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Post-invasion demography and persistence of a novel functional species in an estuarine system

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Abstract Long-term population data of marine invaders are rarely collected although it provides fundamental knowledge of the invasion dynamics that is important for evaluating the impacts, interactions and range expansion of the invader and for management purposes. During a 6-year monitoring period, we studied the dynamics and population demographic characteristics of the newly introduced mud crab *Rhithropanopeus harrisii*. The overall abundance of *R. harrisii* appeared to follow the boom and bust pattern with a rapid initial abundance increase and subsequent decline. The recruitment and growth of juveniles were correlated with the temperature during the larval period indicating that the increase in water temperature caused by climate change could have a positive effect on the recruitment and have potentially facilitated the establishment of *R. harrisii* in the northern Baltic Sea. The changes in the survival of reproductive females influence most the growth rate of the studied population. Hence, native predators feeding on benthic fauna such as fish could regulate the population growth of *R. harrisii* in the study area by reducing female survival. Although the population size seems to be stabilized at the monitoring locations, *R. harrisii* continues to expand its distribution range, and the rapid initial population increase is likely occurring at newly invaded sites.

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Introduction

Introduced marine species are considered a threat to coastal ecosystems, and thus studying marine invasions has received a lot of attention. However, long-term population monitoring data is rarely collected for marine invaders, even though the abundance of introduced species affects its impacts on and interactions with native species (Grosholz 2002; Strayer et al. 2006). The impacts of introduced species tend to increase with increasing population abundance (Virnstein 1977; Ricciardi 2003; Jackson et al. 2015),

although in high abundances the impacts could be evened out by intraspecific interaction (Kornis et al. 2014). In some cases, native species regulate the population growth of the invader through predation (Hunt and Behrens Yamada 2003; de Rivera et al. 2005; Jensen et al. 2007), thus decreasing the impacts of the invader as well as the rate of spread and long term population stability. As the population abundance of introduced species affects various interactions in the invaded community, long-term population monitoring data is needed to reveal the population-level dynamics of introduced species.

The populations of introduced species are not always stable, and drastic changes in population abundance can occur across space and time through demographic and environmental stochasticity (Simberloff and Gibbons 2004; Strayer and Malcom 2006; Burnaford et al. 2011). Introduced species often grow faster and larger and have higher survival and reproductive success in the invaded range (Grosholz and Ruiz 2003; Parker et al. 2013; Sargent and Lodge 2014). The observed enhanced performance in the introduced range is believed to be caused by access to more resources and the absence of predators and/or parasites (Grosholz and Ruiz 2003; Torchin et al. 2003), but several environmental and community level factors (e.g. water temperature, salinity, and intraspecific competition) can also alter survival and reproductive success (Branch 1975; Dorgelo 1976). Capturing the importance of different life stages, together with biotic and abiotic factors, for population abundance is crucial for understanding long-term population viability, stability and regulation (Coale and Trussell 1996).

Newly observed introduced species create a unique opportunity to study the population dynamics of invasions. One such newly observed invader in the northern Baltic Sea is the North American white-fingered mud crab *Rhithropanopeus harrisii* which was first observed in 2009 in the Archipelago Sea on the southwest coast of Finland (Fowler et al. 2013). In comparison to other seas, the brackish waters of the northern Baltic Sea have low species richness (Leppäkoski et al. 1999) and no native crab species (Bonsdorff 2006), which makes *R. harrisii* a novel functional species in the area. Within 3 years after the first observation, *R. harrisii* increased its abundance and rapidly extended its distribution area to include several habitats (i.e. soft sediments, rocky shores, and

macroalgae) (Fowler et al. 2013). This rapid increase in abundance and distribution negatively impacted the diversity and abundance of its prey species, leading to cascading top-down impacts (Forsström et al. 2015; Jormalainen et al. 2016).

Rhithropanopeus harrisii is an excellent model species as it has many characteristics of a successful invader, including a planktonic larval stage, high reproductive capacity, wide tolerance range of salinity (1–41‰) and temperature, and omnivorous feeding habits (Costlow et al. 1966; Turoboyski 1973; Forward 2009; Boyle et al. 2010) that have probably facilitated its spread to two oceans, 10 seas and freshwater inland reservoirs covering 28 countries (D'Incao and Martins 1998; Rodríguez and Suárez 2001; Iseda et al. 2007; Roche and Torchin 2007; Bacevičius and Gasiunaite 2008; Kotta and Ojaveer 2012; Fowler et al. 2013; HELCOM 2015). In its native range, *R. harrisii* are found in habitats that afford some type of shelter, such as oyster reefs, living and decaying vegetation, branches, and other debris (Ryan et al. 1956; Williams 1984; Petersen 2006). In invaded regions, the reproductive season of *R. harrisii* lasts for three to four summer months, and, in the Baltic Sea, the planktonic larval stage is most abundant in August (Turoboyski 1973). The larval survival and duration of the planktonic period (range 7–26 days) are dependent on water temperature and salinity, but in general, higher survival and shorter planktonic periods are found in warmer water and higher salinity (Chamberlain 1962; Costlow et al. 1966; Laughlin and French 1989a, b; Gonçalves et al. 1995). However, larval survival and the duration of the larval period can vary depending on location, as larval adaptations to the local environmental conditions have been observed (Laughlin and French 1989a). In the native range *R harrisii* grows to a maximum size of 15.5 mm (carapace width) (Ryan et al. 1956; Fowler et al. 2013) and in the invaded range maximum of 26 mm (Turoboyski 1973). In the native range females start the reproduction at a size of 4.8 mm (Ryan et al. 1956) whereas in the native range females start to reproduce at a size of 8 mm (Turoboyski 1973).

Here we study the population dynamics, demography and persistence of *R. harrisii* with the data collected during a 6-year monitoring period covering the supposed early invasion (2011–2016) in the Archipelago Sea in the northern Baltic Sea. We examined and evaluated changes in the population

abundance, demographic characteristics and environmental factors that contribute to the viability and stability of the *R. harrisii* population. In addition, we used the collected field data to construct single-sex stage-structured matrices and used a population matrix model to evaluate which life stage (juvenile, young-female or reproductive-female) or overall reproductive success is the driving force determining long-term population stability. We then used this model to assess the persistence of the introduced population in the study area.

Materials and methods

Sampling and measured variables

To monitor the establishment process of the introduced population of *R. harrisii* in the northern Baltic Sea, three sites (Kaarina N 60°24′28 E 22°26′27, Lapila N 60°23′59 E 22°2′49 and Naantali N 60°27′37 E 22°1′51; Fig. 1) were selected for sampling in the Archipelago Sea in the southwestern coast of Finland. The sites were selected from the area that *R. harrisii* individuals were known to occur before the sampling started in 2011, only 2 years after the first observation (Fig. 1). All sampling sites were soft sediment habitats (no large rocks or large bivalve shells present) with the common reed, *Phragmites australis*, growing on the shoreline. Kaarina is situated in a shallow and sheltered strait, Lapila in a shallow, sheltered bay, and Naantali in a deeper and more open strait. The salinity in the study area is ∼ 6, and the water temperature ranges from 4 (winter) to ∼ 20 °C (summer) with the high probability of ice cover during winter (Leppäranta and Myrberg 2009). *R. harrisii* were collected using plastic crates (30 × 30 × 30 cm) containing autoclaved oyster shells, used previously by Fowler et al. (2013) and Roche et al. (2009) to monitor introduced populations of *R. harrisii* globally. The crates provide a habitat for both juvenile and adult *R. harrisii*, and the individuals can freely move in and out of the crates.

Each year (2011–2016), three crates per site were deployed in water depths of 2–3 m in May (except for 2011 when the crates were deployed in July). *R. harrisii* were collected from the crates twice per year (except for 2011 only in fall) after the crates had been in the water for 6–8 weeks; in mid-July (summer

sampling; except for 2012 in early August) and mid- to late-September (fall sampling; except for 2012 in Lapila early October). All collected crabs were stored in 95% ethanol.

The reliability of the used sampling method was evaluated by calculating the repeatability between the three crates per sampling using an analysis of variance (ANOVA): $r = S_A^2/(S^2 + S_A^2)$, where S^2 is the variance in the total number of individuals within the three crates and S_A^2 is variance between the sampling occasions. The repeatability of the sampling method was 0.89 ($P < 0.001$), meaning that the used sampling method is reliable and the observed changes over the monitoring period reflect natural stochasticity in the population rather than the difference in the sampling efficiency between sampling occasions. In two occasions, one crate out of the three deployed in a site could not be found. To equalize the sampling effort for the demographic and population modeling analysis, a mean substitution using the values from the two retrieved crates was calculated for the number of juveniles, females and males and used as the third crate.

In the laboratory, *R. harrisii* were sexed based on abdomen width and the number of pleopods (Barnes 1980). The total number of *R. harrisii* (i.e. juveniles and adults combined) was counted per crate as well as the number of females, males, juveniles (here, defined as young-of-year from that calendar year and hence not reproductively mature), and ovigerous females. In addition, the number of eggs each ovigerous female carried was counted visually after eggs were stripped from the abdomen in 2012, 2014, and 2015. From Naantali, only two ovigerous females were collected across all years; therefore these data were excluded from the statistical analyses on ovigerous females. The carapace width (CW) of each individual was measured with electronic calipers to an accuracy of 0.01 mm.

To assess the number of juveniles in the fall sampling, the cutoff size of the juvenile cohort was determined separately for each site in each year according to the size distribution of the population (Figs. S1–S3) and the known growth rate of *R. harrisii* (Turoboyski 1973). The maximum CW of juveniles ranged between 4.0 and 7.5 mm. Due to the short reproductive season (i.e. short period of time the water temperature is warm enough for females to spawn) and the length of time *R. harrisii* larvae are in the planktonic phase (estimated 2–3 weeks), no young-
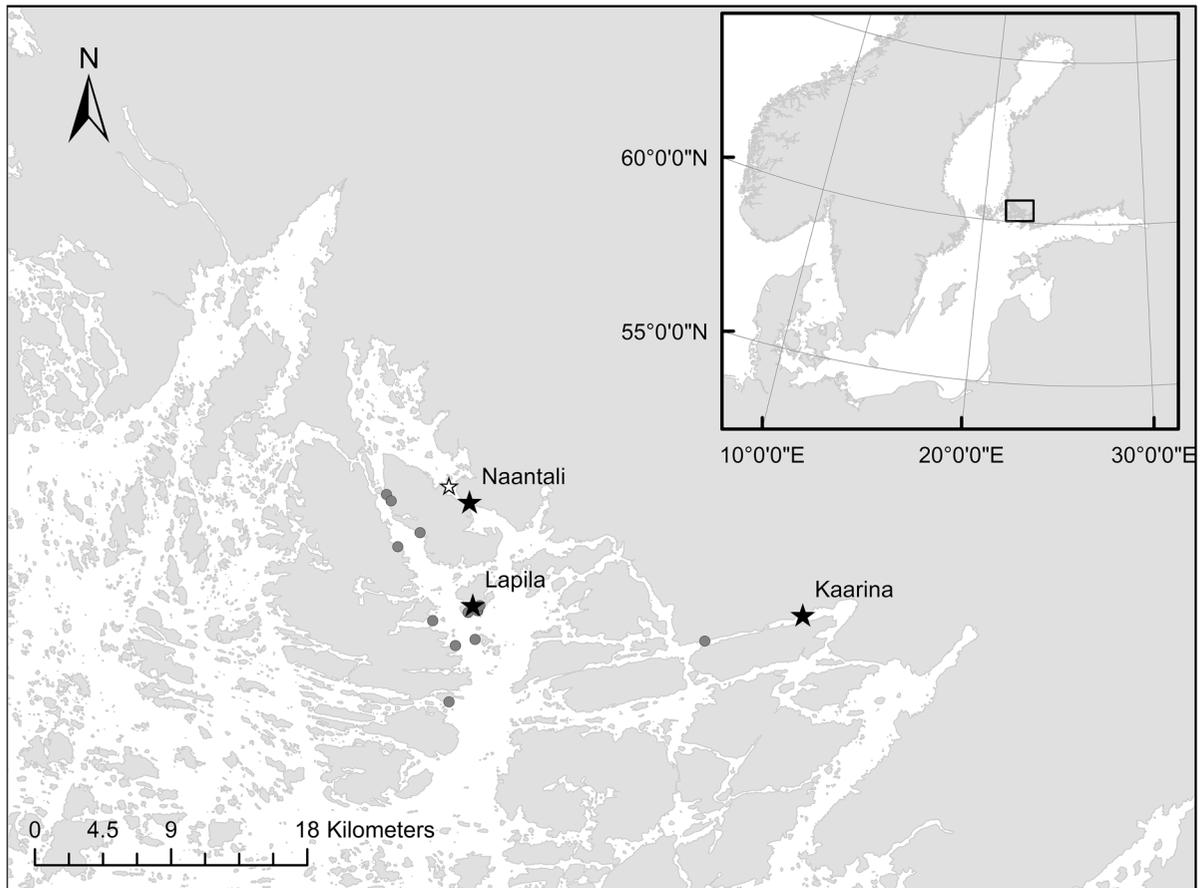
Fig. 1 The map of monitoring sites (black stars) and the observations of *Rhithropanopeus harrisii* prior to the start of the monitoring (grey circle). The white star represents the site of the first observation in 2009

of-year would be present during the summer sampling period in mid-July. Therefore, all individuals in the summer sampling (mid-July) were assigned as adults (personal observation; Turoboyski 1973). In addition, to study the occurrence of the rhizocephalan parasite *Loxothylacus panopei* (Gissler 1884), individuals were examined for the presence of an external form of the parasite (Van Engel et al. 1966).

Statistical analyses

First we examined whether there were changes in abundance and the different demographic characteristics during the 6-year monitoring period with a generalized linear mixed model (GLMM, SAS enterprise guide 6.1; Table 1). We analyzed fixed factors (i.e. sampling year, site, season, and interactions) affecting the population abundance, sex ratio, adult

size, reproductive output of females, recruitment and size of recruits (Table 1). Separate analyses were conducted for the number of adult females and the percentage of females as they are the ones that contribute new individuals to the population. As a measure of reproductive output, we used the variables of percentage and size of ovigerous females as well as the number of eggs that the female carried (Table 1).

To study recruitment and the quality of recruits, we used the number of juveniles, proportion of juveniles and size of juveniles as response variables (Table 1). To explain the variation in the quality of the juveniles [i.e. individual size as carapace width and weight are highly correlated in this species (Czerniejewski 2009; Hegele-Drywa et al. 2014)], mean summer (June–August) water temperature was used as an explanatory variable to cover the whole reproductive period from egg laying to the first crab stages, as maturation into

Table 1 The studied population demographic characteristics of *Rhithropanopeus harrisii* with explanatory variables and the distribution used in the generalized linear mixed model

Response variable	Explanatory variable	Used distribution	Demographic characteristic
Total abundance	Year, site, season, year × site, site × season, crate(site) as random factor	Negative binomial with a log link function	Population abundance
Number of adult females	Year, site, season, year × site, site × season, crate(site) as random factor	Negative binomial with a log link function	Abundance of females
Percentage of adult females	Year, site, season, year × site, site × season, crate(site) as random factor	Binomial distribution with logit link function	Sex ratio
Size of adults	Year, site, season, sex, year × site, site × season, site × sex, season × sex, year × sex, year × site × sex, site × season × sex	Normal distribution with an identity link function	Size of adults
Percentage of ovigerous females (2013–2016)	Year, site, year × site, crate(site) as random factor	Binomial distribution with a logit link function	Reproductive output
Size of ovigerous females	Year, site, year × site	Normal distribution with an identity link function	Reproductive output
Number of eggs a female carries (2012, 2014, 2015)	Size, year, site, year × site, size × site, size × year, size × year × site	Normal distribution with an identity link function	Reproductive output
Number of juveniles	Number of ovigerous females, mean air temperature (July–August), site, temperature × site	Negative binomial distribution with a log link function	Recruitment
Proportion of juveniles	Year, site, year × site, crate(site) as random factor	Binomial distribution with a logit link function	Recruitment
Size of juveniles	Mean summer (June–August) temperature, site, temperature × site	Normal distribution and an identity link function	Quality of recruits

the juvenile stage depends on environmental conditions experienced during the egg and planktonic larval stages (Costlow et al. 1966; Laughlin and French 1989b). In addition, the reproductive output of females in the summer (i.e. the number of ovigerous females) was also used as an explanatory variable. For these analyses, we used data collected from only Kaarina and Lapila; data from Naantali was excluded as only two ovigerous females were collected across all years. Sea surface water temperature data were obtained from the Finnish Meteorological Institute and was measured on Ruissalo mareograph (N 60°25′42 E 22°6′68) near the Lapila sampling site.

The model assumptions for normal distribution and/or homoscedasticity of variances were assessed by visual examination of diagnostic plots. The pairwise comparisons of the analyses were conducted using LSMESTIMATE statement implemented in GLIMMIX procedure (SAS enterprise guide 6.1), and the Bonferroni corrected *P* values are shown.

Population modeling

To assess the importance of the different life history stages for the population growth rate and to examine the persistence of the *R. harrisii* population in the northern Baltic Sea, a single sex stage-structured matrix model (Caswell 2000) was constructed using the population data collected from the Kaarina and Lapila sites combined. In the matrix model, only females were used as the sex ratio of *R. harrisii* is close to 1:1 (Fowler et al. 2013; Hegele-Drywa et al. 2014), and one male can fertilize several females, hence, there should always be enough males to fertilize the females. Juveniles collected in fall and young-females and reproductive females collected in summer in the years 2012–2016 were divided into three size classes

according to CW: juveniles (the same maximum size as in the analyses above), young-females (< 9 mm) and reproductive females (≥ 9 mm). Young-females represent small, non-reproductive females, as all ovigerous females collected throughout the 6-year monitoring were ≥ 9 mm with two exceptions (CW of 7.5 and 8.74 mm).

We assumed that all juveniles in year t that survived, matured into young-females in year $t + 1$, as in the Baltic Sea only a small percentage of females breed in the first summer after the juvenile stage (Turoboyski 1973). Similarly, we assumed that all young-females in year t that survived, matured into reproductive females in year $t + 1$ and all of the reproductive females in year t that survived, remained as reproductive females in year $t + 1$. The survival of juveniles, young-females and reproductive females and the reproductive success of the reproductive females (i.e. the transition probabilities) for each 3×3 transition matrix (2012–2013, 2013–2014, 2014–2015 and 2015–2016) were estimated from the collected field data. The transition probabilities were estimated using a GLMM with a binomial distribution and logit link function to account for the uneven number of collected individuals between the years, as individuals were not tracked using a mark-capture-recapture method.

To examine the proportional contribution of each life history stage (survival of juveniles, young-females and reproductive females) and overall reproductive success to the population growth rate, the deterministic and stochastic elasticity values (Caswell 2000) were estimated using the popbio package in R studio v 1.0.136 (Stubben and Milligan 2007). In addition, both a deterministic growth rate (λ) and stochastic growth rate (λ_s) was estimated for each matrix using a simulation-based approach (20,000 steps) (Caswell 2000).

To test whether the *R. harrisii* population will persist in the study area over the next 50 years, a quasi-extinction probability was simulated with 100 simulations and 10,000 iterations using the popbio package in R studio v 1.0.136 (Stubben and Milligan 2007). In the simulation, the starting number of individuals in each life stage was 91 juveniles, 7 young-females, and 54 reproductive females. These numbers represent the combined number of individuals collected in 2016 from Kaarina and Lapila and are the same population used for the matrix analysis

described above. The quasi-extinction threshold was set at 15 individuals which represents a 90% reduction from the starting population size.

Results

The total abundance of *R. harrisii*

Over the 6-year monitoring period, a total of 3288 *R. harrisii* were collected, sexed and measured. Of those, 1797 were collected from Kaarina with 737 adults (41%) and 1060 juveniles (59%). From Lapila, 976 individuals were collected with 508 adults (52%) and 468 juveniles (48%). From Naantali, 515 individuals were collected with 90 adults (17.5%) and 425 juveniles (82.5%). From all the collected individuals, 1335 (40.6%) were adults with 185 ovigerous females, and 1953 (59.4%) were juveniles. Not a single external form of the parasite *L. panopei* was observed.

The total abundance of *R. harrisii* varied between years and fluctuated differently at the site level (Table 2; Fig. 2a). The overall abundance of *R. harrisii* was the highest in Kaarina (mean 31 individuals per crate) and the lowest in Naantali (mean 6 individuals per crate), whereas in Lapila the mean number of individuals per crate was 28. Overall, the total abundance was higher in fall than summer at each site (Table 2).

Variation in abundance, sex ratio and size of adult *R. harrisii* and reproductive output of females

The abundance of females varied between years and sites (Table 2; Fig. 2b). There were significantly more females in summer (59%) than in fall (45%) overall (Table 2), although site level differences were significant only in Kaarina (9 individuals per crate in summer and 6 in fall; $t_{72} = 2.17$, P 0.03) and Lapila (11 individuals per crate in summer and 4 in fall; $t_{72} = 5.64$, $P < 0.0001$). Over the sampling period, the percentage of females varied between 44 and 58%, but the difference between years was not significant (Table 2). Across all time points, the percentage of females was close to 50% at each site (Kaarina 51%; Lapila 48%; Naantali 57%).

Overall, females were an average of 13.7% smaller than males in CW (Table 3), and significantly so in Kaarina and Lapila but not in Naantali (Table 3). The

Table 2 The results of generalized linear mixed models from separate analyses on the response variables of the total abundance of *Rhithropanopeus harrisii* and the number and percentage of females collected from crates in summer and fall during the years 2011–2016 from three sites in the Archipelago Sea, in the northern Baltic Sea

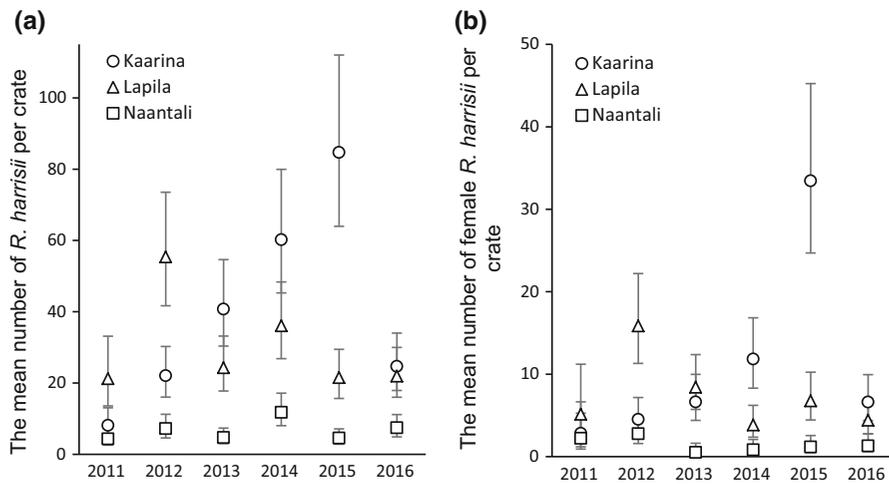| Effect	Number of *R. harrisii*			Number of females			Percentage of females		
	DF	*F*	*P* value	DF	*F*	*P* value	DF	*F*	*P* value
Year	5, 72	12.34	< 0.0001	5, 72	3.95	0.003	5, 64	0.57	0.72
Site	2, 6	73.48	< 0.0001	2, 6	39.97	0.0003	2, 6	0.80	0.49
Season	1, 72	261.8	< 0.0001	1, 72	6.00	0.017	1, 64	9.56	0.0029
Year × site	10, 72	9.34	< 0.0001	10, 72	8.55	< 0.0001	10, 64	1.78	0.083
Site × season	2, 72	32.02	< 0.0001	2, 72	7.78	0.0009	2, 64	0.92	0.41

Fig. 2 The mean number and 95% confidence intervals of **a** *Rhithropanopeus harrisii* individuals and **b** female (young and reproductive) *R. harrisii* per crate collected in summer and fall during the years 2011–2016 from three sites in the Archipelago Sea, in the northern Baltic Sea

Table 3 The mean carapace width (± SE) and range (min–max) of *Rhithropanopeus harrisii* collected from crates in summer and fall during the years 2011–2016 from three sites in the Archipelago Sea, in the northern Baltic Sea, with the *P* values from the pairwise comparisons between sexes

Site	Female			Male			*P* value
	n	Range (mm)	Mean ± SE (mm)	n	Range (mm)	Mean ± SE (mm)	
Overall	671	3.49–20.21	11.32 ± 0.24	663	3.39–23.37	12.99 ± 0.35	0.0002
Kaarina	357	3.49–20.21	12.14 ± 0.29	380	4.90–23.37	13.48 ± 0.30	0.019
Lapila	267	3.54–19.00	10.23 ± 0.30	241	3.39–22.12	11.52 ± 0.27	0.018
Naantali	47	7.84–15.50	11.60 ± 0.60	42	6.72–18.96	11.91 ± 0.96	1.00

mean adult size fluctuated between years and sites (Table 4). Individuals were the largest in 2016 (mean ± SE 12.83 ± 0.40 mm) and smallest in 2014 (10.96 ± 0.41 mm). In Kaarina, adults were larger (mean ± SE 12.81 ± 0.21 mm) than in Lapila

Table 4 Results from separate generalized linear mixed models on the factors affecting the size of adults and the number off eggs female *Rhithropanopeus harrisii* carry from crabs collected from crates in summer and fall during the years 2011–2016 from three sites in the Archipelago Sea, in the northern Baltic Sea

Effect	Size of adults			Effect	Number of eggs		
	DF	F	P value		DF	F	P value
Year	5, 1292	4.93	0.0002	Size	1, 69	221.35	< 0.0001
Site	2, 1292	22.05	< 0.0001	Year	2, 69	0.74	0.48
Season	1, 1292	17.68	< 0.0001	Site	1, 69	0.10	0.76
Sex	1, 1292	5.32	0.021	Year × site	2, 69	2.01	0.14
Year × site	10, 1292	2.67	0.003	Size × site	1, 69	0.02	0.90
Site × season	2, 1292	9.20	0.0001	Size × year	2, 69	1.20	0.31
Site × sex	2, 1292	0.37	0.69	Size × year × site	2, 69	1.74	0.18
Season × sex	1, 1292	2.11	0.15				
Year × sex	5, 1292	0.26	0.93				
Year × site × sex	10, 1292	0.78	0.65				
Site × season × sex	2, 1292	2.28	0.10				

(10.87 ± 0.20 mm) or in Naantali (11.75 ± 0.57 mm) (Table 4).

The relative amount of ovigerous females varied between sites, with more ovigerous females in Kaarina (63% of females) than in Lapila (43%) (Table 5). As noted before, only two ovigerous females were collected across all years from Naantali and were removed from the analyses. The percentage of ovigerous females also varied between years, showing a similar pattern at both sites (Table 5; Kaarina 55–75% and Lapila 24–57%). Overall, the highest percentage of ovigerous females was in 2016 (64% of females) and lowest in 2015 (39%), and the difference was significant ($t_{12} = 2.77$, P 0.017). The mean size of ovigerous females was similar throughout the years within both sites (Table 5; the range of mean: Kaarina 12.13–12.93 mm CW; Lapila 11.79–13.58 mm CW)

and between sites (Kaarina mean 12.65 mm, range 8.74–18.50 mm, n = 104; Lapila mean 12.64 mm, range 7.50–19.00 mm; n = 66). The mean number of eggs carried by a female was 5579 eggs (range 1635–10,536 eggs; CW range 7.5–18.51 mm; n = 81), and female size (CW) was the only tested variable that affected the number of the eggs the female carried (Table 4, Fig. 3).

Variation in the recruitment and the quality of recruits

Juvenile abundance (young-of-year) was positively correlated with the mean water temperature during the larval period (July–August) ($F_{1,3} = 8.72$, $P = 0.0599$) at both sites ($F_{1,3} = 0.25$, $P = 0.7$), but was not correlated with the number of ovigerous females in

Table 5 Results from separate generalized linear mixed model on factors affecting the percentage and size of ovigerous *Rhithropanopeus harrisii* females collected from crates in summer and fall during the years 2011–2016 from three sites in the Archipelago Sea, in the northern Baltic Sea

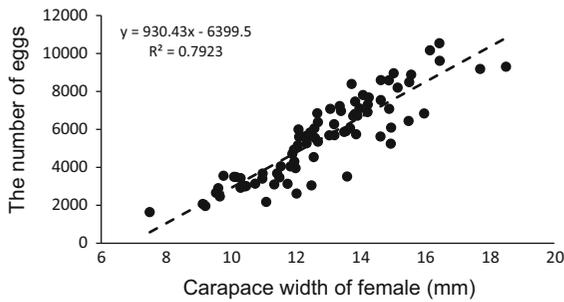| Effect	Percentage of ovigerous females			Size of ovigerous females		
	DF	F	P value	DF	F	P value
Year	3, 12	3.39	0.054	4, 160	1.42	0.23
Site	1, 4	9.94	0.034	1, 160	0.00	0.98
Year × site	3, 12	0.86	0.49	4, 160	0.23	0.92

Fig. 3 The linear relationship of *Rhithropanopeus harrisii* female size (carapace width) to the number of eggs carried. Females (N = 81) were collected from two sites (Kaarina and Lapila) during 3 years (2012, 2014 and 2015)

Fig. 4 The estimated juvenile size of *Rhithropanopeus harrisii* in fall (CW ± 95% CI) at 10th percentile, lower quantile, median, upper quantile and 90th percentile of the mean summer sea surface water temperature (June–August) covering the reproductive period from egg laying to the first crab stage

the summer ($F_{1,3} = 1.73$, $P = 0.3$). The proportion of juveniles varied between years ($F_{2,6} = 7.75$, $P = 0.02$), sites ($F_{5,30} = 19.57$, $P < 0.0001$), and the year × site interaction ($F_{10,30} = 6.43$, $P < 0.0001$; Table 6). Juveniles were larger in Kaarina than in Lapila or Naantali ($F_{2,1943} = 8.80$, $P = 0.0002$; Table 6). The mean summer (June–August) water temperature was positively correlated with the mean size of juveniles ($F_{1,1943} = 135.56$, $P < 0.0001$), but the extent of the effect varied by the site ($F_{2,1943} = 10.56$, $P < 0.0001$; Fig. 4).

Population modeling

According to both deterministic and stochastic elasticities, the population growth rate was proportionally most sensitive to the changes in the survival rate of reproductive females. Deterministic elasticities for the
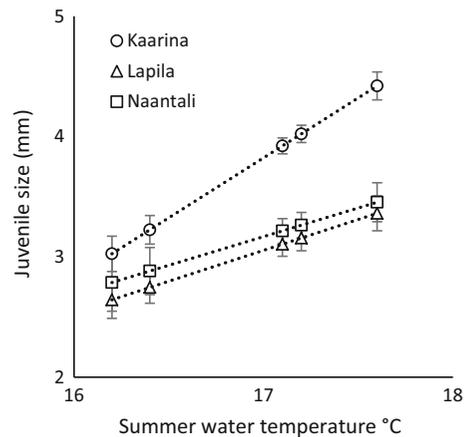
survival of reproductive females ranged from 0.37 to 0.47 (other life stages: 0.18–0.21), and stochastic elasticity for the survival of reproductive females was 0.39 (other life stages: 0.20–0.21). The deterministic population growth rate (λ) in the years 2012–2016 varied between 0.76 and 1.25 (values of λ indicates a constant population growth rate, < 1 declining population growth, and > 1 increasing population growth). The stochastic population growth rate (λ_s) was 0.97 (95% CI 0.967 and 0.98). The mean quasi-extinction probability (with the extinction threshold of a 90% decline in population size) over the next 50 years was 29% (Fig. 5).

Table 6 The mean carapace width, range (min–max) and percentage of juvenile (young-of-year) *Rhithropanopeus harrisii* from all individuals collected in fall from three replicate crates during years 2011–2016 from three sites at the Archipelago Sea, Finland

Year	Kaarina				Lapila				Naantali			
	n	Range (mm)	Mean ± SE (mm)	(%)	n	Range (mm)	Mean ± SE (mm)	(%)	n	Range (mm)	Mean ± SE (mm)	(%)
2011	38	2.30–6.70	4.65 ± 0.16	74	66	1.40–6.50	3.44 ± 0.12	75	35	1.50–5.40	2.43 ± 0.17	67
2012	116	1.08–4.67	3.42 ± 0.09	72	143	1.58–4.04	2.69 ± 0.08	73	41	1.39–3.99	2.21 ± 0.15	71
2013	247	1.73–6.93	3.80 ± 0.06	82	42	1.60–3.55	2.59 ± 0.15	56	57	1.84–5.32	3.02 ± 0.13	98
2014	390	1.76–7.44	4.16 ± 0.05	88	122	1.57–5.98	3.44 ± 0.09	95	159	1.94–6.74	4.04 ± 0.08	93
2015	178	1.45–4.42	2.90 ± 0.07	41	43	1.52–3.42	2.29 ± 0.15	52	46	1.38–3.77	2.70 ± 0.15	87
2016	91	1.92–6.99	4.50 ± 0.10	76	52	1.60–5.11	3.39 ± 0.14	73	87	1.31–4.41	2.86 ± 0.11	89

To assess the number of juveniles (young-of-year) in fall sampling, the cutoff size of the juvenile cohort was determined individually for each site in each year according to the size distribution of the population (Fig. S1–S3)
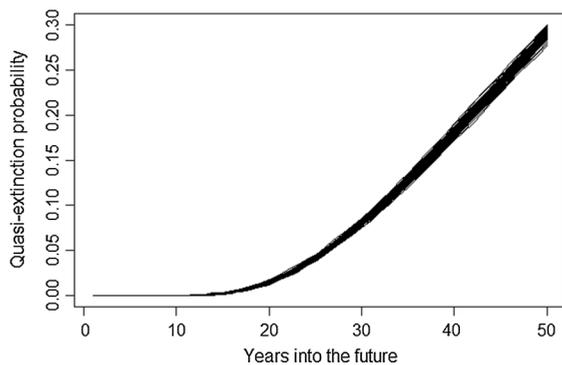
Fig. 5 The quasi-extinction probability of the *Rhithropano-peus harrisii* population in the northern Baltic Sea using 100 simulations with 10,000 iterations with extinction threshold of 15 individuals (90% population size decrease). The starting population size (N = 152) was the number of females collected in 2016 from two sites (Kaarina and Lapila)

Discussion

The total abundance of *R. harrisii*

This work represents the first study on the early invasion population dynamics of the mud crab *R. harrisii* in the northern Baltic Sea. Monitoring the population-level dynamics of an introduced marine species at stationary sites during the initial colonization period and subsequent spread for multiple years has rarely been conducted (but see O'Connor 2014; Gíslason et al. 2017), yet are important to understand population stability and viability and are needed for legislative and management purposes (Lehtiniemi et al. 2015).

The overall abundance of *R. harrisii* in the northern Baltic Sea was lower than in the native range but higher than in the southern Baltic Sea using the same sampling method (Fowler et al. 2013). Our results show that the abundance of *R. harrisii* in the northern Baltic Sea initially increased rapidly, but then declined. Hence, the population seemed to follow the boom and bust pattern that is commonly observed with introduced species where a rapid increase is often followed by a decline that stabilizes at a lower level (Simberloff and Gibbons 2004). The rapid initial increase may be caused by multiple factors such as the escape from predators and parasites, access to more resources (Torchin et al. 2003; Simberloff and Gibbons 2004), and increased population growth as *R. harrisii* is a R-selected species (i.e. high growth

rates and fecundity). Indeed, during the 6-year monitoring not a single externa of the parasite *L. panopei* was observed, indicating that at least this parasite of *R. harrisii* (Blakeslee 2015) has not spread to the northern Baltic Sea. Population declines and collapses, on the other hand, are thought to be caused by intra- and interspecific competition, the exhaustion of resources, and/or subsequently introduced parasites, pathogens (Simberloff and Gibbons 2004). Despite the decline in population abundance and negative stochastic population growth rate, the quasi-extinction probability simulation predicts that *R. harrisii* will persist in the study area for at least the next 50 years. Further monitoring over the next few years is needed to distinguish whether the population stabilizes at a lower abundance level or whether abundances show a more cyclic boom and bust pattern.

Abundance, sex ratio, size and reproductive output of *R. harrisii*

To understand changes in the population dynamics during the monitoring period and to delineate factors potentially affecting the observed dynamics, we studied demographic traits and population characteristics of *R. harrisii*. The abundance of females varied between the monitoring years and sites in a manner similar to the overall *R. harrisii* abundance with an initial increase and subsequent decline. According to the population modeling, changes in the survival of reproductive females have the largest impact on the population growth rate of *R. harrisii* in the northern Baltic Sea as compared to other life stages. This is not surprising given the high reproductive output of females and low survival of larval and juvenile individuals (Costlow et al. 1966; Turoboyski 1973; Laughlin and French 1989b). Taken together, these results indicate that reproductive females drive the overall population dynamics of *R. harrisii* in the northern Baltic Sea, and factors regulating the number of adult females such as predation and winter mortality could regulate population abundance. In the study area, several fish species, such as perch (*Perca fluviatilis*) and four-horned sculpins (*Myoxocephalus quadricornis*) preferentially consume adult *R. harrisii* between 9 and 16 mm CW, which is the size range of reproductively mature *R. harrisii* (Puntila 2016). In addition, cold water temperatures during the winter months may increase the mortality of females, as

observed with Chesapeake Bay (USA) blue crabs (*Callinectes sapidus*) (Rome et al. 2005).

The percentage of females differed significantly only between seasons; in summer there were more females than males and vice versa in fall. These results may indicate sex specific differences either in mortality or habitat occupancy of males and females during the summer months, possibly related to reproduction. Females might prefer warmer water temperatures in shallower areas (where our crates were placed) in summer that decrease the duration of egg development (Costlow et al. 1966; Gonçalves et al. 1995; Forward 2009) and also seek shelter from pelagic predators in these habitats during the egg carrying period. While habitat preference may also help explain the reduction of females in the fall, it is also possible that a large proportion of females die after brooding eggs.

The size of the adults in the northern Baltic Sea was considerably larger than reported from the native range (Ryan et al. 1956; Fowler et al. 2013) which is not surprising as *R. harrisii* grows 44% larger in the introduced range of the Northeast Pacific Ocean (Grosholz and Ruiz 2003). The maximum body sizes of both male (CW 23.37 mm) and female (20.21 mm) *R. harrisii* in the northern Baltic Sea seemed to be slightly larger than individuals from other introduced populations elsewhere (the maximum CW of males 17.30–22.10 mm and females 10.9–19.41 mm; Mizzan and Zanella 1996; Roche and Torchin 2007; Hegele-Drywa et al. 2014; Rodrigues and Incao 2015), except for males in one location in Poland (male CW 26.1 mm; Turoboyski 1973). The larger maximum size of females in the northern Baltic Sea is notable as larger females lay more eggs, potentially increasing the production of offspring to the population in comparison with other introduced or native populations. In addition, the overall percentage of ovigerous females in the northern Baltic Sea (53%) was higher than ∼ 30–40% previously reported from the southern Baltic Sea (Turoboyski 1973) indicating a higher reproductive output in the northern Baltic Sea. However, a reliable comparison is difficult as the sampling methods between the studies were different. This larger size of introduced species in invaded areas is a common phenomenon observed in several species groups (Grosholz and Ruiz 2003; Parker et al. 2013) and may be caused by increased available resources in the invaded area and/or absence of predators and parasites (Torchin et al. 2001; Grosholz and Ruiz

2003). On the other hand, larger body sizes in ectotherms do occur in lower temperatures where individuals grow slower but larger and mature at larger body sizes due to low metabolic rates (Angilletta et al. 2004; Kelley et al. 2015). *R. harrisii* in the northern Baltic Sea represent the northernmost known populations found at some of the coldest winter water temperatures (Fowler et al. 2013), which might explain the larger body size.

Recruitment of juvenile *R. harrisii*

There was a high proportion of recruits (young-of-year) in the northern Baltic Sea population; more than 59% of all the collected individuals were juveniles. This is more than the 30% previously reported from the southern Baltic Sea in Poland from an area where *R. harrisii* has occurred ∼ 10 years (Hegele-Drywa and Normant 2014), although the definition of "juvenile" and the sampling methods were different. Hegele-Drywa and Normant (2014) defined all individuals smaller than 4.4 mm CW as juveniles unlike this study where juveniles were defined separately for each year according to the population size distribution (the maximum size of juvenile ranged < 4.0–7.5 mm CW). Therefore, we defined some individuals as juveniles that Hegele-Drywa and Normant (2014) defined as adults. However, the proportion of juveniles in the northern Baltic Sea is higher than previously reported even if the 4.4 mm maximum carapace width is used (41%). While sampling methods could explain some of the difference in the proportion of juveniles between studies, the higher female reproductive output observed in the northern Baltic Sea may also contribute to the observed difference. From the other introduced sites elsewhere, high proportions of recruits have been reported from one location in Panama (Roche et al. 2009). Despite the high recruitment of juveniles in this study, the majority die during the first winter indicating that aperiodic cold winters may influence the range expansion and population dynamics of this species in the northern Baltic Sea as observed with other species (Canning-Clode et al. 2011; Canning-Clode and Carlton 2017).

The growth of juveniles was positively correlated with the mean water temperature during the larval period and the first crab stages; juveniles grew larger during warm summers than cold summers. Water temperature affects the duration of the planktonic

larval stage of *R. harrisii* (Costlow et al. 1966; Laughlin and French 1989a, b), and juveniles grow to a larger size after a warm summer due to a shorter planktonic larval stage, allowing them to metamorphose into the crab stage sooner. Similar increased growth rates and decreased duration of intermolt periods in warmer water temperatures have been observed in several other crab species (Stoner et al. 2013; Cunningham and Darnell 2015; Ryer et al. 2016; Yuan et al. 2017). This larger juvenile size may also increase the odds of surviving the winter, as seen in larger juvenile blue crabs (*C. sapidus*) (Bauer and Miller 2010). The timing of the fall sampling cannot explain the observed difference in juvenile size between the years. For example, in Lapila the 2014 and 2015 samplings were done on the same date, and there was still a significant difference in juvenile size. Other factors in addition to water temperature, such as juvenile density and the amount of available food, may also affect juvenile sizes due to intraspecific competition (Donahue 2004; Moksnes 2004).

The juvenile abundance in the fall was more correlated with water temperature during the larval period than the reproductive output of females, indicating that the survival of the planktonic larvae has a large impact on the abundance of juveniles. As both the survival and growth of larvae are dependent on temperature, *R. harrisii* may benefit from the warming summer temperature caused by climate change. The surface seawater temperature at the study site has increased by 1.5 °C over the period of May to September during the past 46 years (Mäkinen et al. 2017), potentially facilitating the establishment and spread of *R. harrisii* in the northern Baltic Sea. In the future, the sea surface water temperature is estimated to increase by 4 °C over the next 80 years in the northern Baltic Sea (Meier 2006) which could potentially increase hatching and larval survival. However, salinity is estimated to decrease over this same period, although at a slower rate (Meier 2006). As the larval survival of *R. harrisii* is positively related to both temperature and salinity (Costlow et al. 1966; Laughlin and French 1989a, b), decreasing salinity in the future caused by climate change may counteract the positive effects of increasing temperature (Holopainen et al. 2016).

Differences between the monitoring sites

Even though we sampled only three sites, there were stark differences in population dynamics between the sites. For one, the population abundance in Naantali and Lapila stabilized early, while the population size in Kaarina continued to increase longer. In addition, Kaarina had larger proportion of ovigerous females and larger sized juveniles than other monitoring sites. The observed differences between the sites could reflect the invasion history of *R. harrisii* in the northern Baltic Sea. Naantali, which has the lowest population abundance in 2016, is the closest to the site of the first observation and therefore may be experiencing a stabilizing phase after years of population growth. In comparison, Kaarina is the furthest away and may represent a population that is still in its first phase of the invasion and is experiencing continued population growth.

Due to the relatively close proximity of the three sites (~ 25 km) and the fact that they are all located within sheltered areas of the inner Archipelago, which receive minimal water currents from outside sources, population level differences observed in this study of *R. harrisii* are not due to water temperatures alone. However, there might be differences in habitat quality and environmental factors between the sites. Naantali, which had the lowest abundance, has the least amount of shallow habitat and is prone to wave action due to the high volume of shipping traffic. The highest abundance of *R. harrisii* was observed in Kaarina (1.5 times higher than in Lapila) which could indicate that the carrying capacity at Kaarina is the highest out of the three monitoring sites. In addition, differences in the predatory regime could affect the observed differences in population abundances as the fish species assemblage in Kaarina is different from Naantali and Lapila. In Kaarina perch occur in low numbers and four-horned sculpins that readily consume *R. harrisii* are absent (Puntila 2016) as they prefer deeper and colder habitat (Kottelat and Freyhof 2007).

Conclusions

This study represents one of the first multiyear monitoring programs of an introduced aquatic species in the northern Baltic Sea. As observed in many other introduced species (Simberloff and Gibbons 2004),

the population abundance of the mud crab *R. harrisii* in the northern Baltic Sea increased over the beginning of the monitoring program and then declined although there were differences among monitoring locations. *R. harrisii* has established a population that is expanding its distribution range in the study area, and the local populations seem to be stable with a low probability for extinction over the next 50 years. The survival of the reproductive females is the most important life stage for the population growth rate of *R. harrisii* in the northern Baltic Sea. This information could be used for management purposes to target management efforts that decrease the survival of reproductive females.

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