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Research Article

The North American mud crab *Rhithropanopeus harrisii* (Gould, 1841) in newly colonized Northern Baltic Sea: distribution and ecology

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Abstract

Here we present the known distribution and population demography of the most northern known population of the North American white-fingered mud crab, *Rhithropanopeus harrisii*, from southwest Finland in the Baltic Sea. This species was first reported in Finland in 2009 from the archipelago close to Turku and has been found from 82 locations within a 30 km radius since then. Due to the presence of young of year, juveniles, and gravid females observed at three sites in Finland, *R. harrisii* has established successful populations that are able to overwinter under ice and can opportunistically occupy diverse habitats, such as shafts of dead marsh plants, self-made burrows in muddy bottoms, and the brown algae *Fucus vesiculosus* in hard bottoms. In its native range, a rhizocephalan barnacle parasitizes *R. harrisii*, but this parasite was not found in the introduced Finnish population. While *R. harrisii* is expected to expand its range along the coast of the northern Baltic Sea, the ultimate impact of this species on food web dynamics, both as a predator and prey item, remains to be seen.

Key words: Xanthidae; Finland; biological invasion; introduced species; demography

Introduction

The white-fingered mud crab *Rhithropanopeus harrisii* (Gould, 1841) (Crustacea: Brachyura: Xanthidae) is a highly successful estuarine invader and is one of the most widely distributed brachyuran crab species globally (Roche and Torchin 2007). It has high fecundity, a long planktonic larval period, and a wide tolerance range for several environmental factors that have likely facilitated its invasion success (Williams 1984; Goncalves et al. 1995a, b). The native range of *R. harrisii* extends along the Atlantic coast of North America, from the southern Gulf of Saint Lawrence, Canada to Veracruz in the Gulf of Mexico (Williams 1984). Over the past century, however, *R. harrisii* has invaded over 20 countries, two oceans, ten seas, and ten fresh-water inland reservoirs across four continents, which span over 45 degrees of latitude, most likely due to anthropogenic means (Roche and Torchin 2007). The most recent introductions include those to: Japan (Iseda et al. 2007); inland lakes in Texas, USA (Boyle et al. 2010); and Estonia (Kotta and Ojaveer 2012).

Rhithropanopeus harrisii was first observed in Europe in 1874, when it was originally misidentified as *Pilumnus tridentatus* (Maitland, 1874) in the Netherlands (Wolff 2005). Since then, it has spread to locations around the North Sea and Baltic Sea, including Germany in 1936 (Schubert 1936), Poland in 1951 (Demel 1953), Lithuania in 2000 (Bacevičius and Gasiūnaitė 2008), Finland in 2009, and most recently Estonia in 2011 (Kotta and Ojaveer 2012) Projecto-Garcia et al. (2010) examined the colonization event of other, older European populations of *R. harrisii* and was unable to pin-point whether *R. harrisii* had a single successful invasion, or a series of successful invasions with different mechanisms (e.g., ballast water, hull fouling, as hitchhikers in the oyster aquaculture trade). Due to the large amount of shipping, both from the USA to Europe and within Europe since 1874, the possibility of a single successful invasion seems highly improbable, but there are no data to unequivocally confirm that conjecture at this time.

In this study, we assessed the current distribution of *R. harrisii* along the southwestern coast of Finland and discuss habitat use, temperature and salinity tolerance, size distribution and sex ratio in these introduced populations. We also examined *R. harrisii* for the parasitic barnacle (rhizocephalan) *Loxothylacus panopaei* (Gissler, 1884), which impacts native populations along the east coast of North America and the Gulf of Mexico (Hines et al. 1997).

Material and methods

All observations reported here were made between 2009 and 2012. The main source of the distribution data presented here (Figure 1) was public observations from a web site created by the Finnish Game and Fisheries and Finnish Environmental Institute (RKTL 2012). It is noteworthy that the public in Finland reports observations of suspicious fauna quite readily to the universities or to RKTL, and the Finnish Game and Fisheries and Finnish Environmental Institute confirmed all observations.

Besides sightings from the public, the distribution data consists of sampling by MvN (19 locations) in the northwest corner of the distribution map (Figure 1), and of sightings made while conducting diving surveys (data from the Centre for Economic Development, Transport and the Environment for Southwest Finland). Field observations were also made by OV, AF, TF, and other researchers at the Archipelago Research Institute (University of Turku). We also contacted other marine researchers around Finland to determine the extent of the invasion of *R. harrisii.*

We collected data on sex ratios and body sizes to gain information on population demography using standardized, artificial-habitat crates to compare the morphometrics of juvenile and adults of the Finnish population to native populations as well as other introduced populations. *Rhithropanopeus harrisii* were collected by means of placing artificial collectors (30 × 30 × 30 cm plastic crates filled with dead, autoclaved oyster shells from Maryland, USA). The crates provided habitat for natural recruitment of both juvenile and adult *R. harrisii,* and the animals could move freely in and out of the collectors. The sampling crate used in the current study has been used successfully to monitor native and introduced *R. harrisii* populations in other countries (e.g. Roche et al. 2009), making it possible to compare size classes, sex ratios, and abundance.

Population sampling consisted of placing three replicate crates in each of three locations in Finland (Kaarina, Lapila, Naantali; see Figure 1 and Appendix 1). For both 2011 and 2012, the crates were in the water for 1.5-2 months. Crates were deployed in July/August and retrieved in either September (2011) or October (2012). Crabs collected from the crates were measured (carapace width, CW) and sex determined if possible. The specimens were then preserved in 70% ethanol and later examined for the presence of *Loxothylacus panopei*. When the parasite has completed an internal growth phase, it produces an external growth form, which would have been easily seen by simple external examination. In this study, we concentrated on demersal stages and did not sample the pelagic stages.

We used a generalized linear mixed model (GLMM) with a negative binomial distribution to determine whether the number of crabs (adults, juveniles, and immature) per crate differed between the Finnish locations (Kaarina, Lapila and Naantali, three crates in all locations) and between the years (2011 and 2012). We also tested the interaction between year and location. The model fit the data as judged from the Pearson Chi-Square/df –value, which was 1.53 (close to 1 indicates a good fit). Here and elsewhere in this paper the multiple pairwise comparisons were conducted with Tukey-Kramer method, and we show the adjusted *P*-values. The results (mean, + upper SE, - lower SE) were back transformed. All the analyses were conducted with SAS Enterprise Guide 4.2 and 4.3.

This study is part of a global study to monitor native and introduced populations of *R. harrisii*, and only part of the data is presented here. The Finnish demographic data were compared to unpublished data from Poland (from the Vistula Lagoon and Gdansk) and native Louisiana, USA, from studies that were conducted concurrently in 2011 (AF). We used the same method as above to compare the number of crabs (adults, juveniles, and immature) per crate collected in Finland (three locations Kaarina, Lapila and Naantali, three crates in each), Poland (two

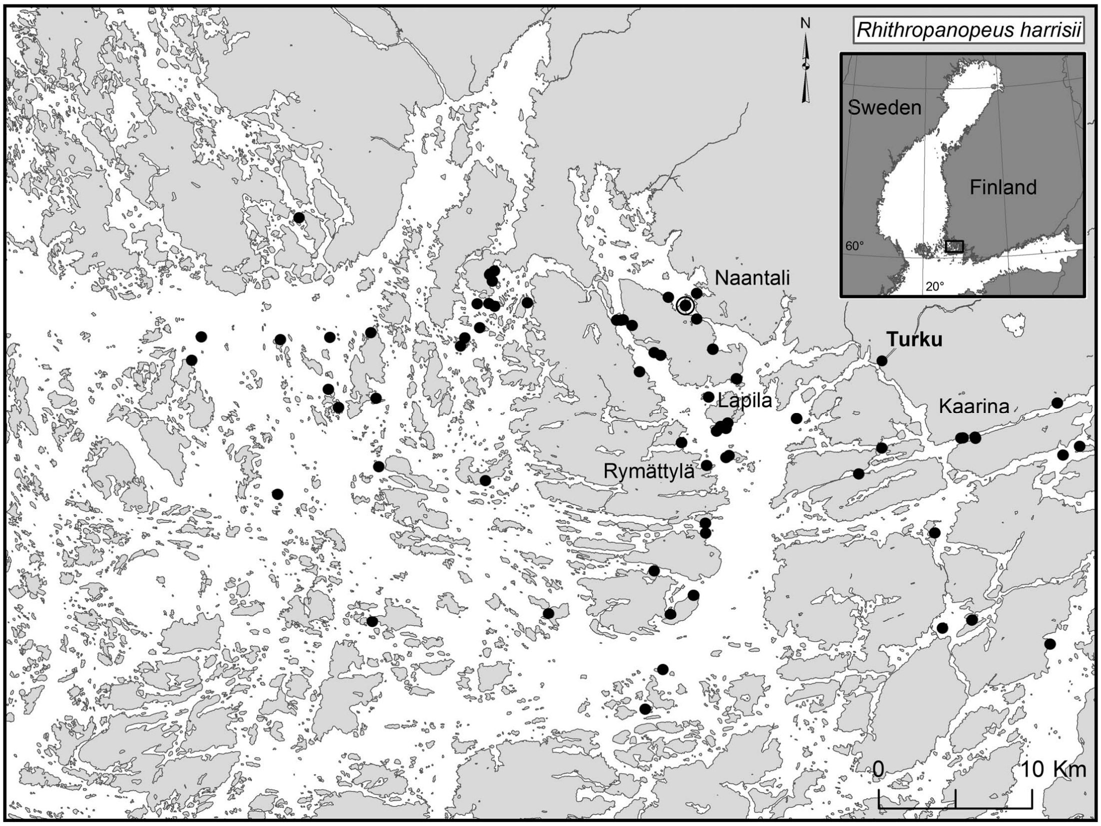

Figure 1. Known locations of individual *Rhithropanopeus harrisii* along the coast of Finland from 2010–2012. Individuals were first observed in Naantali, denoted by the double circle. For details see Appendix 1.

locations Gdansk and Vistula, three crates in both locations) and Louisiana (two locations Cocodrie and Cypremort Point, three crates both locations). (Pearson Chi-Square/df –value 1.13) After removing data on the immature crabs, we used a GLMM with binomial distribution to determine the sex ratios of the Finnish crab populations. The number of males/total number of adult crabs per crate was the response variable, and we examined the proportion of males by location (Naantali, Kaarina, Lapila), year (2011 and 2012), and the interaction of location and year (Pearson Chi Square/df –value 1.16).

We also used a GLMM with negative binomial distribution to compare the carapace widths of the crabs within the Finnish locations. Distribution of size in Finnish populations was not normal, as there were more small individuals than larger ones. We compared the sizes among the locations, sexes and years and all interactions (Pearson Chi-Square/df –value 1.16).

A GLMM with negative binomial distribution was also employed to determine whether the populations in Finland, Poland and Louisiana differed in carapace width and whether there were any size differences between the sexes (Pearson Chi-Square/df –value 1.03).

Results and discussion

Distribution

Rhithropanopeus harrisii was observed for the first time in Finland in 2009, at a site near the town of Naantali in the southwest of Finland in the Northern Baltic Sea (Karhilahti 2010; Figure 1). Based on all available data, *R. harrisii* has been found in 82 locations, all within a radius of about 30 kms from this first observation site. Shipping routes to and from harbors in Turku and Naantali connect to countries such as Poland (e.g. coal cargo to Naantali) and the Netherlands (oil tankers), making it possible for *R. harrisii* to invade the area by hitchhiking on/in the ships' hull or ballast water. However, planktonic dispersal along water currents to Finland cannot be ruled out, especially as the Estonian population in Parnu Bay, about 300km from the present study area, has increased rapidly and almost simultaneously with the Finnish population reported here (Kotta and Ojaveer 2012). However, only population genetic studies could reveal the origin of the Finnish population.

Habitat use

Rhithropanopeus harrisii have been found in a variety of habitats in southwest Finland. In its native range, these crabs are found in habitats that afford some type of shelter, such as oyster reefs, living and decaying vegetation, branches, and other debris to a depth of approximately 37 m (Ryan 1956; Williams 1984; Petersen 2006; AF, personal observation). In non-native locations, *R. harrisii* is found under stones and woody debris (Panama Canal; Roche and Torchin 2007), in sand and silt with shells, and among pieces of wood and remnants of dead vegetation (Poland; Turoboyski 1973).

The Finnish population of *R. harrisii* seems to be opportunistic when it comes to utilizing available habitats. In the field, we have found crabs inside dead and broken marsh reeds (*Phragmites australis* (Cav.) Trin ex Steud), buried in mud, under small stones along the shore, and living amongst the macroalgae *Fucus vesiculosus* even at hard bottom sites heavily exposed to wind and waves. Indeed, in the Northern Baltic Sea, shelters such as oyster shells are not found, and natural structures that form cavities are a limiting resource. This suggests that *R. harrisii* colonizes almost all habitat types available in Finland. The flexible habitat use behaviour also suggests that predicting the invasion potential of this opportunistic species cannot be based on prior knowledge of habitat preference alone.

Rhithropanopeus harrisii is euryhaline and able to tolerate salinities from 0.5 psu in freshwater reservoirs (introduced Texas populations; Boyle et al. 2010) to 20.4 psu in estuarine embayments (native Chesapeake Bay populations; Ryan 1956). Laboratory experiments have shown larvae in the native range survive salinities of 2.5 – 40 psu and 20 – 30ºC (Costlow et al. 1966; Christiansen and Costlow 1975). The salinity of the Baltic Sea ranges from 0–30 psu in the Danish straits (Leppäranta and Myrberg 2009), with high values in the Arkona basin close to the entrance and almost fresh water in the northern parts of the Gulf of Bothnia (Suominen et al. 2010).

In its introduced range in Poland, *R. harrisii* is able to reproduce when the water temperature is above 14ºC (Turoboyski 1973). In the archipelago of southwestern Finland, this temperature is annually reached during the summer months (Leppäranta and Myrberg 2009), and we observed ovigerous females from July through October. Turoboyski (1973) reported that populations in the Vistula River, Poland could survive winter temperatures below 1ºC and could even survive being frozen in ice for a short time. This is not particularly unusual as populations at the northern edge of their natural range in the Miramichi Estuary, Canada are exposed to salt water near freezing for up to six months of the year (Chadwick 1995). The temperature of the Baltic Sea ranges from 4 to 20ºC (Leppäranta and Myrberg 2009), with colder water at the surface during the winter months. However, the temperature of the bottom is likely to be the crucial abiotic factor for *R. harrisii* as it occupies the benthic surface and also buries in the mud. Even in the winter, the bottom of the sea usually remains +4 ºC as dense warmer water sinks to the bottom. In the present distribution area, there is more than 90% probability of annual ice cover during winter, and the average duration of ice cover varies between 81 and 122 days (Mälkki et al. 1979; Leppäranta and Myrberg 2009). The appearance of young of year and reproducing adults during sampling years 2011 to 2012 indicate that *R. harrisii* is able to survive the Northern Baltic Sea winter in conditions similar to those it experiences at the northern extent of its native range.

Number of individuals per crate, sex ratio and size distribution

In 2011, a total of 192 *R. harrisii* were collected from all three locations in Finland, and 416 in 2012 (Table1). The overall mean number of individuals per crate increased from 20.7 (+4.1, -3.5) in 2011 to 40.8 (+6.6, -5.6) in 2012 ($F_{1,12}$ = 40.09, P <0.0001). The mean number of individuals varied significantly among locations ($F_{2,12}$ = 21.88, P < 0.0001); however, the significant interaction "year X location" ($F_{2,12}$ = 6.73, P = 0.011) indicated that mean values increased

Table 1. Average carapace width (± SE) and range (min - max) of *Rhithropanopeus harrisii* collected from three replicate crates in each of three locations in southwestern Finland in September 2011 and October 2012 (raw data). Crabs for which sex could not be determined were categorized as immature individuals.

		2011			**2012**		
Location		n	Mean size±SE (mm)	Range (mm)	n	Mean size±SE (mm)	Range (mm)
Kaarina	Males	32	6.85 ± 0.90	2.3 - 19.9	71	8.46 ± 0.69	3.1 - 22.0
Kaarina	Females	20	8.12 ± 1.07	2.8 - 16.9	55	6.17 ± 0.58	3.1 - 20.2
Kaarina	Immature	-	-	-	35	2.40 ± 0.09	1.1 - 3.7
Kaarina	**Total**	**52**	**7.34 ± 0.69**	**2.3 - 19.9**	**161**	**6.36 ± 0.41**	**1.1 - 22.0**
Kaarina	**Mean # crabs/crate**	**17**			**54**		
Naantali	Males	17	7.33 ± 1.07	2.3 - 14	7	11.26 ± 2.05	4.0 - 18.8
Naantali	Females	16	7.56 ± 1.21	2.3 - 15.2	12	10.73 ± 0.93	3.2 - 15.4
Naantali	Immature	19	1.83 ± 0.05	1.6 - 2.2	39	2.14 ± 0.08	1.4 - 3.2
Naantali	**Total**	**52**	**5.39 ± 0.63**	**1.5 - 15.2**	**58**	**5.02 ± 0.62**	**1.4 - 18.8**
Naantali	**Mean # crabs/crate**	**17**			**19**		
Lapila	Males	38	7.65 ± 0.99	2.3 - 19.9	74	5.29 ± 0.45	2.2 - 18.4
Lapila	Females	42	5.74 ± 0.61	2.4 - 15.4	89	5.04 ± 0.34	2.1 - 13.7
Lapila	Immature	8	1.81 ± 0.10	1.4 - 2.2	34	2.08 ± 0.05	1.6 - 2.7
Lapila	**Total**	**88**	**6.21 ± 0.55**	**1.4 - 19.9**	**197**	**4.62 ± 0.24**	**1.6 - 18.4**
Lapila	**Mean # crabs/crate**	**29**			**66**		

differently among locations: the mean value increased in Lapila (t = 5.09, df=12, P = 0.0003) and in Kaarina (t = 6.12, df=12. P = 0.0006), but not in Naantali (t = 0.51, df=12. P = 0.995).

The mean number of *R. harrisii* per crate differed between Finland, Poland, and Louisiana, USA ($F_{2,18}$ = 68.03, P <0.0001), with more crabs per crate in Louisiana (202.3, + 108.0, – 70.4) than Finland (21.3, + 9.8, -6.7) or Poland (4.5, + 3.6, -2.0) (Tukey's all pairwise comparisons P < 0.001). Both introduced populations sampled have substantially lower abundance than have been observed in Louisiana, USA.

There were no significant differences in the sex ratios between the three Finnish locations ($F_{2,12}$ = 3.16, P =0.079), with slightly more males in Kaarina (59%) than Lapila (46.5 %) or Naantali (44.1%). The sex ratios remained the same between the years ($F_{1,12}$ = 1.51, P = 0.243) and among locations in both years (year X site $F_{2,12}$ = 0.32, P = 0.733).

In both years 2011 and 2012, we caught a broad size range of individuals, including young of the year, juveniles, adults, and ovigerous females (Table 1). Two ovigerous females were found in 2011 and 29 in 2012 (carapace widths: 7.42 mm - 10.78 mm). In Finnish populations, females and males did not differ in overall mean carapace width ($F_{1,488}$ = 0.98, P = 0.322). There was variation in carapace width between locations ($F_{2,488}$ = 9.38, P = 0.0001), but this depended on the year (interaction $F_{2,488}$ = 10.58, P < 0.0001) as sampled crabs were much bigger in Naantali in 2012 than in 2011 (t = 4.12, df = 488, P = 0.0006). The increase in carapace width in crabs from Naantali also changed the combined size distribution for all three sites towards larger individuals from 2011 to 2012 ($F_{1,488}$ = 5.04, P = 0.025). In 2011 there were no differences in carapace width between the locations, but in 2012 the crabs were smaller in Lapila than in Kaarina (t = 4.23, df= 488, P = 0.0004) and in Naantali (t = 4.9, df = 488, P < 0.0001).

When comparing the carapace widths of Finnish crabs to crabs from Poland and Louisiana, we found that the size (mean, +SE, -SE) of Louisiana crabs was significantly smaller (4.03, + 0.014, -0.14) than Finnish (6.3, + 0.5, -0.47) and Polish (9.33, + 0.86, -0.54) crabs (all pairwise comparisons P < 0.001). Only in the Polish population were males larger than females (12.9, +3.3-2.63 *vs* 5.22, + 1.87 -1.34; t = 4.64, df=1471, P < 0.0001); in Louisiana and Finland there were no significant size differences between the sexes. This could be due to the small sample size in Poland (N=27), but others have shown this pattern in Polish populations (Table 2; Czerniejewski and Rybczyk 2008, Czerniejewski 2009). The mean number of individuals in the crates, their sex ratios, and carapace width distributions in Finland resembled the introduced population of *R. harrisii* in Panama, which was sampled using the same method (44 *R. harrisii* in one site, 26 in another; Roche et al. 2009). For further comparison of carapace widths among native and invasive populations, see Table 2.

Table 2. Estimates of *Rhithropanopeus harrisii* carapace widths from various native and introduced regions. * Non ovigerous females. Note that the sampling methods for collecting individuals were not constant between surveys.

Males			Females			Place	Native/ Invasive	Reference
n	Range	Mean±SD	n	Range	Mean±SD			
149	5.60-22.90	16.81±3.98	115	5.30-19.80	15.05±3.33	Odra estuary, Poland	Invasive	Czerniejewski (2009)
125	5.0-22.40	13.37±3.95	95	4.9-18.30	12.16±2.56	Dead Vistula River, Poland	Invasive	Normant et al. (2004)
45	3.1-17.7	9.3	19*	4.9-10.9	8.0	Panama Canal	Invasive	Roche and Torchin (2007)
637	4.4-26.1	11.32±3.49	555	4.4-19.0	10.76±2.43	Dead Vistula River, Poland	Invasive	Turoboyski (1973)
82	7.69-22.80	17.10±3.99	64	11.23-17.80	15.87±2.27	Odra estuary, Poland	Invasive	Czerniejewski and Rybczyk (2008)
44	3.2-22.8	10.4±4.0	28	3.1-16.3	10.5±3.8	Gulf of Gdańsk, Poland	Invasive	Hegele-Drywa and Normant (2009)
2	2.2-7.5	4.85±3.75	3	2.1-3.2	2.57±0.57	Gdynia, Poland	Invasive	AF, unpublished data
20	9.6-21.6	15.0±3.6	26	8.9-19.4	11.5±2.6	Dead Vistula River, Poland	Invasive	Hegele-Drywa and Normant (2009)
13	2.3-19	14.14±5.54	10	1.8-16	6.02±5.79	Vistula Lagoon, Poland	Invasive	AF, unpublished data
527	4.1-14.6	8.04±2.31	391	4.4-12.6	7.25±1.31	Chesapeake Bay, USA	Native	Ryan (1956)
532	1.8-12.8	4.39±2.38	591	1.8-15.4	4.29±2.03	Louisiana, USA	Native	AF, unpublished data
239	2.21-22.0	7.14±5.29	234	2.07-20.21	6.16±4.1	Archipelago Sea, Finland	Invasive	This study

We found no external evidence of the rhizocephalan *Loxothylacus panopei* in Finnish populations of *R. harrisii*. This, together with the larger mean values in carapace width, suggests that the crabs in Finland may be released from a parasite load and are able to invest more resources in growth. How parasite release influences fecundity in Finnish populations remains to be studied.

Concluding remarks

The first record of the white-fingered North American mud crab, *Rhithropanopeus harrisii*, in Finland was from the southwest Finnish archipelago (Naantali) in 2009. While this may not be the site of the point of original invasion, by 2012, *R. harrisii* has been observed from over 82 sites within a 30 km radius from there. At present, no observations exist outside this range in Finland. However, the distribution range of *R. harrisii* is likely to increase along the coast of the northern Baltic Sea in the future, based on the successful invasion history of this species throughout Europe and other parts of the world. Future genetic studies may reveal whether the colonization occurred only once or in multiple events, and whether the local population has multiple or single origins. Comparing the genetics of Finnish and newly found Estonian and Swedish populations of *R. harrisii* could also answer whether the vector is natural dispersion or shipping vessels (e.g. in ballast water or in/on hulls). In Finland, *R. harrisii* individuals are able to withstand cold winters and low salinities, as they do in Canadian waters and elsewhere, and exhibit flexibility in their ability to use various habitats. The existence of young of year and juveniles, together with gravid females and increasing abundance, confirms that the species was reproducing in Finland. The lack of parasites and larger body sizes suggests a release from parasite load in the Finnish waters, which may allow the crabs to invest more energy in growth and reproduction. At this point, it is unknown how interactions with native species may impact the dispersal and future population demography of *R. harrisii*. Several *R. harrisii* have been found in the stomachs of perch (*Perca fluviatilis* (Linnaeus, 1758)), fourhourned sculpin (*Myoxocephalus quadricornis* (Linnaeus, 1758)), roach (*Rutilus rutilus* (Linnaeus, 1758)), and pike-perch (*Sander lucioperca* (Linnaeus, 1758)) (RKTL 2012) (OV, personal communication with local fishermen). This indicates that top-down regulation through predation by fish may be taking place. More detailed studies on the ecology of *R. harrisii* in these recently introduced regions are needed to assess their effects on food webs in the northern Baltic Sea ecosystem. Alterations to the benthic community are expected, as this is a completely new functional species to the area. Successful invasive species such as *R. harrisii* provide a natural experiment to study rapid adaptations to new environments and conditions and novel interactions with the local flora and fauna.

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Supplementary material

The following supplementary material is available for this article.

Appendix 1. Known locations of individual *Rhithropanopeus harrisii* along the coast of Finland from 2009–2012.

This material is available as part of online article from:
http://www.aquaticinvasions.net/2013/Supplements/AI_2013_Fowler_etal_Supplement.pdf