

Research Article

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

Dominique G. Roche^{1,2} and Mark E. Torchin²*

¹Department of Biology, McGill University, 1205 Avenue Doctor Penfield, Montreal, Quebec, H3A 1B1, Canada ²Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Panama, Republic of Panama

*Corresponding author

E-mail: torchinm@si.edu (MET)

Received: 1 May 2007 / Accepted: 1 June 2007

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.

Key words: Rhithropanopeus harrisii, Brachyura, Xanthidae, Panama Canal, estuaries, nonindigenous, invasion

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 brachyuran invaders distributed 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, Goncalves 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

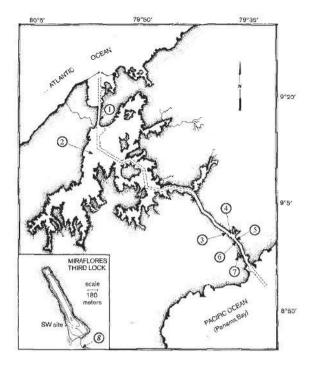


Figure 1. Map of the Panama Canal showing the location of the Miraflores Third Lock Lake (modified from McCosker and Dawson 1975). From the Pacific coast to the Atlantic coast: (1) Gatun Locks, (2) Gatun Lake, (3) Pedro Miguel Locks, (4) Miraflores Lake, (5) Miraflores Locks, (6) Miraflores Spillway;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

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 ($8^{\circ}58'45''N$, $79^{\circ}35'04''W$ - 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



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.

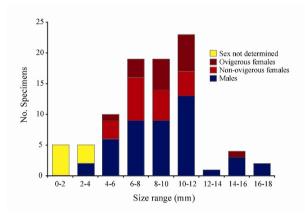


Figure 3. Size distribution of *Rhithropanopeus harrisii* collected in the Miraflores Third Lock Lake, Panama, on 2 March 2007.

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 freshwater 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 = 3.1-17.7mm), 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 will also be deposited at the National Museum of Natural History. Smithsonian Institution. Washington D.C.

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

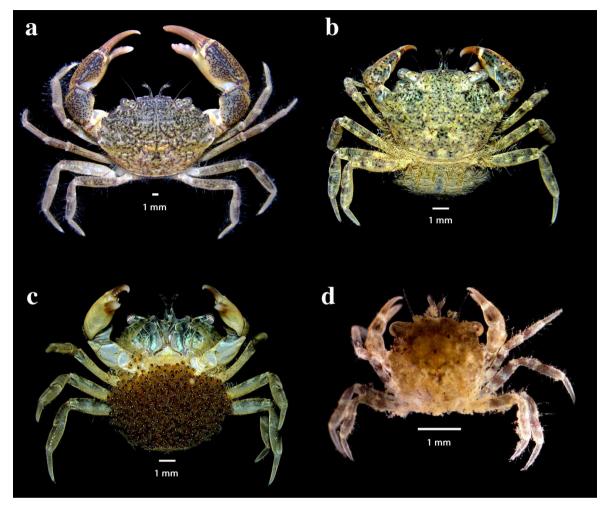


Figure 4. *Rhithropanopeus harrisii* collected in the Miraflores Third Lock Lake adjacent to the Panama Canal: (a) male specimen, 17.1 mm carapace width, dorsal view (photo by A. Anker); (b) ovigerous female specimen, 7.8 mm carapace width, dorsal view and (c) ventral view; (d) juvenile, 2.25 mm carapace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

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, although the latter may prove difficult.

Acknowledgements

We thank B Leung for assistance in the field, LG Abele, JH Christy and A Anker for confirming identification of adult specimens and larvae. Photos credits for Figure 1a: A Anker. We acknowledge the contribution of SA Binning, A Anker and an anonymous reviewer for comments on an earlier version of this manuscript. We are also grateful to A Aguirre for help in obtaining numerous useful publications and to the ACP for granting access to restricted sites. We acknowledge STRI and SENACYT for financial support and grants from NSERC, OQAJ and McGill NEO to DGR.

References

- Abele LG, Kim W (1989) The decapod crustaceans of the Panama Canal. *Smithsonian Contributions to Zoology* 482: 1–50, http://dx.doi.org/10.5479/si.00810282.482
- Andreyev NI, Andreyeva SI (1988) A crab Rhithropanopeus harrisii (Decapoda, Xanthidae) in the Aral Sea. Zoologichesky Zhurnal 67: 135–136
- ACP Autoridad del Canal de Panamá (2006) Proposal for the expansion of the Panama Canal, Third Set of Locks Project. http://www.pancanal.com/eng/plan/documentos/propuesta/acp-expansion-proposal.pdf. Cited 30 March 2007
- Băcescu MC (1967) Fauna Republicii Socialiste România. Crustacea Decapoda. Editura Academiei Republicii Socialiste România 4(9): 1–351
- Ben Souissi JI, Zaouali J, Rezig M, Neimeddine Bradai M, Quignard JP, Rudman B (2004) Contribution à l'étude de quelques récentes migrations d'espèces exotiques dans les eaux Tunisiennes. Rapports de la Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée 37: 312
- Buitendijk AM, Holthuis LB (1949) Note on the Zuiderzee crab *Rhithropanopeus harrisii* (Gould) subspecies tridentatus (Maitland). Zoologische Mededelingen 30(7): 95–106
- Carlton JT (1985) Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. Oceanography and Marine Biology. An Annual Review 23: 313–371

- Cohen AN (2006) Chapter III Species Introductions and the Panama Canal. In: Gollasch S, Galil BS and Cohen AN (eds) Bridging Divides - Maritime Canals as Invasion Corridors. Monographiae Biologicae, vol. 83. Springer, Berlin Heidelberg New York
- Cohen AN, Carlton JT (1995) Nonindigenous aquatic species in a U.S. estuary: a case study of the biological invasions of the San Francisco Bay and delta. A Report for the US fish and wildlife service, Washington D.C.
- Christiansen ME (1969) Crustacea Decapoda Brachyura. Marine invertebrates of Scandinavia, No. 2 Universitetsforlaget, Oslo, Denmark
- Demel K (1953) Nowy gatunek w faunie Baltyku. Kosmos 2: 105–106
- Eno NC, Clark RA, Sanderson WG (1997) Non-native marine species in British waters: a review and directory. Joint Nature Conservation Committee, Peterborough, 152 pp
- Gadzhiev DV (1963) Dutch crab in the Caspian Sea. Priroda 10: 126
- Gmelin JF (1791) Vermes. Regnum animale. Caroli a Linné Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. *Lipsiae: Impensis Georg. Emanuel. Beer.* 1(6): 3021–3910
- Gonçalves F, Ribeiro R, Soares AMVM (1995) *Rhithropanopeus harrisii* (Gould), an American crab in the estuary of the Mondego River, Portugal. *Journal of Crustacean Biology* 15(4): 756–762, http://dx.doi.org/10.2307/1548824
- Google Earth™ mapping service (2007) http://earth.google.com. Cited 30 Apr 2007
- Grosholz ED, Ruiz GM (1996) Predicting the impact of introduced marine species: Lessons from the multiple invasions of the European green crab Carcinus maenas. Biological Conservation 78: 59–66, http://dx.doi.org/10.1016/ 0006-3207(94)00018-2
- Gould AA (1841) Crustacea. In: Report on the Invertebrata of Massachusetts, comprising the Mollusca, Crustacea, Annelida, and Radiata. Cambridge, Massachusetts, Folsom, Wells, and Thurston, pp 321–341
- Howells R (2001) Introduced non-native fishes and shellfishes in Texas waters: an updated list and discussion. Texas Parks and Wildlife Department, Management Data Series 188
- Jazdzewski K, Konopacka A (1993) Survey and distribution of Crustacea Malacostraca in Poland. Crustaceana 65: 176–191, http://dx.doi.org/10.1163/156854093X00540
- Jones LL (1940) An introduction of an Atlantic crab into San Francisco Bay. *Proceedings of the Sixth Pacific Science Congress of the Pacific Science Association* 3: 485–486
- Keith DE (2007) Occurrence of the estuarine mud crab, *Rhithropanopeus harrisii*, in Texas reservoirs. http:// www.tarleton.edu/~biology/MudCrab.html. Personal communication. Cited 23 April 2007
- Linnaeus C (1758) Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis Synonymis, Locis. Edition 10. Holmiae. 1: iii + 1–824
- McCosker JE, Dawson CE (1975) Biotic passage through the Panama Canal, with particular references to fishes. *Marine Biology* 30: 343–351, http://dx.doi.org/10.1007/BF00390639
- Maitland RT (1874) Naamlijst van Nederlandsche Schaaldieren. *Tijdschrift der Nederlandsche Dierkundige Vereeniging* 1: 228–269
- Makarov AK (1939) Certain new elements in the composition of the fauna of the Black Sea Limans as an effect of maritime navigation. C.R. (Doklady) Adacemy of Sciences of the USSR 23: 819–822
- Marchand J, Saudray Y (1971) Rhithropanopeus harrisii Gould tridentatus Maitland (Crustacé – Décapode. Brachyoure),

dans le réseau hydrographique de l'ouest de l'Europe en 1971. *Bulletin de la Société Linnéenne de Normandie* 102: 105–113

- Mariscal JAC, Garcia-Raso JE, Gonzilez Gordillo JI (1991) Primera cita de *Rhithropanopeus harrisii* (Gould, 1841) (Crustacea, Decapoda, Brachyura, Xanthidae) en la Peninsula Iberica. *Boletin del Instituto Espanol Oceanografia* 7: 149– 153
- Mizzan L, Zanella L (1996) First record of *Rhithropanopeus* harrisii (Gould, 1841) (Crustacea, Decapoda, Xanthidae) in the Italian waters. *Bolletino del Museo civico di Storio* naturale di Venezia 46: 109–120
- Milne Edwards H (1853) Mémoires sur la famille des Ocypodiens. Annales des Sciences Naturelles série 3 (Zoologie) 20: 163–228
- Morgan SG, Goy JW, Costlow JD (1988) Effect of density, sex ratio, and refractory period on spawning of the mud crab *Rhithropanopeus harrisii* in the laboratory. *Journal of Crustacean Biology* 8: 245–249, http://dx.doi.org/10.2307/ 1548316
- Noël P (2001) Le crabe américain *Rhithropanopeus harrisii* étend-t-il actuellement son aire de distribution en Méditerranée? Rapports de la Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée 36: 407
- Pagad S (2007) Global Invasive Species Database. Personal communication. Cited 20 April 2007
- Payen GG, Bonami JR (1979) Mise en évidence de particules d'allure virale associées aux noyaux des cellules mésodermiques de la zone germinative testiculaire du crabe *Rhithropanopeus harrisii* (Gould) (Brachyura, Xanthidae). *Revue des Travaux de l'Institut des Pêches Maritimes* 43: 361–365
- Petersen C (2006) Range expansion in the northeast Pacific by an estuary mud crab a molecular study. *Biological Invasions* 8: 565–576, http://dx.doi.org/10.1007/s10530-005-0160-1
- Rubinoff RW, Rubinoff I (1968) Interoceanic colonization of a marine Goby through the Panama Canal. *Nature* 217: 476– 478, http://dx.doi.org/10.1038/217476a0

- Ruiz GM, Carlton JT, Grosholz ED, Hines AH (1997) Global invasions of marine and estuarine habitats by non-indigenous species: Mechanisms, extent, and consequences. *American Zoologist* 37(6): 621–632
- Ruiz GM, Fofonoff PW, Carlton JT, Wonham MJ, Hines AH (2000) Invasion of coastal marine communities in North America: Apparent patterns, processes, and biases. *Annual Review of Ecology and Systematics* 31: 481–531, http://dx.doi. org/10.1146/annurev.ecolsys.31.1.481
- Ruiz GM, Lorda J, Arnwine A, Lion K (2006) Shipping Patterns Associated with the Panama Canal: Effects on Biotic Exchange? In: Gollasch S, Galil BS and Cohen AN (eds), Bridging Divides - Maritime Canals as Invasion Corridors. Monographiae Biologicae, vol. 83. Springer, Berlin Heidelberg New York
- Saudray Y (1956) Présence de *Heteropanope tridentatus* Maitl. Crustacé brachyoure dans le réseau hydrographique normand. *Bulletin de la Société Zoologique de France* 81: 33–35
- Schubert K (1936) *Pilumnopeus tridentatus* Maitland, eine neue Rundkrabbe in Deutschland. *Zoologischer Anzeiger* 116: 320–323
- Turoboyski K (1973) Biology and ecology of the crab Rhithropanopeus harrisii ssp. tridentatus. Marine Biology 23: 303–313, http://dx.doi.org/10.1007/BF00389338
- Wasson K, Zabin CJ, Bedinger L, Diaz MC, Pearse JS (2001) Biological invasions of estuaries without international shipping: the importance of intraregional transport. *Biological Conservation* 102: 143–153, http://dx.doi.org/10.10 16/S0006-3207(01)00098-2
- Williams AB (1965) Marine decapod crustaceans of the Carolinas. Fishery Bulletin 65: 1–298
- Williams AB (1984) Shrimps, lobsters, and crabs of the Atlantic Coast of the Eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, D.C.
- Wolff T (1954) Occurrence of two east American species of crabs in European waters. *Nature* 174: 188–189, http://dx.doi.org/ 10.1038/174188a0
- Zaitsev Y, Öztürk B (2001) Exotic species in the Aegean, Marmara, Black, Azov and Caspian Seas. Turkish Marine Research Foundation, Istanbul, Turkey, pp 125–126

Supplementary material

The following supplementary material is available for this article:

Annex. 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
Germany	Black Sea	1936	Makarov 1939
Ukraine	Azov Sea	1930	Zaitsev and Öztürk 2001
United States	NE Pacific	1948	Jones 1940
	Black Sea	late 1800s	Marchand and Saudray 1971
Russia	Azov Sea	1948	Zaitsev and Öztürk 2001
		1948	Gadzhiev 1963
Delassis	Caspian Sea Black Sea	1939	
Bulgaria			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

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