| Apr 1972 | 27 | | | | | 1–3[a] | 0[a] | 0[a] | 0[a] | 0.1[a] | 5–11[a] | | | 17[a] | 5 |
| Nov 1972 | 23[a] | | | | 14–15 | 3[a] | 0–1[a] | 0[a] | 0[a] | 0.2–0.3[a] | 6–8[a] | | | 10–17[a] | 5 |
| Mar 1974 | | | | | | | | | 0.2 | 0.02–0.8 | | | | | 6 |
| Jun 2007 | | 4[c] | 0[c] | | | | | | | | | | | | 7 |
| Jul 2007 | | 3[c] | 0[c] | | | | | | | | | | | | 7 |
| Aug 2007 | | 3.3 | 0.4–0.6 | 0.1–3.4[d] | | | 0.3–0.4 | | | | | | | | 7 |
| Sep 2007 | 19.3–20.3 | | | | | | 0.2–0.5 | | | | | | | | 7 |
| Oct 2007 | | 2.8–2.9 | 0.4 | 0.9–7.6[d] | | | | | | | | | | | 7 |
| Nov 2007 | | 2.3 | 0.4 | | | | 0.2–0.4 | | 0.1 | | | | | | 7 |
| Dec 2007 | | 2.1–2.2 | 0.4 | | | | 0.1–0.5 | | | | | | | | 7 |
| Jan 2008 | | 2.1 | 0.4 | | | | 0.4[e] | | 0.1 | | | 0.2 | 0.1–0.2[d] | 14.4–24.4 | 7 |
| Feb 2008 | 14.1–20.0 | 2.5–2.6 | 0.5 | | | | 0.5[e] | | | | | 0.2 | 1.5–10.5 | 23.3–24.5 | 7 |
| Mar 2008 | | 3.1–3.6 | 0.6 | | | | 0.6–0.7[e] | | | | | | | | 7 |
| Apr 2008 | | 4.1–4.3 | 0.6 | | | | 0.6[e] | | | | | | | | 7 |

Abbreviations: MF = Miraflores, SL = Southern Lagoon, NL = Northern Lagoon

[a] Values estimated by Cohen (2006)

[b] In sump areas after dewatering

[c] Measured with a refractometer

[d] At low tide

[e] At the culvert connection with the NL

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