Discovery, distribution, and eradication potential of the introduced mud crab,

***Rhithropanopeus harrisii*, in the Panama Canal**

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Abstract

Eradication of invasive species is an eminent concept in conservation biology. After prevention is no longer an option, many ecologists argue that eradication is the most effective way to mitigate the risk of impacts from invasive species, given the elevated costs and often prolonged environmental effects of long-term control strategies. In the majority of systems, eradication is most likely to succeed early in the invasion process, when an invader is localized. However, rarely is early eradication considered in practice. This paradox may result from the many uncertainties regarding the future spread and impacts of novel invaders and managers lacking practical guidance to make logical decisions to manage them. In this thesis, I use a case study of an introduced mud crab, *Rhithropanopeus harrisii*, to propose guidelines for rapidly assessing and communicating the feasibility and the benefits of early eradication. First, I document the recent discovery of an established population of *R. harrisii* in the Panama Canal, highlighting how maritime traffic in this hub of international shipping may further increase the spread of this invader worldwide. Second, I evaluate the distribution, abundance, and demographics of *R. harrisii* across the Panama Canal with a standardized quantitative survey; I also assess the crab's potential for spread beyond its distribution in the Canal with two laboratory experiments. Third, I develop an analytical framework for evaluating the feasibility of a rapid response to eradicate *R. harrisii* and for communicating the potential benefits of this management strategy to decision-makers. My results indicate that *R. harrisii* currently occupies a limited range within two manmade lagoons adjacent to the Panama Canal, suggesting that eradication may be feasible. Furthermore, salinity

tolerance experiments revealed that adults and juveniles could survive in locations within the Canal proper, should their habitat be modified according to the Panama Canal expansion plan. Building on this case study, I suggest a general framework to contend with major challenges of rapid response efforts: limited information about novel invaders, limited time for management, and limited communication between scientists and decision-makers.

Résumé

L'éradication d'espèces introduites invasives est un concept populaire dans le domaine de la biologie de la conservation. Lorsque la prévention d'une invasion échoue, de nombreux écologistes soutiennent que l'éradication est la méthode la plus efficace afin d'éviter que les espèces introduites ne causent de dommages, considérant les coûts élevés et les effets parfois prolongés du contrôle à long-terme. Notamment, dans la majorité des systèmes, le succès d'un programme d'éradication est supérieur s'il est entrepris tôt lors du processus d'envahissement, lorsqu'une espèce est peu dispersée. Cependant, cette stratégie qui consiste à éradiquer les espèces introduites de façon hâtive est rarement mise en pratique. Ce paradoxe peut résulter d'un haut niveau d'incertitude concernant le potentiel qu'ont les espèces nouvellement introduites à se propager et à causer des impacts, et par le fait que les administrateurs responsables de leur gestion manquent souvent de conseils pratiques afin de réagir promptement suite à leur découverte. Pour remédier à cette lacune, cette thèse se base sur une importante étude de cas et suggère un modèle théorique servant à analyser de façon rapide la possibilité d'implémenter un programme d'éradication hâtif et d'en évaluer les bénéfices. Premièrement, je documente la découverte récente du crabe *Rhithropanopeus harrisii* dans le Canal de Panama. Le Canal de Panama est une plaque tournante du trafic maritime international et pourrait jouer un rôle important dans l'accroissement de la propagation de *R. harrisii* au niveau mondial. Deuxièmement, au moyen d'un échantillonnage quantitatif standardisé, j'évalue la distribution, l'abondance et la démographie de *R. harrisii* à l'échelle du Canal de Panama. J'évalue également le potentiel de dispersion du crabe au-delà de sa

distribution actuelle dans le Canal avec l'aide de deux expériences en laboratoire. Troisièmement, je développe un modèle analytique pour évaluer la possibilité de réagir rapidement afin d'éradiquer *R. harrisii* et de communiquer les avantages de cette stratégie aux gestionnaires intéressés. Les résultats de cette étude indiquent que *R. harrisii* occupe présentement une distribution restreinte au sein de deux lagons artificiels adjacent au Canal de Panama, ce qui suggère la possibilité d'un éventuel programme d'éradication. De plus, des expériences examinant la tolérance physiologique du crabe à différents niveaux de salinité démontrent que les adultes et les juvéniles on la capacité de survivre dans plusieurs sites à l'intérieur même du Canal, advenant une imminente modification de leur habitat selon les futurs plans d'expansion du Canal. Finalement, je présente de façon générale, puis j'applique à l'étude de cas de *R. harrisii* un modèle théorique afin de surmonter les difficultés majeures qui entravent les initiatives d'éradication hâtive, notamment le manque d'information à propos d'espèces invasives, le manque de temps disponible pour prendre des décisions, et le manque de communication entre chercheurs et gestionnaires.

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Contributions of Authors

The three chapters of this thesis were prepared for submission to peer-reviewed journals. The initial topic of my thesis was a test of the enemy release hypothesis using native and introduced cichlids in the Panama Canal watershed; Dr. Brian Leung helped to develop the questions and the experimental design and Dr. Mark Torchin later provided expertise in parasitology and help with dissections. This data is not presented in my thesis, but I will finish the analysis in the fall of 2008 and it is intended for publication, co-authored with both my advisors and E.F. Mendoza Franco, CINVESTAV Institute of Parasitology, Mexico.

I conceived and executed the field and laboratory work presented in this thesis in close consultation with both my advisors, Dr. Mark Torchin and Dr. Brian Leung, and with additional guidance from members of my supervisory committee, Dr. Lauren Chapman and Dr. Andrew Hendry. Dr. Torchin provided much guidance in the writing of Chapter 1, on which he is co-author. Following the publication of this first article in *Aquatic Invasions*, I decided, with support from both my advisors, to continue working on *R. harrisii* in Panama due to the importance and the timeliness of this discovery. Dr. Torchin and Dr. Leung provided substantial help in the development and writing of Chapter 2. Sandra Binning assisted with field and laboratory work in Panama, provided insightful comments, and edited the manuscript prior to submission. As such, all three are co-authors on this article published in *Biological Invasions*. Lastly, Dr. Leung and Dr. Torchin provided much guidance in the development and writing of the third chapter, which is intended for submission to the journal *Conservation Biology*. While assistance from all co-authors contributed to the successful completion of these three manuscripts, the work presented in this thesis is largely the result of my independent research.

Acknowledgements

I would like to acknowledge the people who have assisted with the completion of this thesis in a more or less chronological order of their contribution. First, I wish to thank both my advisors, Brian and Mark, for guidance throughout the process, particularly at times of uncertainty and stress, when I was eager to get things rolling. Their patience, advice, constructive criticism, and support were greatly appreciated. In particular, I am grateful to both of them for encouraging me to seize various opportunities as they arose throughout this thesis - there were several and it would have been a shame to pass them by. I progressively realized that success in science requires more than just hard work; a certain element of luck and the ability to generate good ideas and pursue them are key. The experience I gained from working on several projects during my time as a master student is invaluable and yielded many unexpected benefits, including collaborations with remarkable people in Panama and publications. Sandra, my fiancée, was also my third advisor. She provided relentless feedback on ideas, help with fieldwork and writing, and an invaluable companionship throughout these two years. I am ever grateful to her for so many things, including sampling crabs with me on weekends, collecting tilapia in Uganda, but above all, for her support and patience when we were apart during my eight month stay in Panama.

I would also like to thank my parents, grandmother, aunt, and brother who provided continual support and showed much interest in my thesis although they were sometimes surprised by my enthusiasm for such a small and uncharismatic crab. My family’s visit to Panama was a real treat of which I have many good memories. I am also grateful to Jeff and Kecia, my roommates in Panama, who provided an ample

source of friendship and distractions away from the lab and sometimes laborious fieldwork. I will fondly remember our tuna fishing expeditions and the many evenings on the apartment's balcony with a Balboa in hand and "Le Palace" for entertainment. Yulang Kam was equally important in making this thesis and Panama a positive and successful experience; not only did she keep me sane in the lab [as we scrutinized 2kg fish to find every single parasite!], but she also taught me Spanish and (some) salsa dancing [my Spanish remains much better than my salsa…]. This thesis would not have been possible without her. Likewise, Carmen Schloeder provided essential assistance for the completion of this work and I am very much appreciative. Both Yulang and Carmen were instrumental in completing the research for Chapter 2, helping with field collections and lab experiments when I was in Panama and away. My biggest regret - and apology to both of them - is for not having been present to fight off the crocodiles in the Miraflores spillway.

Other people I would like to thank include members of my committee, Andrew Hendry and Lauren Chapman, for useful advice throughout this thesis; Edgar Mendoza Franco for invaluable help with parasite identifications and the opportunity to collaborate on the manuscript "New species of Diplectanum Diesing 1858 (Monogenoidea) and a new genus and species of the Dactylogyridae from the gills of Gerreid (Teleostei) fishes from Mexico and Panama" in press in *Folia Parasitologica*; Arthur Anker for moral support, "scientific counseling", and introducing me to the wonderful world of snapping shrimp and Photoshop; Angel Aguirre from the STRI Library for facilitating access to obscure papers; Aileen Terrero, Alejandra Jaramillo, Sr. Anibal, Carlitos, Nacho, and many other people at STRI who offered their help an perhaps innocently agreed to look

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General Introduction

Species introductions can cause considerable ecological and economic harm (Wilcove et al. 1998; Mack et al. 2000), and their threat to global biodiversity is ranked alongside major concerns such as habitat loss and climate change (Chapin et al. 2000; Kokko and Lopez-Sepulcre 2006). Once established, non-native populations can dominate invaded communities, numerically or functionally, and generate widespread impacts by altering ecosystem processes, disrupting economic activities, and affecting human health (Elton 1958; Mack et al. 2000). In past decades, the problem of species transfers has intensified due to the globalization of the world's economies and a dramatic increase in international trade (Jenkins 1996; Meyerson and Mooney 2007). In response to this growing concern, much effort in ecology has focused on documenting the effects of introduced species (e.g. Vitousek 1990; Grosholz 2002b) and studying their population biology in order to better understand the mechanisms driving biological invasions (e.g. Keane and Crawley 2002; Shea and Chesson 2002).

While there has been considerable progress in this field, more proactive research is needed to make use of these advances and apply them towards improving management strategies (Allendorf and Lundquist 2003; Simberloff et al. 2005; Hulme 2006). Solutions to reduce the impacts of invasive species are desperately needed since current policies largely fail to prevent new introductions from occurring (Mack et al. 2000; Ricciardi 2003) and the rate of biological invasions is predicted to increase in the near future (Levine and D'Antonio 2003). In fact, some authors argue that the management of invasive species may be the biggest challenge facing conservation biologists in the next few decades (Allendorf and Lundquist 2003).

Once prevention is no longer an option, a growing number of authors argue that eradicating exotic species at the outset of an invasion is the next best management strategy (Coblentz 1990; Myers et al. 2000; Rejmánek and Pitcairn 2002; Simberloff 2003b; Crooks 2005), since the costs of treating a few newcomers is usually trivial compared to the costs and efforts of delayed management after a population has established and spread (Mack et al. 2000; Byers et al. 2002). Indeed, early eradication efforts are typically more environmentally sound and ethically acceptable than long-term control, which can require prolonged use of unsafe measures and generate many more casualties than a brief eradication campaign (Clout and Veitch 2002). Past examples of successful eradications illustrate the benefits of this powerful conservation tool (Myers et al. 2000; Simberloff 2003a); however, successes are largely restricted to islands and further development is required to broaden the applicability of this management strategy (Donlan et al. 2003). The overall objective of this thesis is thus to build upon the case study of an important marine invader in the Panama Canal and provide general guidelines to facilitate rapid response efforts for eradicating newly discovered exotic species.

Study system

Biological invasions are particularly prevalent in marine and estuarine environments due to shipping activities, which have been identified as a major mechanism of species transfers to new biogeographic regions (Carlton and Geller 1993; Ruiz et al. 1997; Cohen and Carlton 1998). Ships move organisms generally associated with ballast water and hull fouling as an unintended result of normal operations (Carlton 1985; Ruiz et al. 2000b). As such, ships have contributed strongly to the cumulative number of invasions in coastal habitats, and are largely responsible for the dramatic increase in the recent rates of invasions in these systems (Ruiz et al. 2000a). In the Americas, Panama has the potential to be a major center of ship-mediated species transfers due in large part to the Panama Canal, connecting the Pacific and the Atlantic Oceans since 1914. In addition to the extensive maritime traffic through the Canal [more than 12,000 ship transits on average between 2000 and 2004 (Ruiz et al. 2006)], Panama's bi-coastal ports serve as hubs for international shipping, elevating the potential for invasions (Ruiz et al. 2006).

Recently, in February 2007, I discovered an established population of an introduced mud crab, *Rhithropanopeus harrisii*, in the waters of the Panama Canal (Roche and Torchin 2007). *R. harrisii* is a small estuarine crab, which can travel long distances on the hull fouling or in the ballast water of ships (Turoboyski 1973; Carlton 1985) and can tolerate a wide range of salinities and temperatures (Christiansen and Costlow 1975; Grosholz and Ruiz 1995). Unlike the majority of marine and estuarine species, it has relatively closed recruitment dynamics which limit dispersal but enable populations to increase locally (Cronin 1982; Cronin and Forward 1986). All of these characteristics have contributed to make it a prolific world-wide invader (Williams 1984; Peterson et al. 2003). Given the potential for shipping in Panama to act as an important dispersal vector of this species at the global scale, the goals of this thesis were to (1) document the discovery of *R. harrisii* in Panama and review its invasion history globally, (2) determine its distribution and potential for spread in the Panama Canal, and (3) use this case study to formulate a general framework for evaluating the possibility of eradicating novel invaders.

Chapter synopsis

Chapter one reports evidence of an established, reproducing population of *R. harrisii* in the Miraflores Third Lock Lake, an area designated for future expansion of the Panama Canal. Despite a well documented history of introductions in Europe and North America (e.g. Christiansen 1969; Williams 1984), reports of *R. harrisii*'s recent introductions are scattered in the scientific literature, weakening its importance as an increasingly widespread invader; thus, I review *R. harrisii*'s invasion history to date and the impacts it is reported to have had in it introduced range. I also highlight the historical importance of the Miraflores Third Lock Lake for biological invasions in Panama and the potential for its pending modification to alter the ecology of *R. harrisii* in the Canal, with consequences for dispersal at a much broader scale.

In chapter two, I evaluate the potential for the spread and eradication of *R. harrisii* in the Panama Canal. This chapter presents a rapid assessment of *R. harrisii*'s distribution across the entire Panama Canal using a standardized quantitative approach. I used the same methodology to monitor the population discovered initially in order to evaluate the crab's abundance and demographics. I also assessed the potential for the crab to spread in the Canal with laboratory experiments based on salinity, since this environmental characteristic is known to be the most important in limiting the distribution of *R. harrisii* at the local scale (Costlow et al. 1966; Cronin 1982). The rational behind the survey and experiments in this chapter were the stepping stone to develop practical guidelines for evaluating the potential to eradicate newly discovered exotic species in general.

Chapter three builds on the case study of *R. harrisii* outlined in chapters one and two to formulate an analytical framework for assessing the feasibility and desirability of eradicating novel invaders. By integrating basic arguments across the invasion biology and the general environmental management literature, I attempt to develop a framework which addresses major challenges of responding to new invasions: limited information about novel invaders (e.g., Byers et al. 2002; Ricciardi 2003), limited time for management (e.g., Simberloff 2003b; Anderson 2005), and limited communication between scientists and decision-makers (e.g., Temple 1990; Donlan et al. 2003; Bossenbroek et al. 2005). At the heart of this framework, I propose a toolbox for conducting a rapid risk analysis. In doing so, I evaluate the utility of recent research in invasion biology for rapid response in order to formulate practical recommendations which can help decision-making under time-constraints and uncertainty. The underlying purpose of this framework was to provide guidance for evaluating the feasibility of eradicating *R. harrisii* in Panama, but it was developed to contend with general challenges of rapid response which extend beyond this case study (limited information, time, and communication), in order to facilitate early eradication efforts across a range of different systems.

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Chapter 1. Established population of the North American Harris mud crab, *Rhithropanopeus harrisii* (Gould 1841) (Crustacea: Brachyura: Xanthidae), in the Panama Canal

Roche DG and Torchin ME (2007) Aquatic Invasions 2: 155-161

In this chapter, I report the discovery of an established population of a globally widespread invader, the North American Harris mud crab (*Rhithropanopeus harrisii*), in the Miraflores Third Lock Lake, adjacent to the Panama Canal. I briefly review the crab's invasion history and available evidence of impacts in its introduced range. I also highlight the importance of *R. harrisii*'s presence in the Canal since this important route of maritime traffic may serve as a source for secondary introductions of the crab elsewhere in the world.

Abstract

Rhithropanopeus harrisii (Gould, 1841) is an estuarine crab native to the East Coast of North America. This species has invaded both the West Coast of the United States and several European countries since the late 1800s where it has reportedly altered native ecosystems. This crab can tolerate a broad range of salinities and temperatures, which probably contributes to its success as an invader. In 1969, five specimens of *R. harrisii* were recorded in Panama, but subsequent surveys suggest it was not established. Here, evidence is reported of an established, reproducing population of *R. harrisii* in the Panama Canal. The crab's entire distribution within this waterway remains to be determined and potential changes in its ecology, especially given the imminent expansion of the Canal, need to be evaluated.

Introduction

Alongside the notorious green crab, *Carcinus maenas* (Linnaeus, 1758), and the Chinese mitten crab, *Eriocheir sinensis* (H. Milne Edwards, 1853), the Harris mud crab, *Rhithropanopeus harrisii* (Gould, 1841), is among the most widely distributed brachyuran invaders worldwide (Grosholz and Ruiz 1996, Pagad 2007 pers. comm.). In its native range, this species inhabits fresh to brackish waters along the East Coast of North America from New Brunswick, Canada, to Veracruz, Gulf of Mexico (Williams 1984). Although recent publications cite a record of this species from Brazil, (Morgan et al. 1988, Abele and Kim 1989, Gonçalves et al. 1995, Zaitsev and Öztürk 2001), the specimens originally reported by Williams (1965) were later reexamined and reclassified as another species by the same author (Williams 1984).

Rhithropanopeus harrisii is a small (< 26 mm carapace width), euryhaline crab typically associated with sheltered estuarine habitats. This crab usually inhabits oyster reefs, woody debris and shoreline vegetation and it occurs to a depth of approximately 37 m (Turoboyski 1973, Williams 1984, Petersen 2006). Currently, *R. harrisii* is reported as a nonindigenous species in 21 different countries (Annex). Initial reports of introduction in the Americas (Jones 1940) and in Europe (Wolff 1954) date back to the first half of the 20th century. It is noteworthy that Maitland (1874) initially described this crab as a native species, *Pilumnus tridentatus*, in the Netherlands and that the synonym *Rhithropanopeus harrisii tridentatus* has often been used to designate this species in Europe (Buitendijk and Holthuis 1949, Christiansen 1969).

In the United States, *R. harrisii* invaded San Francisco Bay between the late 1800's and the early 1900's presumably via translocations of the Atlantic oyster, *Crassostrea virginica* (Gmelin, 1791), from Chesapeake Bay in an attempt to initiate commercial oyster aquaculture (Cohen and Carlton 1995, Ruiz et al. 1997, Wasson et al. 2001). Since, *R. harrisii* has spread along the coast of California and Oregon, reaching several bays and rivers where populations persist (Petersen 2006). Interestingly, the crab also appears to have expanded its native coastal range inland and has successfully invaded freshwater reservoirs in Texas, where it has established reproducing populations (Howells 2001, Keith 2007 pers. comm.).

While no studies were found quantifying the impact of *R. harrisii* on the communities where it is introduced, there is evidence that it may alter species interactions and cause some economic damage. In Europe and on the West Coast of

North America, it competes with native crabs (Marchand and Saudray 1971, Jazdzewski and Konopacka 1993, Cohen and Carlton 1995) as well as benthophagous fishes (Zaitsev and Öztürk 2001) and alters food webs by acting as a predator and serving as prey of native species (Turoboyski 1973, Cohen and Carlton 1995, Zaitsev and Öztürk 2001). Furthermore, in the Caspian Sea, where it has reached very high densities, the crab is responsible for pipe fouling and causes economic loss to fishermen by spoiling fishes in gill nets (Zaitsev and Öztürk 2001). In Texas, *R. harrisii* has also caused fouling problems in intake pipes and may have displaced a native species of freshwater crayfish (Keith 2007 pers. comm.). Finally, this species can host white spot baculoviruses, making it a potential vector for crustacean diseases (Payen and Bonami 1979).

Abele and Kim (1989) reported five specimens (one male, three non-ovigerous females and one juvenile) of *R. harrisii* from Panama, collected in the Pedro Miguel Locks in 1969 (Figure 1). According to more recent studies, however, the crab was not considered to be established (Cohen 2006). The purpose of this study is to report a reproducing population of *R. harrisii* in the Miraflores Third Lock Lake on the Pacific side of the Panama Canal.

Results and Discussion

Collection Site

Rhithropanopeus harrisii was discovered on the southwestern shore of the Miraflores Third Lock Lake on February 6, 2007 (8°58'45" N, 79°35'04" W - Figure 2). The crab was common under stones and on woody debris along the shore. One of the authors (MET) immediately recognized this species as *R. harrisii*. Identification was confirmed with photographs and live specimens by A Anker, JH Christy and LG Abele.

The general habitat features of the Miraflores Third Lock Lake were first described by Rubinoff and Rubinoff (1968) in a study reporting the occurrence of an Atlantic fish species crossing the Panama Canal and successfully establishing on the Pacific Coast. McCosker and Dawson (1975) also recognized the distinctiveness of this lake, which they characterized as "a unique Pacific habitat which supports a mixed biota of Atlantic and Pacific organisms". The Miraflores Third Lock project was initiated by the Panama Canal Company in the early 1940's in order to build an auxiliary set of locks. However, these efforts were rapidly abandoned in 1943. The resulting excavation, 1,340 m long by 90-150 m wide and 18-26 m deep, was filled with Pacific sea water and fresh-water runoff from the Canal (Rubinoff and Rubinoff 1968). The lake was initially connected to the Pacific Ocean below the Miraflores Lock via five metal culverts and a drainage stream two to three meters wide (McCosker and Dawson 1975; Figures 1 and 2).

Currently, the drainage stream no longer exists, and the condition of the underground culverts is uncertain. According to Rubinoff and Rubinoff (1968) and McCosker and Dawson (1975), the lake experiences very small tidal oscillations, but Pacific water may enter several times a month during exceptionally high spring tides. In contrast to the higher salinity measurements taken by these authors at the time, salinities of 0 ppt at the surface and 4 ppt at 0.75 m depth were recorded along the southwestern shore of the Lake, where crabs were collected (Figure 2).

Specimens collected

On 2 March 2007, 88 crabs were collected within an hour of examining the shoreline of the Miraflores Third Lock Lake. These were measured, sexed and preserved in 95% ethanol (Figure 3). Of the 88 crabs collected, 45 were males (avg cw = 9.3 mm, range cw = 3.1-17.7 mm), 19 were non-ovigerous females (avg cw = 8.0 mm, range cw = 4.9-10.9 mm), 16 were ovigerous females (avg cw = 9.3 mm, range cw = 5.8-12.8 mm) and eight were juveniles of undetermined sex (< 2.5 mm cw; Figure 4 a-d). Ovigerous females with late-stage eggs were kept alive to observe larvae. Within one week of collection, six females released their zoeae. Voucher specimens of adult crabs were deposited at the University of Panama (CRU-07-01) and at the National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM 1111073).

Vectors of introduction

Ship activity through the Canal is a likely mechanism of introduction of *R. harrisii* to Panama, either via hull fouling or release of ballast water. Vectors responsible for other introductions of the crab, such as aquaculture on the west coast of the U.S. (Ruiz et al. 2000; Wasson et al. 2001), are considerably less probable. The Panama Canal is a major center of shipping activity in the Americas, allowing transit of approximately 13 to 14 thousand vessels per year from around the globe (Ruiz et al. 2006). In Panama, little is known about ballast water exchange on either side of the waterway. However, sightings of ships discharging bilge and ballast within the Canal have been documented, despite regulations of the Autoridad del Canal de Panama prohibiting such activities (Cohen 2006). Carlton (1985) suggests that ballast water is a probable transport mechanism of *R. harrisii* into the Canal. However, boats do not transit via the Miraflores Third Lock Lake; thus, crabs (either adults or larvae) likely entered from adjacent Canal waters, perhaps during a spring tide flooding event.

Rhithropanopeus harrisii has an extensive history as a world-wide invader and its potential impacts where it is introduced warrant further evaluation of its distribution throughout the entire Panama Canal. Currently *R. harrisii* is established in a semi-contained lake, which is designated as an area for future expansion of the Canal (ACP 2006). Further research will determine the probability that imminent changes will promote its spread as well as identify the possibility of eradicating localized populations within Panama.

Conclusion

A population of *R. harrisii* is now established in Panama, almost four decades after the first specimens were observed in the Pedro Miguel Locks. This population may have established after a different introduction event or perhaps from a larger population of this species that has remained undetected in the Canal. Given the many world-wide locations where *R. harrisii* has established, the source population of this invasion remains to be determined with the use of molecular genetics. In view of the impending expansion of the Panama Canal through the Miraflores Third Lock Lake, it is crucial to consider the potential spread of this crab and the possibility for its eradication.

Acknowledgements

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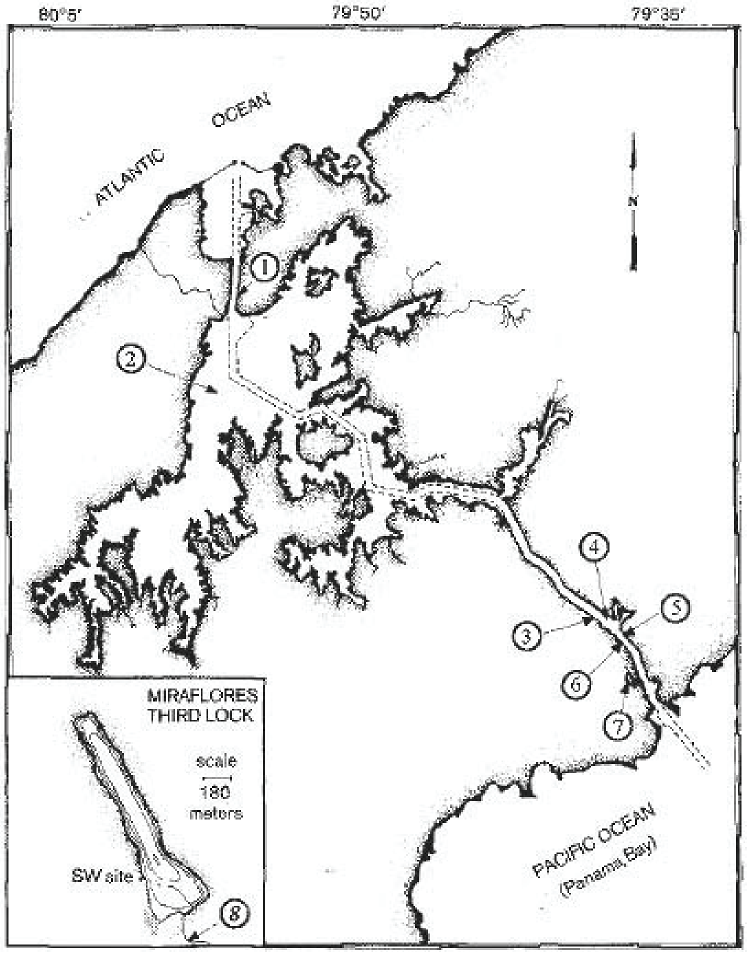

Figure 1. Map of the Panama Canal showing the location of the Miraflores Third Lock Lake (modified from McCosker and Dawson 1975). From the Pacific coast to the Atlantic coast: (1) Gatun Locks, (2) Gatun Lake, (3) Pedro Miguel Locks, (4) Miraflores Lake, (5) Miraflores Locks, (6) Miraflores Spillway; (7) Miraflores Third Lock Lake, (8) drainage stream present in 1971.

Figure 2. Satellite image (Google Earth™ mapping service 2007) of the collection site where *Rhithropanopeus harrisii* was found in Panama – the Miraflores Third Lock Lake adjacent to the Panama Canal: (1) Miraflores Third Lock Lake, (2) location of the underground culverts connecting the Lake to the Pacific Ocean, (3) Miraflores Locks, (4) fresh water lake, (5) Miraflores Lake, (6) Pacific entrance to the Panama Canal, (∗) site where crabs were collected

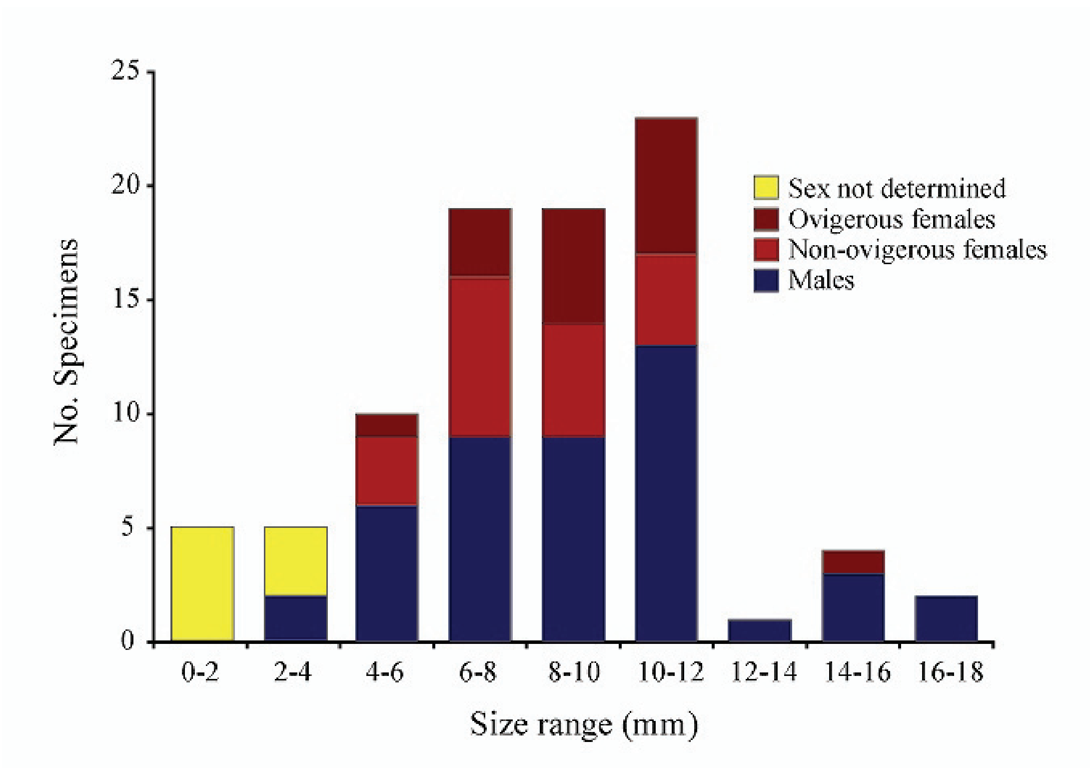

Figure 3. Size distribution of *Rhithropanopeus harrisii* collected in the Miraflores Third Lock Lake, Panama, on 2 March 2007.

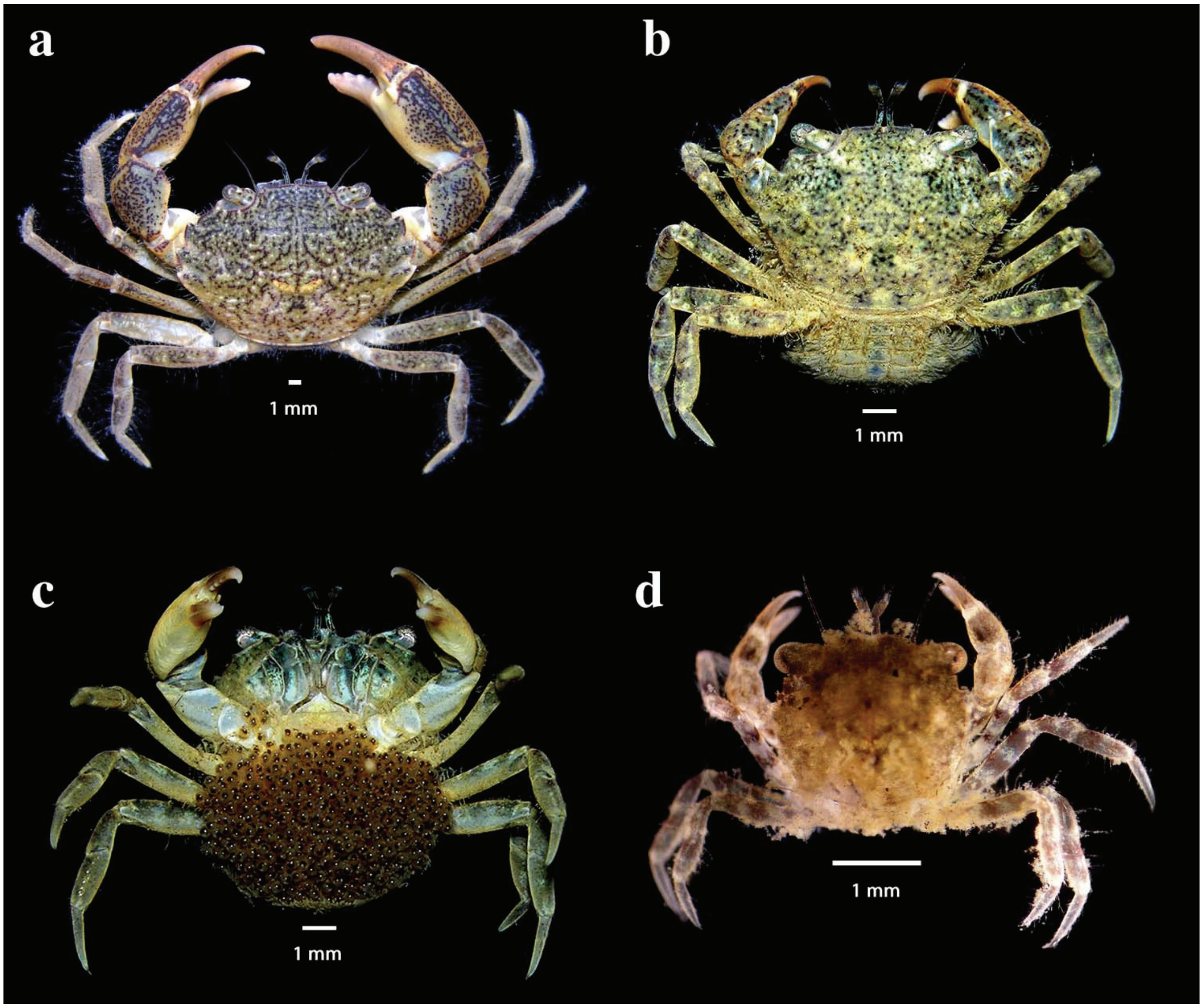

Figure 4. *Rhithropanopeus harrisii* collected in the Miraflores Third Lock Lake adjacent to the Panama Canal: (a) male specimen, 17.1 mm carapace width, dorsal view (photo by A. Anker); (b) ovigerous female specimen, 7.8 mm carapace width, dorsal view and (c) ventral view; (d) juvenile, 2.25 mm carapace width, dorsal view (photos by D.G. Roche).

Appendix

List of the countries where *Rhithropanopeus harrisii* has been reported as a nonindigenous species.

Country	Ocean / Sea	First report	Reference
Netherlands	North Sea	1874	Maitland 1874
Germany	Baltic Sea	1936	Schubert 1936
Ukraine	Black Sea	1936	Makarov 1939
	Azov Sea	1948	Zaitsev and Öztürk 2001
United States	NE Pacific	1937	Jones 1940
Russia	Black Sea	late 1800s	Marchand and Saudray 1971
	Azov Sea	1948	Zaitsev and Öztürk 2001
	Caspian Sea	1959	Gadzhiev 1963
Bulgaria	Black Sea	1948	Marchand and Saudray 1971
Romania	Black Sea	1951	Băcescu 1967
Poland	Baltic Sea	1951	Demel 1953
Denmark	Baltic Sea	1953	Wolff 1954
France	NE Atlantic	1955	Saudray 1956
	Mediterranean	2000	Noël 2001
Iran	Caspian Sea	---	Zaitsev and Öztürk 2001
Azerbaijan	Caspian Sea	1961	Gadzhiev 1963
Turkmenistan	Caspian Sea	1961	Zaitsev and Öztürk 2001
Panama	Panama Canal	1969	Abele and Kim 1989
Kazakhstan	Aral Sea	1971	Andreyev and Andreyeva 1988
	Caspian Sea	---	Zaitsev and Öztürk 2001
Uzbekistan	Aral Sea	1971	Andreyev and Andreyeva 1988
Spain	NE Atlantic	1990	Mariscal et al. 1991
Portugal	NE Atlantic	1991	Goncalves et al. 1995
Italy	Adriatic Sea	1994	Mizzan and Zanella 1996
England	NE Atlantic	1996	Eno et al. 1997
Tunisia	Mediterranean	2003	Ben Souissi et al. 2004

Chapter 2. Localized invasion of the North American Harris mud crab, *Rhithropanopeus harrisii*, in the Panama Canal: implications for eradication and spread

Roche DG, Torchin ME, Leung B and Binning SA (2008) Biological Invasions DOI: 10.1007/s10530-008-9310-6

In the first chapter, I reported the presence of *Rhithropanopeus harrisii* in the Panama Canal. I also emphasized the potential for ship traffic to serve as a dispersal vector of this species at the global scale, and the need to assess the possibility of eradicating *R. harrisii* in Panama. Here, I evaluate the crab's distribution and population demographics across the Panama Canal and its potential for spread to determine whether eradication is warranted.

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 of 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 indicate that populations of *R. harrisii* are currently limited to two manmade lagoons which will soon be modified as a result of the impending expansion of 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.

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 2002a). Indeed, aquatic invasions appear to be increasing at an accelerating pace (Cohen and Carlton 1998; Ruiz et al. 2000a), 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 2003a). 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. 2001; 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 (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 1800's and is now established in 21 different countries on the European and the American continents (Roche and Torchin 2007), and most recently in 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 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 degrees 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 1940's (Fig. 1b; Rubinoff and Rubinoff 1968; Roche and Torchin 2007). During the course of this study, the salinity in the Southern 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 2006b; Fig. 1b). Already, the Southern Lagoon was partially drained into the Pacific approach to the Canal in 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. 8L) 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 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™ 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 ≥ 5.5mm and juvenile crabs with a carapace width ≤4.5mm (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 0-35‰. 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 100ml 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 10am and 12pm 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 native crabs, none contained *R. harrisii* (Table 1). Although this species 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 (8.41mm, range 4.58-18.89mm) compared to the Southern Lagoon (8.16mm, range 4.53-17.96mm) (t_{1459}= -2.28, $p<0.05$).

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 hours 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 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 mean abundance 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. Since the Panama Canal is an international hub for global shipping, the invasion of *R. harrisii* in the Canal may not only be Panama's problem but rather a global problem pending future invasions from this potential source. 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. This may be a small price to pay to avoid possible spread of the crab in Panama and elsewhere in the world.

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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	N08º58'37" W79 º35'02"	05-Jun-07	2	N
		10-Sept-07	4	N
		21-Feb-08	8	N
2. Southern Lagoon	N08º59'03" W79º35'18"	05-Jun-07	2	Y
		01-Aug-07	8	Y
3. Northern Lagoon	N08º59'38" W79º35'41"	05-Jun-07	1	Y
		01-Aug-07	6	Y
4. Culvert Miraflores Lake	N08°59'45" W79°35'42"	14_Jan-08	3	Y
		21-Feb-08	2	Y
		24-Mar-08	2	Y
		28-Apr-08	2	Y
5. Miraflores Lake	N09º00'28" W79º36'05"	05-Jun-07	4	N
		11-Sept-07	6	N
		07-Dec-07	18	N
6. Miraflores spillway	N08º59'41" W79º35'06"	10-Oct-07	12	N
7. Gatun Lake – Gamboa	N09º07'12" W79º42'58"	7-Nov-07	5	N
8. Gatun Lake – BCI	N09º09'55" W79º50'03"	7-Nov-07	10	N
9. Gatun Lake at Gatun Locks	N09º15'43" W79º55'24"	08-Jan-08	21	N
10. Gatun Third Lock Lagoon	N09º16'52" W79º54'49"	20-Jan-08	6	N
11. Gatun spillway/French Canal	N09º15'51" W79º56'01"	20-Jan-08	7	N
12. Atlantic approach	N09º17'30" W79º54'54"	20-Feb-08	5	N

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

Site (n=measurements)	Date	Salinity (‰)	Temp (ºC)	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	32.1E03	79.7

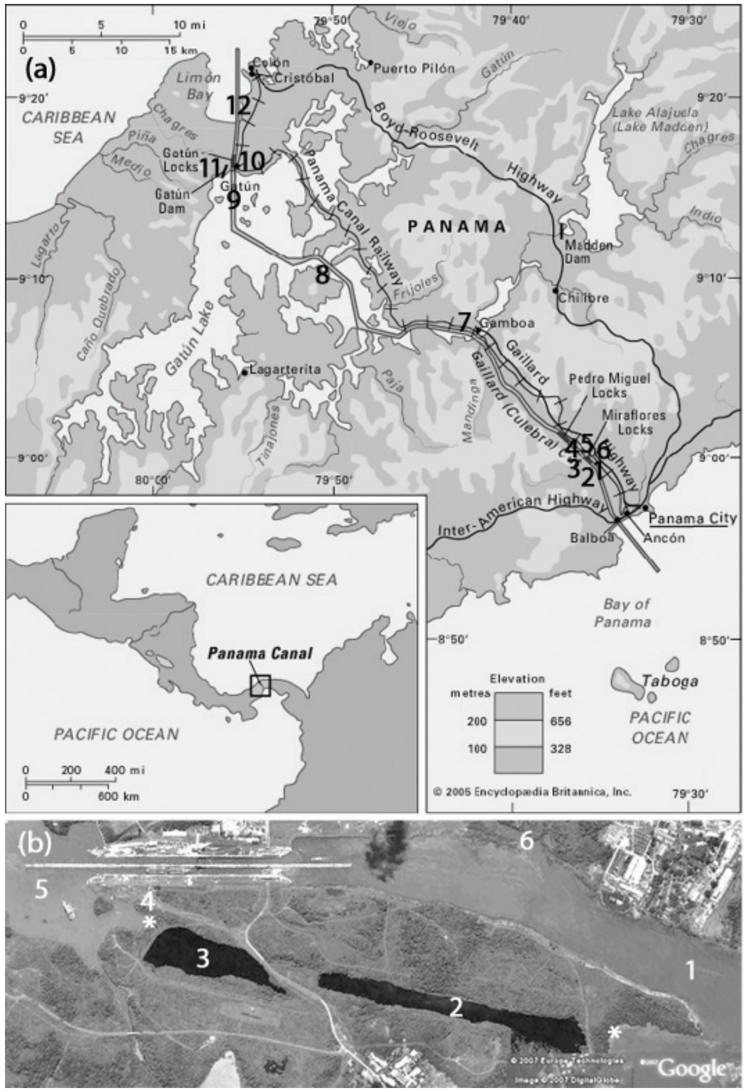

Figure 1. (a) Map of the Panama Canal with sites surveyed for *R. harrisii*: 1. Pacific approach - 2. Southern Lagoon - 3. Northern Lagoon - 4. Culverts at the Miraflores Lake - 5. Miraflores Lake - 6. Miraflores spillway - 7. Gatun Lake - Gamboa - 8. Gatun Lake - Barro Colorado Island - 9. Gatun Lake - 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) – (*) indicate sites where water will be drained out of the lagoons

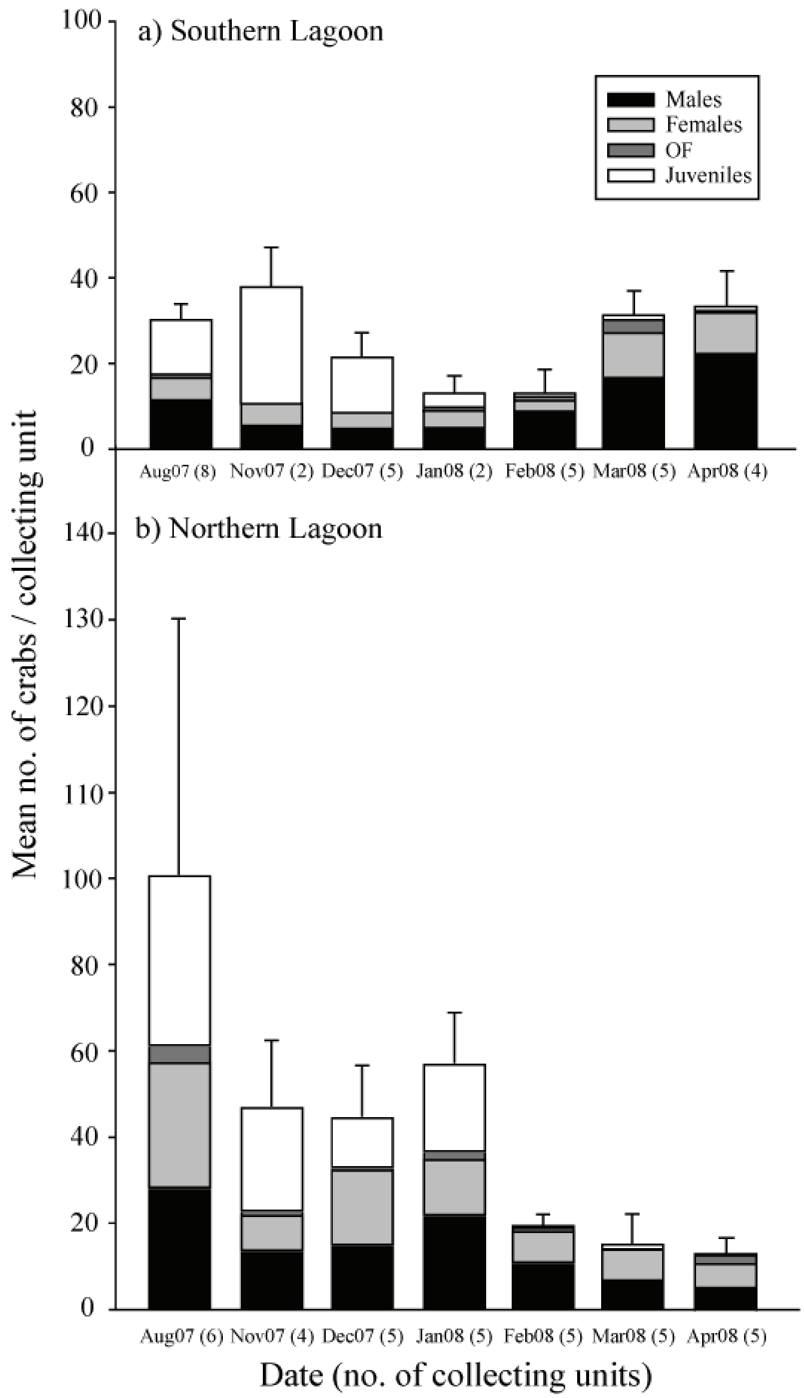

Figure 2. Mean number of *R. harrisii* per life-stage per collecting unit in (a) the Southern Lagoon and (b) the Northern Lagoon, between August 2007 and April 2008. The number of collecting units analyzed per month is indicated in parenthesis; error bars are SE for the mean total crabs per collecting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

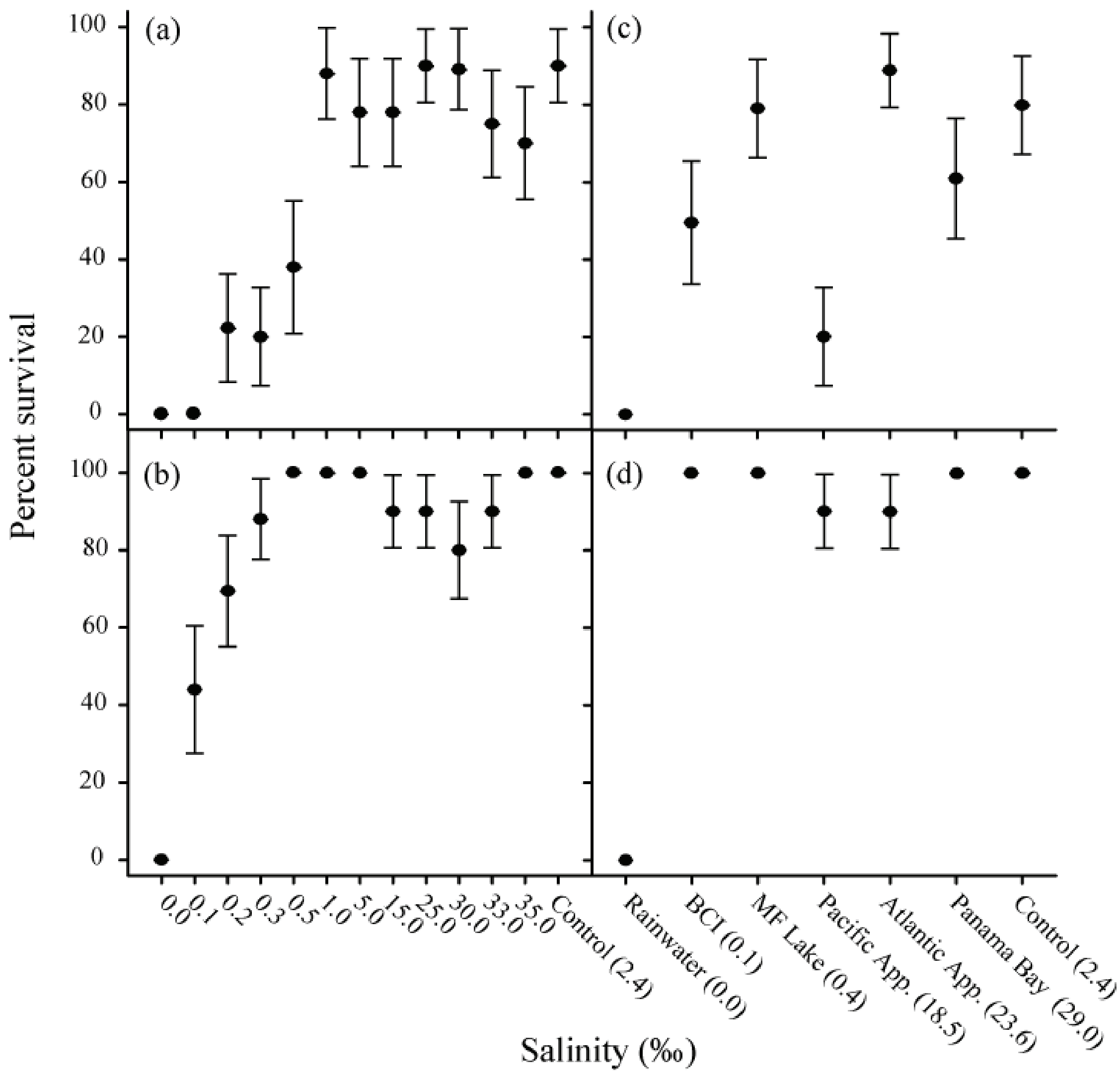

Figure 3. Survival of juvenile (top) and adult (bottom) *R. harrisii* subjected to 30 days of treatments of different salinities in water (a,b) artificially prepared and (c,d) collected in the field. Error bars are SE for a binomial distribution

Appendix

Measurements of surface salinity (parts per thousand) at different sites along the Panama Canal (modified from Cohen 2006). Abbreviations: MF=Miraflores, SL=Southern Lagoon, NL=Northern Lagoon. *=values estimated by Cohen (2006), **=in sump areas after dewatering,†=measured with a refractometer, ††=at low tide, §=at the culvert connection with the NL. References: (1) Hildebrand 1939, (2) Menzies 1968, (3) Abele 1972, (4) Dawson 1973, (5) Jones & Dawson (1973), (6) Jones & Rützler 1975, (7) this study

Date	Pacific ap-proach	SL	NL	MF spill-way	MF Lower Locks	MF Upper Locks	MF Lake	Pedro Miguel Locks	Gatun Lake	Gatun Upper Locks	Gatun Lower Locks	Gatun TLL	Gatun spill-way	Atlantic ap-proach	Ref
Jun 1935										0	10-16			18-20	1
< 1939	16-20						0.1-3.0		≤0.02					18-20	1
≤ 1968	30*				26*		1.0*	0.0*	0.0*		24*			28.5*	2
Feb 1969								0.0-0.4							3
Jan 1972						20**									4
Apr 1972	27					1-3*	0*	0*	0*	0.1*	5-11*			17*	5
Nov 1972	23*				14-15	3*	0-1*	0*	0*	0.2-0.3*	6-8*			10-17*	5
Mar 1974									0.2	0.02-0.8					6
Jun 2007		4†	0†												7
Jul 2007		3†	0†												7
Aug 2007		3.3	0.4-0.6	0.1-3.4††			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††											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§		0.1			0.2	0.1-0.2††	14.4-24.4	7
Feb 2008	14.1-20.0	2.5-2.6	0.5				0.5§					0.2	1.5-10.5	23.3-24.5	7
Mar 2008		3.1-3.6	0.6				0.6-0.7§								7
Apr 2008		4.1-4.3	0.6				0.6§								7

Chapter 3. A balancing act: uncertainty and timely decision-making in eradicating invasive species

Intended for submission to *Conservation Biology*

In the previous chapter, I examined the possibility of eradicating *Rhithropanopeus harrisii* from the Panama Canal to avoid the potential for local spread and broader dispersal elsewhere in the world. In this third chapter, I develop a general framework, based on the case study of *R. harrisii*, to provide guidance on how to best evaluate the feasibility of a rapid response to eradicate newly discovered invaders and communicate the potential benefits of this management strategy to decision-makers.

Abstract

When prevention falls short, responding rapidly to eradicate novel invaders is often the most cost-effective way to mitigate the risk of future impacts from biological invasions. Yet, rapid responses may be impeded due to uncertainty and a lack of practical guidance to determine whether an eradication effort is warranted. Here, we argue that rapid responses are hindered by limited information, time, and communication, and we formulate an analytical framework for evaluating the feasibility and desirability of early eradication by integrating arguments from the literature on invasion biology and environmental management. We apply this framework to a case study of a global invader, the Harris mud crab (*Rhithropanopeus harrisii*), recently discovered in the Panama Canal. Useful ideas to help manage invasive species exist, but explicit quantification of even simple models may be difficult for novel invasions. In the absence of predictive models, establishing probability thresholds to determine whether an eradication attempt is warranted can help clarify management options. Specifically, our results suggest that it is worthwhile eradicating *R. harrisii*, given a very conservative impact scenario, if the combined probability of impacts occurring and eradication being successful exceeds as little as 4.4%.

Introduction

The increasing integration of the world's economies has intensified the global spread of invasive species (Mack et al. 2000; Meyerson & Mooney 2007), which are considered a leading threat to biodiversity and cost the US almost $120 billion annually (Pimentel et al. 2005; Wilcove et al. 1998). However, recent advances in invasion biology research allow conservationists a growing opportunity to help decision-makers conduct logical, well-reasoned actions to manage invaders.

Eradication is an important tool in conservation biology as current policies cannot entirely prevent new biological invasions from occurring (Mack et al. 2000; Ricciardi 2003). After prevention, eradicating populations when they are small, at the outset of an invasion, is considered the next best management strategy (Crooks 2005; Genovesi 2007; Myers et al. 2000; Rejmánek & Pitcairn 2002; Simberloff 1997, 2003a, b). Yet, the benefits of early eradication are often not communicated to managers (Coblentz 1990; Donlan et al. 2003), creating a gap between detection and response. A major difficulty lies in the paradox of rapid response: the best opportunity for eradication is when we know the least about an invader (Crooks 2005). Therefore, uncertainty regarding the potential spread and damage by invaders often results in a tendency to "wait and see". Unfortunately, hesitation to act rapidly may prevent the best opportunity for eradication and avoiding future impacts (Crooks & Saoulé 1999; Rejmánek & Pitcairn 2002; Simberloff 2003a).

This costly inaction was the case for the "killer alga", *Caulerpa taxifolia*, introduced to the Mediterranean Sea (Meinesz 2007). The original patch detected in 1984 could likely have been eradicated, but efforts were delayed for years allowing it to spread over thousands of hectares (Simberloff 2003a). Now, more than twenty years later, we would hope that things have changed. If invasion biology is to become a policy-relevant science, communication with managers must be effective, and decisions must be timely.

Recently, the Harris mud crab, *Rhithropanopeus harrisii*, was discovered in the Panama Canal, perhaps early enough to allow eradication (Roche & Torchin 2007). *R. harrisii* is a global invader with known, albeit un-quantified impacts and its potential for spread in Panama is uncertain. Once again, managers are pressed for time and faced with the decision of whether to attempt eradication (Roche et al. 2008). Now however, with half a century of research on biological invasions (e.g., Elton 1958), science may be able to provide useful recommendations to management. Additionally, the case study of *R. harrisii* provides an opportunity to evaluate the utility of recent research in invasion biology for rapid response and to identify challenges that need to be addressed.

Aside from cost, we argue that responses to most new invasions are characterized by three major challenges: limited information about novel invaders, limited time for management, and limited communication between scientists and managers. However, we believe that the invasion biology and environmental management literature can provide the tools to address these challenges. Our objective is to integrate key arguments from these two disciplines to formulate a practical framework for assessing and communicating the potential value of rapid response to eradicate novel invaders, given limitations of information, time, and communication. In so doing, we refine previous management frameworks (e.g., Bax et al. 2001; NISC 2003) and provide a step-by-step toolbox to inform rapid risk analysis for early eradication, which we apply to *R. harrisii* in the Panama Canal.

***Rhithropanopeus harrisii* in the Panama Canal**

Rhithropanopeus harrisii is native to the Atlantic and Gulf Coasts of North America, but established populations now occur in almost 20 countries in Europe, on the West Coast of the United States, in Texas, and most recently in Panama and Japan (GISD 2008). Anecdotal reports indicate that the crab can reach high densities, alter food webs, and compete with native species. Additionally, it has been reported to foul pipe systems and spoil catches of fish (Roche & Torchin 2007). Recently, fouling of the cooling system in a nuclear power plant in Glen Rose, Texas, compelled managers to hire a consulting firm to control *R. harrisii* (G. Hildebrand, pers. comm.). The presence of the crab in Panama is thus of particular concern given not only its potential to affect biodiversity and infrastructure in the Canal itself, but also high amounts of shipping traffic which may lead to secondary introductions elsewhere in the world (see Hayes & Sliwa 2003). Given impending plans to expand the Canal at the site of *R. harrisii*'s discovery, the decision to attempt eradication is highly time dependent (Roche et al. 2008).

Eradication Framework

Below, we highlight each step of the framework (Fig 1), the methods to achieve these steps, and potential challenges. We further illustrate each component by relating them to our case study of *R. harrisii* and exemplify practical applications of our framework to a real life situation.

Monitoring, early detection, and authoritative identification (steps 1-2)

As the first step, we need to determine whether and where an invasion has occurred. Monitoring facilitates eradication efforts through early detection of exotic species (Anderson 2005; Crooks 2005), improving the time- and cost-effectiveness of responses to potential invaders (Meinesz 2007; Simberloff 2003a). While structured scientific surveys and chance reports from individuals are still central to monitoring (Meinesz 2007), current research recognizes that time and resources limit the extent of surveillance efforts. Thus, researchers recommend targeting likely points of entry, vulnerable areas, and species of particular concern (Genovesi 2007; Meinesz 2007; NISC 2003), and increasing available effort by involving the general public and citizen scientists (Delaney et al. 2008; Fore et al. 2001). Technology can also aid in minimizing the limitations in information/expertise and time: recent innovations include molecular tools (Darling & Blum 2007), and the use of digital photography, online data bases, and email for rapid help from experts to confirm the identity of new invaders (FICMNEW 2003; see Hewitt & Martin 2001). Taken together, these advances in conjunction with traditional techniques represent our best current possibility for early detection.

Case study

Based on the targeted monitoring approach, we recently surveyed the Miraflores Third Lock Lagoon, adjacent to the Panama Canal. We chose this particular site due to its history as a habitat prone to invasions (e.g., McCosker & Dawson 1975) and its designation for future expansion of the Canal. A previous report of *R. harrisii* in the Canal (Able and Kim 1989) and our experience with decapod crustaceans helped to discover an established population in the lagoon in

February 2007 (Roche & Torchin 2007). This discovery exemplifies the necessity of taxonomic knowledge for identifying introduced species, as *R. harrisii* belongs to a very cryptic family, the Xanthidae, several species of which are native to Panama. We further confirmed the identity of the crab with taxonomic experts (see Roche & Torchin 2007).

Survey (step 3)

Next, a survey of an exotic species' distribution and abundance will provide the necessary baseline information to document an invasion and inform managers whether remedial action is possible. Stohlgren and Schnase (2006) offer the best practical guidelines for increasing the efficacy of a survey after an exotic species is discovered. They suggest iterative sampling using a subjective selection of sites based on the affinity of a species for particular habitats. Much like monitoring, post-detection surveys should avoid complete randomness as they are often constrained by costs and the patchy distribution of emergent species (Hewitt & Martin 2001; Stohlgren & Schnase 2006).

Case study

Consistent with the idea of non-random search, we chose key sites to survey in the Canal based on our assessment of habitat suitability for *R. harrisii*. We focused on salinity since it is the most important factor limiting the crab's distribution at the local scale (Costlow et al. 1966; Cronin 1982; Turoboyski 1973). Additionally, we sampled areas of particular concern (adjacent to the site of discovery) more extensively. We used standardized collecting units, which provided substrate for colonization similar to settlement plates (Roche et al. 2008). These collecting units best fulfilled the criteria of a good surveying tool: rapidly applicable, technically accessible, cost-effective, and accurate (Darling & Blum 2007). Our findings indicated that *R. harrisii* was restricted to two manmade lagoons designated for the expansion of the Canal (Roche et al. 2008).

Despite our desire for rapidity, the entire survey across the Canal took twelve months to complete (Roche et al. 2008). However, we initiated the survey at locations close to the site of *R. harrisii*'s discovery. Although new populations may have been discovered later, initial data suggesting the crab's containment allowed the Panama Canal Authority (ACP) the option to eradicate localized populations without further delay. Given our time constraints, we also began the analysis of subsequent steps of the framework before the completion of the survey.

Risk analysis (steps 4-5)

Although the benefits of rapid response are known to ecologists (Byers et al. 2002; Rejmánek & Pitcairn 2002; Simberloff 2003b), managers are less likely to adopt this approach without tangible arguments, given the large degree of uncertainty typically associated with the threat of new invasions. Thus, communication is critical and risk analysis can provide a quantitative evaluation for communicating different management options under uncertainty (Leung et al. 2002). In its simplest form, risk analysis is a two step process; risk assessment (step 4, Fig 1) to identify the likelihood and severity of adverse effects, and risk management (step 5, Fig 1) to evaluate and select methods of reducing risk.

Previous studies have employed this approach and developed guidelines to facilitate the management of invasive species (e.g., Bax et al. 2001; FICMNEW 2003; NISC 2003; Stohlgren & Schnase 2006). Yet, despite important contributions, the practical use of these frameworks may be limited for rapid response as they require extensive information gathering. Previous guidelines highlight all the information that is desirable, but what is most needed is an analysis of available approaches to allow rapid decisions, given the limited data that characterize most new invasions (Byers et al. 2002; Ricciardi 2003) and the limited time available for eradication (Anderson 2005; Simberloff 2003b). Therefore, we synthesize major ideas from the invasion biology and environmental management literature to address these problems, and we put them in the context of rapid response and eradication, highlighting *R. harrisii* as an example.

Establishment / Spread (step 4-A)

Much of the current literature in invasion biology focuses on predicting establishment and spread. Below, we summarize these approaches in the context of rapid risk assessment (ranked by information requirements in Fig. 1 - from least to greatest).

To successfully establish/spread, exotic species must get to new areas in sufficient numbers and survive. Current methods of predicting establishment and spread rely on estimating the number of arrivals (propagule pressure) or survival ability as predicted by species traits or environmental conditions. Propagule pressure is a central factor in determining whether an exotic species will successfully establish

(Kolar & Lodge 2001; Lockwood et al. 2005; Williamson 1996) and can be used to build quantitative spread models (e.g., Leung et al. 2004). Additionally, traits of novel species can be compared with those of known invaders to assess the risk of invasion (Keller et al. 2007; Kolar & Lodge 2001; e.g., Lodge 1993). Characteristics of recipient sites can also be used to assess habitat suitability for potential invaders using predictive models (e.g., GARP, MAXENT, Evangelista et al. 2008) or, alternatively, empirical observations based on field or experimental data (Anderson 2005; Byers et al. 2002; Mack 1996). When data permits, the interaction between habitat suitability and propagule pressure can be incorporated into a joint model (Leung & Mandrak 2007).

Ultimately, any or all of these approaches can be used, with the accuracy of predictions increasing as several methods are combined. However, the availability of information, the timeliness of a decision, and the magnitude of a problem are key factors in guiding the choice of approach for a risk assessment (see Andersen et al. 2004a).

Case study

Current ideas in invasion biology proved very useful to estimate the spread of *R. harrisii* - we combined three approaches from the list provided in Fig. 1: a comparison with traits of invasive species and an assessment of habitat suitability and of propagule pressure. We were unable to produce explicit spread models given the limited availability of published data on past invasions of *R. harrisii*, recent range expansions beyond known physiological tolerances (Keith 2008), and the difficulty of quantifying propagule pressure. These constraints exemplify the universal challenge of building predictive models for recent invasions; rather than waiting for more data, we chose to use the approaches possible and weigh the balance of evidence based on existing information.

Results suggest that *R. harrisii* has the potential to spread in the Panama Canal. First, *R. harrisii* possesses several characteristics linked with invasiveness; notably, high fecundity (Keller et al. 2007), a wide range of physiological tolerances (van der Velde et al. 1998), a broad history of invasion (Kolar & Lodge 2001), and all but one of the attributes hypothesized to characterize invasive aquatic species (Ricciardi & Rasmussen 1998). Second, salinity tolerance experiments suggested that juvenile and adult crabs can survive in a broad range of habitats in the Canal, including areas of high shipping traffic on either side of Canal locks [the Miraflores Locks] (Roche et al. 2008). Third, monthly samplings in the lagoons where *R. harrisii* is currently found indicated high densities averaging 26-44 crabs per collecting unit (approx. 8L) (Roche et al. 2008). In comparison to past and current levels, draining these habitats would considerably increase propagule pressure, a known driver of invasions, to the Canal proper. Taken together, these lines of evidence suggest a high risk that *R. harrisii* may spread in Panama, given impending plans to expand the Canal.

Impacts (step 4-B)

To quantify potential impacts of an invader, researchers argue that the best method is via a synthesis of data, either from a species invasion history (Ricciardi 2003; Ricciardi & Rasmussen 1998) or that of functionally similar organisms (Byers et al. 2002). Alternatively, when information is limiting, we suggest scenario planning. Scenario planning is a useful approach to tackle uncertainty and can allow managers to quantitatively forecast impacts where other methods are not possible. Although rarely used for biological invasions (but see Chapman et al. 2001; Rodríguez-Labajos 2006), scenario planning is common practice in business, government, and other fields of conservation (Bohensky et al. 2006; MEA 2005; Peterson et al. 2003).

Case study

We found that insufficient quantitative data exists to estimate the magnitude of impacts from *R. harrisii*'s invasion history or that of functionally similar species. Indeed, the case of *R. harrisii* is similar to the majority of invaders whereby the necessary information is lacking (Ricciardi 2003). Thus, we chose a scenario planning approach to integrate existing information about risk and illustrate a possible range of outcomes.

We limited our analysis to four economic scenarios regarding possible impacts of *R. harrisii* in the Canal, assuming that the lagoons with current populations would be drained without additional treatment. Fouling of water pipes is arguably the most detrimental impact the crab may have on economic activities due to its small size and the high densities in can reach (e.g., Zaitsev & Öztürk 2001). Fouling by *R. harrisii* in Panama could affect the functioning of the Miraflores Locks, adjacent to the lagoons where the crab is currently established. We limited the scope of our scenarios to effects on shipping and excluded other potential impacts, including consequences of increased global spread.

Currently, lockages in the Canal depend on regular maintenance to remove fouling and prevent equipment failure. This maintenance requires temporarily closing a shipping lane, which decreases the Canal's daily operational capacity from 38 to 28-26 transits (ACP 2006). Between 2000 and 2005, the ACP performed an average of five annual maintenance lane shutdowns, totaling 56 days per year (ACP 2006). Given an average transit toll of US $80,000 (ACP 2007), and the fact that the canal typically operates at full capacity, increased maintenance could result in significant losses.

In our first scenario, the crab does not establish in the Canal proper or remains at low abundance, causing no direct economic impacts. In the second, third, and fourth scenarios, the crab spreads into the Canal proper and causes fouling in the Miraflores Locks. In the second, most conservative of these last three scenarios, *R. harrisii* only causes a one-time slowdown of Canal traffic by a single ship and a loss of US $80,000. In the third scenario, accrued maintenance requires a single additional day of lane outage in the Miraflores Locks, amounting to a one-time loss of US $800,000. In the fourth scenario, one additional day of maintenance shutdown is required every year, for a total cost of US $16.8 million calculated at a 5% annual discount rate.

Eradication feasibility (step 5-A), costs and constraints (step 5-B)

The feasibility of eradication as identified in the invasion biology literature requires one of the three following conditions: (1) the invader occupies a limited distribution (Bomford & O'brien 1995; Myers et al. 2000), (2) the invader exhibits one or several susceptible pre-reproductive life-stages allowing repeated treatments to extirpate the population (Edwards & Leung 2009), or (3) a full population biology model shows that it can be driven to extinction (Courchamp & Sugihara 1999). If one of these criteria is met, the next step towards eradication is identifying the best protocol.

Without seeking to completely understand an organism's population biology, basic species information should be reviewed to avoid inefective efforts (Edwards & Leung 2009; Simberloff 2003b). For instance, manual removal may fail if targeted species reproduce asexually from fragments. It is also important to review national and regional legislation to insure that (1) the legal status of the invader is compatible with removal measures (Genovesi 2007), (2) removal methods are approved for use (Anderson 2005; Bax et al. 2002), and (3) adequate procedures are undertaken to respect protected habitats and private property rights (Stohlgren & Schnase 2006). If predetermined protocols are unavailable for a given invader, adequate eradication methods should be sought with advice from experts and tested in the laboratory and with small scale field experiments to avoid unforeseen catastrophes (Bax et al. 2001, 2002).

For any strategy employed, assessing the costs of an eradication program must consider four key elements: preliminary trials, materials and labor, collateral damage to non-target species, and indirect economic losses. Once these costs are calculated, they can be compared to the estimated impacts of the invader with a cost-benefit analysis.

Case study

Criteria listed in the current literature proved useful to assess the feasibility of eradicating *R. harrisii* from the Panama Canal. While its contained distribution facilitates extirpation, knowledge of the crab's biology was necessary to devise the most effective method of treating all life-stages. We identified the simplest protocol as a combination of steps: first killing the larvae (the smallest and most sensitive life-stage) in the lagoons by mixing the anoxic and highly sulfurous bottom layers into the water column (McCosker & Dawson 1975, pers. observ.), second, filtering the drainage through a gravel pit to remove surviving adults; and third, diverting the drainage to the Pacific Ocean to allow the tidal flushing of contaminated waters and dilute propagule pressure. Alternatively, a more expensive, but perhaps more effective protocol, would involve chemically treating the larvae in the water column with the pesticide Dimilin (McEnnulty et al. 2001), prior to filtration and drainage (Appendix).

We estimated the cost of eradicating *R. harrisii* to \$3,500 based on the first protocol, and \$64,470 based on the second protocol (Appendix). We excluded collateral damage from our calculations since the habitat in the Third Lock Lagoons will be completely modified by Canal expansion plans, and effects to non-target species would be minimized by the use of a targeted chemical treatment (Appendix). We also omitted indirect economic losses since ships do not transit through the lagoons and Canal traffic would not be affected by either eradication program.

Cost-Benefit analysis (step 6)

We suggest a minimal equation as a starting point for cost-benefit analyses;

$$E < I * PI * PE \quad (1)$$

where, for management to be worthwhile, the costs of an eradication program (E) should be lower than the magnitude of predicted impacts from an invader (I) multiplied by both the probability of impacts occurring (PI) and eradication being successful (PE). Collateral damage is not explicit in our equation, but restoration expenses can be added to the costs of the eradication program. This straightforward equation is simple, logical and likely the best way to communicate with managers the benefits of rapid response.

Case study

Although existing cost-benefit equations provided a good starting point (e.g., Bax et al. 2001), we found that even this very simple one (eqn 1) was difficult to parameterize. While the approaches employed allowed us to estimate a variety of impact scenarios (I) and eradication costs (E) for *R. harrisii*, we were unable to quantitatively express the probability of these impacts occurring (PI) and eradication being successful (PE). Beyond our case study, we deem that this challenge is likely to characterize most new invasions. However, we also believe that putting thresholds on these parameters and distinguishing between high versus low probability may often be sufficient to provide sensible recommendations to management, even in the absence of full quantification.

For instance, our risk assessment for *R. harrisii*, based on favorable invasive traits, habitat suitability, and propagule pressure, suggests that the crab may spread beyond its current range, with little support for the first scenario (see Roche et al. 2008). Thus, as a conservative lower bound of impact, we use the second scenario (slowdown of Canal traffic by a single ship worth $80,000). In this case, the first eradication protocol (cost of $3,500) is worthwhile if the combined probability of impacts and eradication exceeds 4.4% (PI*PE>0.044; eqn 1); however, the second eradication protocol is not worthwhile. Alternatively, if managers judge that a less conservative impact scenario is likely (e.g., the third scenario - single day of lane shutdown costing $800,000), the second eradication protocol (cost of $64,470) now becomes worthwhile if PI*PE>0.08.

Assessing the worst case impact scenario (annual day of lane shutdown; $16.8 M) is not necessary since attempting to eradicate *R. harrisii* already appears profitable. Similarly, the analysis is conclusive without further need to include the risk of *R. harrisii* causing ecological harm in Panama or spreading elsewhere in the world.

Consultation of stakeholders and public outreach (step 7)

Previous reports of eradications assert that communication with local stakeholders is paramount to success (Anderson 2005; Bax et al. 2001, 2002; NISC 2003). Indeed, public policy decisions require that managers consider economic, political, social, and cultural values of interested parties (Andersen et al. 2004b; Bomford & O'brien 1995; Bossenbroek et al. 2005). However, given time limitations of early eradication efforts, we believe that, much like deciding on whether to implement a management strategy, deciding on whom to consult is itself a cost-benefit tradeoff; bypassing key stakeholders will generate roadblocks, but involving too many will complicate and delay action.

Public outreach is also critical to facilitate a community's understanding of rapid response efforts (Bossenbroek et al. 2005; NISC 2003) and can be achieved through open information meetings or the media (Bax et al. 2002; Williams & Grosholz 2008). Alternatively, the importance of public outreach may be less if eradication measures are safe and limited to private property or areas of restricted access. If these criteria are fulfilled and economic or environmental damages reduced, eradication efforts may avoid strong resistance from the public (Bomford & O'brien 1995; see Temple 1990).

Case study

We identified the ACP as the only major stakeholder likely to be directly affected by *R. harrisii*. The fact that it has full jurisdiction over the invaded site facilitates the decision-making process. We involved the ACP from the start of the study and held three official meetings to discuss the discovery of the crab, progress regarding our survey and experiments, and potential eradication strategies. Without this continued collaboration, solutions to avoid the spread of *R. harrisii* may not have been reached on time or may have remained unheard.

Thus far, beyond scientific publications, several articles were published online and in local newspapers in Panama to inform the general public of *R. harrisii*'s discovery (e.g., Arcia 2007; King 2007). Given the opportunity to implement a safe and well thought-out eradication program with anticipated ecological and economic benefits, the ACP may further gain from public outreach by "greening" the image of its expansion plan in the eyes of the Panamanian public and the international community.

Rapid response and monitoring (steps 8-9)

Beyond even the best opportunity for eradication, cooperation on behalf of major stakeholders is critical to success. Cost-benefit analysis may be an effective way of securing the necessary funding from stakeholders, but support is also highly dependent upon the consideration of stakeholders' constraints and concerns.

After an eradication attempt, researchers argue that prolonged monitoring efforts are central to insure that removal objectives are met (Anderson 2005; Genovesi 2007; Mack & Lonsdale 2002; Panetta 2007). While this is ideal, we argue that monitoring costs should not deter valuable opportunities for rapid response and can be distinguished from the cost-benefit decision to attempt early eradication. Deciding to monitor post-hoc is itself a separate cost-benefit analysis, dependent on the cost and likelihood of eradication if the initial attempt fails and the invader spreads.

Case study

The importance of addressing stakeholders' constraints was critical in the case of *R. harrisii*. The ACP, initially concerned with the cost of an eradication program and possible interference with Canal expansion plans, requested a cost-benefit analysis. So far, the arguments presented in this study have been positively received by managers, who are currently evaluating eradication strategies.

The case of *R. harrisii* also highlights the importance of distinguishing post-hoc monitoring from the cost-benefit decision of whether to attempt eradication. If the initial eradication fails in the Third Lock Lagoons, subsequent attempts in the Canal proper may be disproportionately more difficult and therefore much less cost-effective. As such, post-hoc monitoring may not be relevant for eradication and current efforts more important. Monitoring may nonetheless be valuable to allow other management strategies if crabs are detected in the future.

Discussion

After prevention, researchers advocate early eradication as the most cost-effective response to biological invaders (e.g., Coblentz 1990; Crooks 2005; Genovesi 2007). The analytical framework developed in this study provides a toolbox to evaluate the feasibility and desirability of eradicating novel invaders. Its application to *R. harrisii* was informative from several perspectives:

On one hand, an obvious lack of data shaped the application of the framework at all stages of the decision-making process. To assess the value of an eradication program and communicate its benefits to the ACP, we had to balance limited information about *R. harrisii* with limited time for decision-making. Indeed, the drainage of the Third Lock Lagoons will proceed, regardless of whether we fully understand the potential for *R. harrisii* to spread and cause damage in Panama. Information was lacking to develop complex models for predicting spread (e.g., Leung et al. 2004) or to use invasion history for estimating impacts (e.g., Ricciardi 2003). Although elaborate models are useful for controlling well-studied invaders, they may be less practical for recent invasions where rapid decisions are necessary. Likewise, previous frameworks have been instrumental in identifying useful information for managing invaders (e.g., Bax et al. 2001; NISC 2003), but this data is often difficult to obtain in a time frame relevant for rapid response. In the case of R.

harriii, for instance, we were unable to explicitly quantify all parameters even in the simplest cost-benefit equation we could derive (eqn 1).

On the other hand, important concepts from the invasion biology (e.g., traits of invaders, habitat suitability, propagule pressure) and the environmental management (e.g., scenario planning, risk analysis) literature proved extremely useful in our analysis, despite limited data. These concepts enabled us to use all available information and give rejection and acceptance thresholds to inform decision-making. We presented alternative impact scenarios and management options to allow managers a choice of strategy based on the balance of evidence from existing scientific knowledge. Even with a very conservative impact scenario, we showed that it is worthwhile to attempt eradicating *R. harrisii* if the combined probabilities of impacts and successful eradication exceed as little as 4.4%. In this way, our framework provides a novel and useful means of synthesizing limited information to communicate with managers. Although complete quantification may be preferable, we believe that rejection and acceptance thresholds will often be necessary to inform decisions for rapid response. Inevitably, if risk analysis is to be relevant for early eradication, a balance must be met between satisfying scientific criteria and the need for rapid decisions.

While we demonstrate the usefulness of this framework for *R. harrisii* in the Panama Canal, it is broadly applicable and can serve to evaluate eradication opportunities in several other systems. At its core, the framework is intended to contend with challenges of limited information, limited time, and limited communication, which fundamentally hamper responses to new invasions. Fifty years of research since Elton (1958) have provided much insight into how to manage biological invasions. Our framework uses these insights to tackle uncertainty and communicate with decision-makers the advantages of timely decisions to avoid future impacts from biological invaders.

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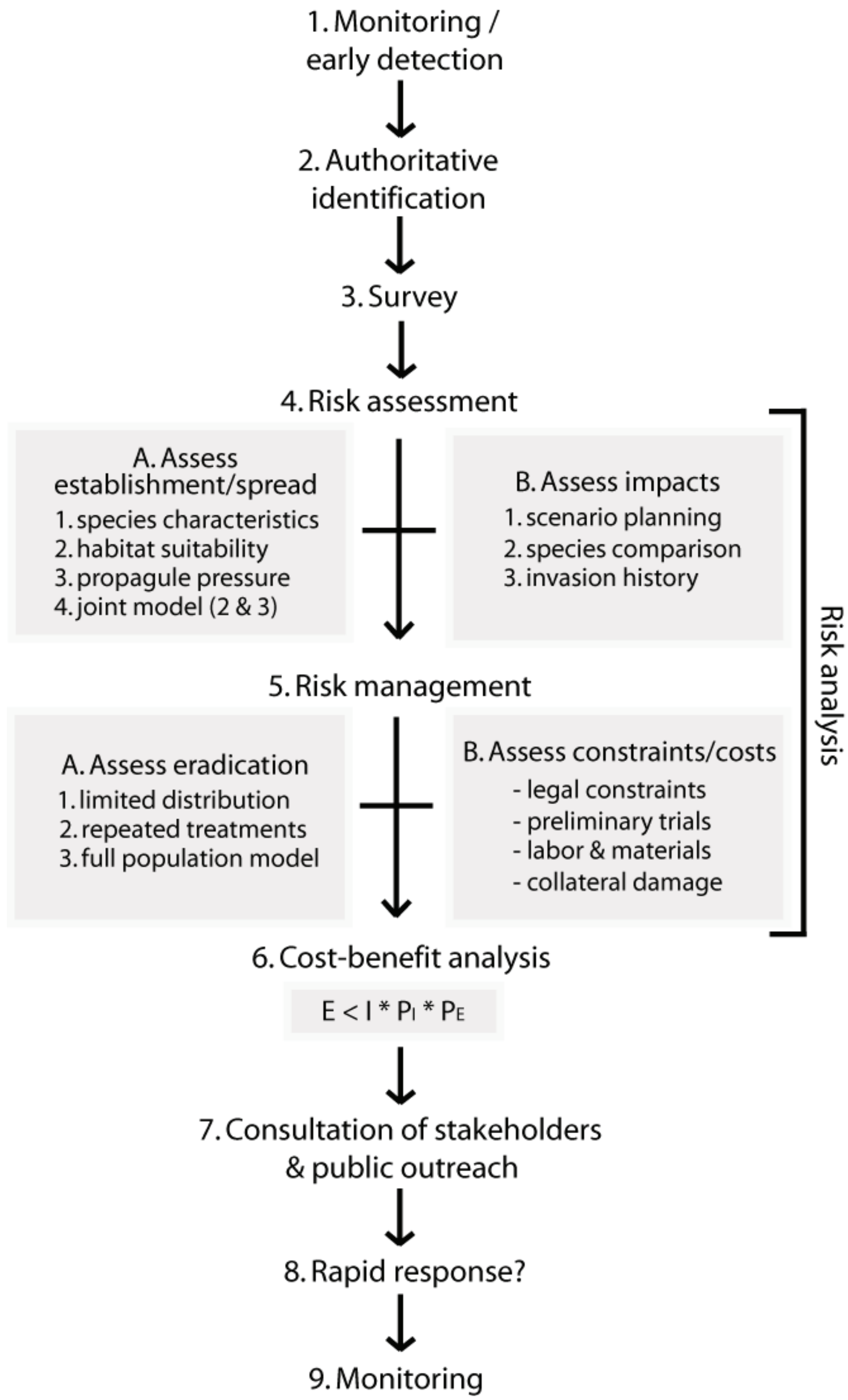

Figure 1. Flow-chart of the steps to evaluate the feasibility of rapid response to novel invaders and communicate the potential benefits of an eradication effort. Techniques within each component of risk analysis (e.g., establishment/spread) are ranked by information requirements, numbered from lowest to highest.

Appendix – Eradication costs

Protocol 1. Mixing of water layers in the Third Lock Lagoons, filtration, and diversion of the drainage to the Pacific Ocean

Component	Details	Cost ($US)
Mixing of water layers	Additional use of pumps	1,000
Filtration	Gravel pit	2,500[†]
Drainage	Blocking culvert between NL and MF Lake	*
	Installation and removal of pipes	*
	Pumping	*
	Relocation of crocodiles/removal of dead biota	*
	Total:	**3,500**
Monitoring post eradication	Two technicians part time $400/month for 1 year	9,600
	Materials (crates, rope, buoys, gas, vials, ethanol)	600
	Boat and truck use (provided by STRI)	0
	Total:	13,700

Protocol 2. Use of the pesticide Dimilin in the Third Lock Lagoons, filtration, and diversion of the drainage to the Pacific Ocean

Component	Details	Cost ($US)
Dimilin field trial (12 days)	Pesticide for trial in section of Northern Lagoon	326
	Labor and materials	1,500
	Concentration assays	1,800
	Plankton tows	500
Dimilin treatment (12 days)	Pesticide for application	52,144
	Concentration assays	1,800
	Labor (10 workers*6 days)	2,400
	Materials for pesticide application	1,000
	Boats (2 - provided by ACP)	0
	Gas for boats	500
Filtration	Gravel pit	2,500[†]
Drainage	Blocking culvert between NL and MF Lake	*
	Installation and removal of pipes	*
	Pumping	*
	Relocation of crocodiles/removal of dead biota	*
	Total:	**64,470**
Monitoring post eradication	Two technicians part time $400/month for 1 year	9,600
	Materials (crates, rope, buoys, vials, ethanol)	600
	Boat and truck use (provided by STRI)	0
	Total:	74,670

* Costs not increased: part of Canal expansion

† Costs could be further reduced as gravel can also be used for landfill

Diflubenzuron, the active compound in the pesticide Dimilin, is a chitin inhibitor which prevents cuticle formation in arthropods. Since it disrupts molting, diflubenzuron is highly toxic to early life stages of crustaceans and has been suggested for chemical control of *R. harrisii* (McEnnulty et al. 2001). Christiansen et al (1978) found that it was lethal to all larval stages of *R. harrisii* at a concentration of 10 ug/l and observed 100% mortality within twelve days of exposure (95% mortality was observed after three days). Advantages of Dimilin include the absence of mutagenic or carcinogenic effects and extremely low toxicity to vertebrates (Fischer & Hall 1992; NPIC 1996), minimizing the possibility of collateral damage. Dimilin is registered for agricultural use in the U.S. and Canada, and approved for controlling mosquitoes in isolated water bodies in California and Canada (Fischer and Hall 1992). Approval for special use in Panama would have to be sought from the Ministry of the Environment (ANAM) by the ACP.

To successfully remove all larvae in the Miraflores Third Lock Lagoons, Dimilin would have to be applied at a concentration of 10 ug/L active ingredient for a period of 12 days, and the water subsequently drained. Waiting for the pesticide to degrade below a safe concentration would compromise its efficacy, since adults appear to continually produce larvae (Roche et al. 2008). Christiansen and Costlow (1980) observed no reduction in mortality rates of the larvae until 21 days after the application of diflubenzuron in brackish water and found that eight weeks were required for the compound to degrade below a level at which *R. harrisii* larvae were no longer affected (1 ug/l; Christiansen et al 1978). These results suggest that a single application of the pesticide may be sufficient; however, a range of degradation rates have been reported in the literature based primarily on temperature and pH differences (*sensu* Fischer and Hall 1992). Additionally, some larvae may only be exposed to the pesticide on day twelve of the treatment, unless development is also affected within the egg stage of development. These points highlight the need to conduct preliminary trials to determine the effectiveness and persistence of diflubenzuron in the Third Lock Lagoons.

Finally, given the specificity of Dimilin, collateral damage to non-crustacean native species would be minimal. Effects to non-target crustaceans would also be decreased by diverting the drainage of both lagoons to the Pacific Ocean at the entrance of the Panama Canal, which would dilute treated waters by an estimated 14 fold. Large tidal amplitudes in this area (2.7 - 5 m) would further increase this dilution factor considerably. However, although minimized by dilution, environmental damage will be unavoidable in both protocols due to the flushing of sulfurous and anoxic waters from the Third Lock Lagoons. These costs are excluded from calculations in either protocol since they will occur independent of any eradication program.

Dimilin 25W costs (Chemtura Corp)

N.B. The top 10m meters of the Miraflores Third Lock Lagoons need to be treated since water layers do not mix and *R. harrsii* cannot survive in the sulfurous and anoxic bottom waters.

Volume of Southern Lagoon:

Narrow section = 986m (L) * 83m (W) * 10m (D) = 818,380 m^3

Wide Section = 343m (L) * 127m (W) * 10m (D) = 435,610 m^3

V_{SL} = 1,253,990 m^3

Volume of Northern Lagoon:

V_{NL} = 615m (L)*120m (W)*10m (D) = 738,000 m^3

Total Volume

V_T = 1,991,990 m^3 ~ $2*10^6$ m^3 ~ $2*10^9$ L

Diflubenzuron required

$2*10^9$ L / $10*10^{-6}$g/L =20,000 g = 20 kg

One bag Dimilin 25W contains 125g diflubenzuron

20,000g/125g/bag = 160 bags

One bag (500g) Dimilin 25W = $325.90

Total cost = 160 bags * $325.90/bag = $52,144

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General Conclusion

In this thesis, I evaluate the possibility of eradicating the North American Harris mud crab, *Rhithropanopeus harrisii*, recently discovered in the Panama Canal. Further, I use this case study to examine how ideas in invasion biology and environmental science can be integrated to best manage newly discovered exotic species and allow managers to make timely decisions when faced with uncertainty. In Chapter one, I report the presence of an established and reproducing population of *R. harrisii* in the Panama Canal and review the crab's invasion history to date. In Chapter two, I evaluate *R. harrisii*'s distribution and population demographics throughout the Canal and test its ability to survive in different locations across the waterway. Results indicated that *R. harrisii* is contained within two manmade lagoons but that it has the potential to spread beyond its current distribution if it were to be displaced due to the impending expansion of the Panama Canal. In Chapter three, I use the example of *R. harrisii* in Panama to formulate a series of applied guidelines for assessing the feasibility and the desirability of eradicating newly discovered exotic species. The goal of this framework is to facilitate communication between scientists and decision-makers when faced with limited information about emerging invaders, in order to allow informed decision-making and improve rapid response efforts for eradication. Using these guidelines, I show how eradicating *R. harrisii* in Panama not only seems possible but may in fact be economically beneficial. Arguably, the applicability of this framework extends beyond the specific example considered in this thesis, and I hope that it will prove useful to help managers and conservationists identify valuable opportunities for eradication in many other systems.

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