Ecology, 98(9), 2017, pp. 2241–2247

The double edge to parasite escape: invasive host is less infected but more infectable

Carolyn L. Keogh,[1,2,4] Osamu Miura,[2] Tomohiro Nishimura,[2,3] and James E. Byers[1]

[1]*Odum School of Ecology, University of Georgia, Athens, Georgia 30602 USA*
[2]*Oceanography Section, Science Research Center, Kochi University, 200 Otsu, Monobe, Nankoku, Kochi 783-8502 Japan*
[3]*Laboratory of Aquatic Environmental Science, Faculty of Agriculture and Marine Science, Kochi University, 200 Otsu, Monobe, Nankoku, Kochi 783-8502 Japan*

Abstract. Nonnative species that escape their native-range parasites may benefit not only from reduced infection pathology, but also from relaxed selection on costly immune defenses, promoting reallocation of resources toward growth or reproduction. However, benefits accruing from a reduction in defense could come at the cost of increased infection susceptibility. We conducted common garden studies of the shore crab *Hemigrapsus sanguineus* from highly parasitized native (Japan) populations and largely parasite-free invasive (USA) populations to test for differences in susceptibility to infection by native-range rhizocephalan parasites, and to explore differences in host resource allocation. Nonnative individuals showed at least 1.8 times greater susceptibility to infection than their native counterparts, and had reduced standing metabolic rates, suggesting that less of their energy was spent on physiological self-maintenance. Our results support an indirect advantage to parasite escape via the relaxation of costly physiological defenses. However, this advantage comes at the cost of heightened susceptibility, a trade-off of parasite escape that is seldom considered.

Key words: biological invasions; common garden experiment; ecological immunology; enemy release hypothesis; infection susceptibility; Polyascus; *trade-offs.*

Introduction

Dramatic reductions in both the prevalence and intensity of parasite infection (i.e., parasite escape) have been documented for numerous nonnative populations of both plants and animals, across terrestrial, freshwater, and marine ecosystems (Mitchell and Power 2003, Torchin et al. 2003, Blakeslee et al. 2013). A reprieve from parasite infection could benefit nonnative populations in two key ways. First, escape from parasites alleviates the negative impacts of parasite infection on host survivorship or fecundity. A second, less obvious benefit of parasite escape is that of "compensatory release" (sensu Colautti et al. 2004), whereby parasite-free nonnative organisms may free up internal resources no longer needed in the maintenance and deployment of the immune system and reallocate them toward growth and reproduction (Blossey and Notzold 1995, White and Perkins 2012).

This expected compensatory benefit to nonnative hosts is based on the observation that hosts pay costs (either evolutionarily, physiologically, or both) to develop, maintain, and deploy immune defenses (Sheldon and Verhulst 1996, Zuk and Stoehr 2002, Graham et al. 2011). However, the possible energetic benefit that nonnatives gain by reducing immune defense investment may impose long-term risks. Specifically, a lack of immune defense maintenance or a reallocation of resources to other traits could lead to increased susceptibility of nonnative populations to both newly introduced natural enemies from their native range, and generalist or fast-evolving parasites in the introduced range (Perkins et al. 2008), as has been observed in invasive plants (Wolfe et al. 2004).

Whether nonnative populations differ from native-range populations in their ability to defend against infection by native-range parasites provides a critical test of the proximate and ultimate consequences of relaxed parasite-mediated selection among introduced populations. However, to our knowledge, only one study comparing the susceptibility of nonnative vs. native host populations to native parasites has been carried out in a nonnative animal, the freshwater snail *Potamopyrgus antipodarum*

Manuscript received 21 November 2016; revised 1 June 2017; accepted 12 July 2017. Corresponding Editor: Jonathan H. Grabowski.
[4] E-mail: ckeogh@uga.edu

(Fromme and Dybdahl 2006). Importantly, the clonal reproduction of the snail host in that study probably limited the snails' likelihood of adapting rapidly to the change in trematode parasite infection risk. More recent studies of immune traits in invasion-front cane toads in Australia that have escaped parasites have provided insight to changes in immunity that may result from altered selection pressures at the invasion's expanding edge, but the susceptibility of toads across the temporal invasion gradient has not yet been studied (Llewellyn et al. 2012, Brown et al. 2015).

Here we explore a possible double edge of parasite escape using the shore crab *Hemigrapsus sanguineus* that is native to Asia, ranging from the southern coast of Russia to Hong Kong, including Taiwan and the Japanese archipelago. The crab was introduced to the northeastern coast of the United States likely as larvae in ballast water and has been established since at least 1988 (McDermott 1991, Epifanio 2013, Blakeslee et al. 2017). Reaching average densities of >200 individuals/m^2 in central parts of its nonnative range in the Northwest Atlantic, *H. sanguineus* has become the dominant rocky intertidal crab in this system (Lohrer and Whitlatch 2002, Griffen and Byers 2009, O'Connor 2014).

In its native range, *H. sanguineus* is host to five species of digenean trematodes and one unidentified microsporidian parasite, along with three species of castrating rhizocephalan barnacles in the genera *Polyascus* and *Sacculina* (Takahashi and Matsuura 1994, Yamaguchi et al. 1994, Blakeslee et al. 2009, McDermott 2011). These rhizocephalan parasites are widespread throughout the crab's native range, and can reach prevalences exceeding 80% (Yamaguchi et al. 1994). In contrast, invasive populations on the Northeast coast of North America experience a near complete reprieve from parasite infection (Blakeslee et al. 2009, McDermott 2011). Importantly, none of the three species of rhizocephalan parasites have been introduced (Blakeslee et al. 2009), and we have never seen a rhizocephalan infection in any of the >1,000 *H. sanguineus* we have collected in the invasive range between 2009 and 2015 (C. L. Keogh, *personal observation*). Because rhizocephalan barnacle parasites should exert strong selective pressure on their crab hosts and are prevalent in native-range populations of *H. sanguineus* while being fully absent in the invasive range, we focused our infection experiment on this group of natural enemies.

To explore whether a reprieve from infection pressure could result in heightened susceptibility to infection among nonnative populations, we conducted a common garden experiment to compare the susceptibility of *H. sanguineus* from native and nonnative populations to their castrating rhizocephalan barnacle parasites. Further, we measured standing metabolic rate as an indicator of physiological self-maintenance costs in uninfected native and nonnative individuals to determine if nonnatives may be spending less of their available energy on physiological upkeep of immune defenses.

METHODS

Collections and background infection prevalence

Between 27 March and 1 April 2014, we collected *Hemigrapsus sanguineus* from three spatially distant sites in their native range in Japan (Appendix S1: Table S1, Fig. S1A; $N = 407$ total crabs, carapace width = 18.53 ± 5.12 mm [mean ± SD] measured at the widest point of the carapace just anterior to the third spine), incorporating both the Pacific Ocean and Sea of Japan coasts in order to better represent regional population genetic diversity (Yoon et al. 2011). Live specimens were collected between 1 and 2 April 2014 from three sites spanning the introduced range on the U.S. East Coast (Appendix S1: Table S1, Fig. S1B; $N = 201$, carapace width = 18.66 ± 3.60 mm), and shipped to a laboratory site at Kochi University, Kochi, Japan. All crabs collected in both source regions were held during transport to the lab in coolers with ice packs and moistened cloths to prevent desiccation. Despite the greater geographic distance travelled by the crabs collected in the nonnative range (U.S.), transit times between collection and arrival in the laboratory were approximately equal between U.S. and Japan sites (48–72 h). Upon arrival in the laboratory, crabs were transferred to aerated, locally collected seawater in closed aquaria (i.e., with no possible outflow of invasive-range crabs or larvae to the environment). All crabs were starved for one week to standardize nutrition status, and were subsequently provided ad libitum access to the seaweed *Undaria* spp. two to three times per week.

The prevalence of reproductively mature (i.e., externally visible) rhizocephalan infections was 0% in crabs from the nonnative U.S. sites (consistent with the continued absence of rhizocephalan parasites throughout the invasive range) and ranged from 0% to 14% in the three native-range sites (Appendix S1: Fig. S1). Because rhizocephalan infections are not externally detectable before they reach maturity, and internal phases of early-stage infections are difficult to distinguish microscopically within the crab, we developed an 18S rDNA PCR assay to detect the presence of latent pre-reproductive *Polyascus* and *Sacculina* infections within host tissues (Appendix S2). We used this assay to quantify the prevalence of pre-reproductive infections by randomly subsampling 20–30 crabs per collection site from the native range with no external signs of infection. Background internal infection was not assayed in invasive-range crabs because rhizocephalan parasites do not infect *H. sanguineus* in the invasive range.

Common garden susceptibility experiment

To test for differences in susceptibility to rhizocephalan parasite infection between invasive- and native-range crabs, we carried out a common garden experiment using between 20 and 30 individuals per site for two invasive- and two native-range sites, as well as some additional (≤10) individuals from a third invasive- and native-range site, for a total of 66 invasive- and 54 native-range sentinel crabs (Appendix S1: Table S1). We excluded a small percentage of native-range crabs that showed external signs of rhizocephalan infection. Thus, the sentinel crabs showed no external signs of infection prior to the start of the experiment, and ranged in size from 12 to 26 mm carapace width.

All experimental crabs were held in a common 60-L tank filled with approximately 45 L of aerated seawater from a nearby coastal area where neither the host crab nor the parasite were observed (thus the seawater should not contain parasite infective stages). This common holding tank was partially submerged in a basin of chilled water to maintain a constant temperature between 18 and 22°C (18.29° ± 0.04°C [mean ± SE]). Inside the common tank the sentinel crabs were maintained in 14.5 × 6.5 × 9 cm plastic mesh boxes (0.1 × 0.5 cm mesh size) in groups of two to four to reduce cannibalism, and were given access to *Undaria* spp. every 2–4 days.

To achieve seminatural exposure to rhizocephalan infective stages, we added to the common tank ~45 infected native-range crabs with reproductively mature rhizocephalan infections. To reduce the potential bias in experimental infection rates from local adaptation between sympatric host parasite populations, the infected crabs that were the source of infective rhizocephalan parasite larvae were collected at a site that was distinct from any of the three native-range sentinel crab collection sites (Appendix S1: Fig. S1A). The infected crabs were contained individually in 5 × 6 cm compartments within two 35 × 22 × 5 cm plastic storage boxes with 0.5 cm diameter holes that allowed released parasite larvae to move freely into the water column. Each of three water samples taken from the tank at two-week intervals after the addition of the sentinel crabs confirmed the frequent presence of parasite larvae in the common garden tank.

During exposure, the boxes with sentinel crabs floated near the top of the water column, while the infected crabs were at the bottom of the tank. Such vertical stratification of the infected and sentinel crabs allowed us to capitalize on the positive phototaxic behavior of the parasite larvae (Hoeg 1984) to ensure a high contact rate of infective larvae with the sentinel crabs, and cages were redistributed randomly within the tank regularly during feeding and water changes to promote even exposure in case of a non-uniform distribution of parasite larvae. Approximately 30% of the tank water was changed weekly.

To ascertain the effect of exposure duration on infection as a function of source region, we staggered the introduction of sentinel crabs into the common garden tank in three exposure blocks containing an even mix of native and invasive-range individuals, thus creating three different exposure lengths (4, 3, or 2 weeks). After all crabs had been exposed for at least 2 weeks, the infected source crabs were removed from the tank, and the sentinel crabs were maintained for an additional 4 weeks to allow any successful infections to establish and reach a detectable level. No infections were externally detectable after the 4-week incubation period, and the time needed from initial infection to release of a visible externae is not known for rhizocephalan species infecting *H. sanguineus.* Therefore, all crabs were dissected and target tissues harvested for PCR detection of infection (Appendix S2).

We used generalized linear mixed models (GLMM) with a binomial distribution to determine the likelihood of experimental infection as a function of host source region (native or invasive), exposure block, crab size (carapace width), and sex as fixed effects, and collection site within the two source regions as a random effect in the initial full model. GLMM models were implemented in R v3.1.2 (R Development Core Team 2015) via the package lme4 (Bates et al. 2014). From the full model, we used backward elimination based on conditional AIC values to select the best fitting model. As a measure of model fit, the proportion of variance explained by fixed effects alone (marginal R^2) and by both fixed and random effects (conditional R^2; Nakagawa and Schielzeth 2013) were extracted using the rsquared.GLMM function in the MuMIn package.

Standing metabolic rate

As an indicator of the energetic cost of self-maintenance in uninfected crabs, we measured resting oxygen consumption as a proxy for standing metabolic rate (SMR) in a separate group of crabs from the same three native-range and invasive-range sites (approximately six individuals per site) using an intermittent-flow respirometry system (Q-Box AQUA; Qubit Systems, Kingston, Ontario, Canada). These crabs were collected and maintained in a separate tank under the same conditions as the common garden experimental crabs. All crabs used in this assay were acclimated to the laboratory holding conditions and feeding schedule for approximately 10 weeks prior to measurement. After the assay was completed, all individuals were dissected to assess rhizocephalan parasite infection status using a PCR assay (Appendix S2), and only data from individuals that were negative for infection were included in the analysis (n = 10 native-range and n = 12 invasive-range individuals). Mass-specific oxygen consumption for each crab was calculated as the rate of oxygen consumption per kg per hour (see Appendix S3 for detailed measurement methods). We used a linear mixed effects model to test for an effect of source region on resting oxygen consumption rate, with crab size (carapace width) and sex as covariates, and individual collection site as a random effect.

RESULTS

Common garden susceptibility experiment

In our survey of field-acquired infection in native-range crabs without external signs of infection, we found

TABLE 1. Results of reduced generalized linear mixed model of infection (binomial) outcomes from common garden exposure experiment.

Variable	Estimate	SE	*z*	*P*	Variance	Variance SD
Intercept	−0.1	0.50	−0.21	0.84		
Source Region	1.45	0.72	2.02	0.04		
Site (random)					0.40	0.63

Note: Native source region is the reference category, with site as a random effect.

rates of internal infection ranging from 32% to 45% (mean = 38%; Appendix S1: Table S1, Fig. S1A), suggesting that hosts at all three native-range sites experience sizable parasite infection risk in their natural habitat.

Experimental susceptibility to parasite infection was significantly higher among invasive-range *H. sanguineus* compared to native-range crabs (Table 1, Fig. 1). Assuming all infections in native-range crabs were acquired during the experiment, the infection susceptibility in invasive-range crabs was 1.8 times greater. A model including Source region as a fixed effect and Site as a random effect best described crab infection prevalence (Appendix S1: Table S2).

Standing metabolic rate

Across body sizes, non-infected native range crabs had significantly higher resting oxygen consumption rates than non-infected invasive-range crabs (Table 2), indicating higher standing metabolic rate (SMR). Mass-specific oxygen consumption rates decreased significantly with increasing crab size (Table 2, Fig. 2). Male crabs had significantly higher SMR than females (Table 2; Appendix S1: Fig. S2). Temperature varied by ≤1.5°C across data collection dates.

DISCUSSION

Populations of nonnative species provide a unique opportunity to test hypotheses about trade-offs between infection resistance and other fitness components by capitalizing on the ostensibly relaxed selection pressure from disease that occurs upon a species' introduction to a novel range (Perkins et al. 2008, Duncan et al. 2011, Dunn et al. 2012). The shore crab *Hemigrapsus sanguineus* shows a dramatic pattern of parasite escape in its nonnative range in terms of both parasite richness and infection prevalence. However, the nonnative populations experiencing parasite-free space were the most susceptible to our standardized parasite challenges. Specifically, after exposure to infective larvae in a laboratory common garden experiment, invasive-range crabs conservatively harbored ~1.8 times more infections than native-range crabs. This value is likely to represent a conservative estimate of the difference in the rate of experimentally induced infection between native and invasive-range crabs. While infected invasive-range crabs must have acquired all of their rhizocephalan infections during the brief (two to four week) exposure period in the lab, the number of internal infections detected in the native-range individuals represents not only lab-acquired infection, but also incipient infections acquired through natural exposure in the field prior to collection (i.e., background internal infection prevalence; dashed line in Fig. 1). Thus, preexisting latent infection (estimated mean 38%) may account for a large proportion of the infection detected in our experimental native-range sentinel crabs, suggesting that infection susceptibility in invasive-range crabs could be as much as six times greater than in native-range individuals (Appendix S1: Fig. S3). Thus, our experimental results reveal a double edge to parasite escape: although hosts in the introduced range suffer less infection, they may ultimately be more infectable.

Our finding of an increase in susceptibility to infection among sexually reproducing nonnative hosts likely reflects a response to selection favoring decreased

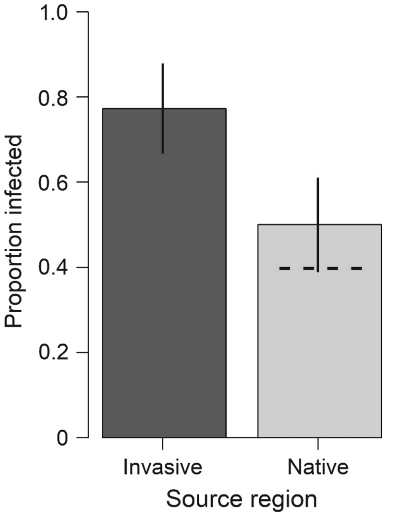

FIG. 1. Proportion of *Hemigrapsus sanguineus* infected after common garden exposure to rhizocephalans, expressed as the weighted mean of the three sites within each source region. Error bars represent standard error of the mean proportion infected across the three sites per region. Dashed line represents our estimate of latent ambient rhizocephalan prevalence averaged across the native range sites (as detected by PCR), indicating that a substantial amount of the prevalence detected in the native-range sentinel crabs that were obtained from this same source pool may represent preexisting natural infections acquired in the field.

TABLE 2. Results of linear mixed effects model of the contribution of source region, size, and sex to rates of resting oxygen consumption.

Variable	Estimate	SE	z	P	Variance	Variance SD
Intercept	−24.14	221.31	−0.11	0.91		
Source (invasive)	−72.96	25.29	−2.88	0.009		
Size	−18.67	4.92	−3.80	<0.001		
Sex (male)	119.07	24.15	4.93	<0.001		
Site (random)					0.0	0.0

Notes: Native range is the reference category for source region, and female is the reference category for sex. Individual collection site within region is included as a random effect.

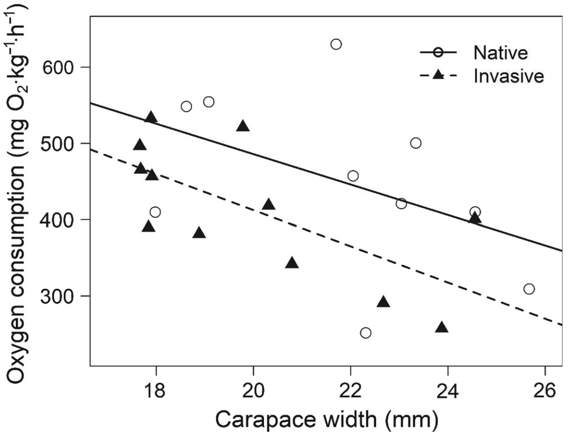

FIG. 2. Resting oxygen consumption rates for uninfected *Hemigrapsus sanguineus* from native (open circles, solid line) and introduced (filled triangles, dashed line) source regions, across carapace width (body size).

investment in immune defense in the nonnative range where rhizocephalan parasites do not occur. This is the scenario expected if resistance against rhizocephalans is costly, and imposes trade-offs with other fitness-related traits such as growth or reproduction. However, differences in parasite selection between the nonnative and native ranges may work in concert with other mechanisms of change. For example, reductions in genetic diversity resulting from population bottlenecks during the invasion process may contribute to a nonnative host's decreased ability to defend against parasites. Epigenetic inheritance and prior exposure to cues of infection risk (i.e., during residence in the parent habitat) may also play a role in determining host defense levels (Sternberg et al. 2015). An experiment using lab-reared crabs from both within-region (native × native) and cross-region (native × invasive) matings could provide a powerful test of the roles of induced vs. inherited differences in defense in susceptibility to future infection.

Although the present study did not specifically undertake to identify the mechanisms behind our finding of differences in infection susceptibility between nonnative- and native-range populations of *H. sanguineus*, a few characteristics of this particular host–parasite system point to the likely role of divergent selection. First, because rhizocephalan parasites castrate their hosts, they are expected to exert strong selection on host defenses, such that a reprieve from infection risk would represent a strong relaxation of parasite-mediated selection. Second, the encapsulation of putative rhizocephalan internal infection stages by host immune cells (Kuris et al. 2007; Appendix S2) is costly, as evidenced by studies reporting lower encapsulation responses in the absence of parasite selection in both laboratory selection experiments (Kraaijeveld et al. 2001) and natural populations (Bryan-Walker et al. 2007), and reduced encapsulation under resource limitation (Konig and Schmidhempel 1995). Finally, reduced physiological energy expenditure on immune defenses is one adaptive change expected among hosts that have escaped infection risk (Duncan et al. 2011), and our finding of lower SMR in invasive-range crabs supports that reduced immune defense may provide a fitness advantage to invaders when parasites are absent.

In particular, native-range crabs that experience consistent selection to defend against rhizocephalans may expend more of their available energy on the production of hemocytes, proteins (e.g., phenoloxidase) and other macromolecules needed to mount a successful encapsulation response. Increased enzyme activity has been linked to higher standing metabolic rate across nine species of *Drosophila* (Berrigan and Hoang 1999), and a positive correlation between an induced encapsulation response and metabolic rate has been found among multiple species of insects (Ardia et al. 2012).

Thus, higher SMR among native crabs may reflect the physiological cost of maintaining constitutive supplies of molecules and enzymes needed for recognizing pathogens and mounting a successful encapsulation response, a cost that may be avoided by nonnatives that have escaped their parasites. If nonnative individuals ultimately spend less energy on immune defense, they may in turn allocate a higher proportion of their assimilated energy to other fitness related traits such as growth and reproduction. Though fitness has not been directly compared in *H. sanguineus* in the native vs. introduced range, a previous exploratory study that held field-collected juvenile crabs in common laboratory conditions did find faster growth (measured as size gain per molt) in invasive-range compared to native-range individuals (C. L. Keogh, *unpublished data*), and population densities appear higher in the U.S. nonnative vs. Japanese native range of the crab (Fukui 1988, Fuji and Nomura 1990, Takada 1999, Lohrer et al. 2000, O'Connor 2014).

In general, and in marine environments in particular, nonnative individuals are often characterized by achieving large sizes and higher fecundity relative to native-range individuals (Grosholz and Ruiz 2003, Darling et al. 2011, McGaw et al. 2011, Gribben et al. 2013, Parker et al. 2013), characteristics that could contribute to their often overwhelming demographic success and that could in some cases represent an indirect consequence of parasite escape. Our exploration of resting energy expenditure supports that the nonnative hosts in our system may have more energy available to invest in fitness due to relaxed immune defense investment. This mechanism of invader success may work in concert with a reprieve from infection pathology to allow nonnative populations to thrive in invaded ecosystems. Here we show that parasite escape has an important trade-off, whereby hosts in the nonnative range, though less infected, are more susceptible to infection. Future studies that incorporate multiple host taxa will be valuable not only for testing the generality of our findings of altered susceptibility and energy expenditure, but also for further disentangling potential mechanisms of immunological change in populations of nonnative hosts.

Acknowledgments

The authors thank Y. Kamakura for her assistance in the field, and A. M. H. Blakeslee, S. Heck, J. Grabowski, J. T. Carlton, and M. Flennigan for field collections in the invasive U.S. range. C. L. Keogh was funded by the NSF-GRFP and a Japan Society for the Promotion of Science Short Term Fellowship. This study was also facilitated by JSPS KAKENHI Grant Number 25840160.

Literature Cited

Ardia, D. R., J. E. Gantz, B. C. Schneider, and S. Strebel. 2012. Costs of immunity in insects: an induced immune response increases metabolic rate and decreases antimicrobial activity. Functional Ecology 26:732–739.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-7. http://CRAN.R-project.org/package=lme4

Berrigan, D., and A. Hoang. 1999. Correlation between enzyme activities and routine metabolic rate in *Drosophila*. Journal of Evolutionary Biology 12:258–262.

Blakeslee, A. M. H., A. E. Fowler, and C. L. Keogh. 2013. Marine Invasions and Parasite Escape. Advances in Marine Biology 66:87–169.

Blakeslee, A. M. B., C. L. Keogh, J. E. Byers, A. M. Kuris, K. D. Lafferty, and M. E. Torchin. 2009. Differential escape from parasites by two competing introduced crabs. Marine Ecology Progress Series 393:83–96.

Blakeslee, A. M. H., et al. 2017. Reconstructing the Invasion History of the Asian shorecrab, *Hemigrapsus sanguineus* (De Haan 1835) in the Western Atlantic. Marine Biology 164:19.

Blossey, B., and R. Notzold. 1995. Evolution of increased competitive ability in invasive non-indigenous plants—a hypothesis. Journal of Ecology 83:887–889.

Brown, G. P., B. L. Phillips, S. Dubey, and R. Shine. 2015. Invader immunology: invasion history alters immune system function in cane toads (*Rhinella marina*) in tropical Australia. Ecology Letters 18:57–65.

Bryan-Walker, K., T. L. F. Leung, and R. Poulin. 2007. Local adaptation of immunity against a trematode parasite in marine amphipod populations. Marine Biology 152:687–695.

Colautti, R. I., A. Ricciardi, I. A. Grigorovich, and H. J. MacIsaac. 2004. Is invasion success explained by the enemy release hypothesis? Ecology Letters 7:721–733.

Darling, E. S., S. J. Green, J. K. O'Leary, and I. M. Cote. 2011. Indo-Pacific lionfish are larger and more abundant on invaded reefs: a comparison of Kenyan and Bahamian lionfish populations. Biological Invasions 13:2045–2051.

Duncan, A. B., S. Fellous, and O. Kaltz. 2011. Reverse evolution: selection against costly resistance in disease-free microcosm populations of *Paramecium caudatum*. Evolution 65: 3462–3474.

Dunn, A. M., et al. 2012. Indirect effects of parasites in invasions. Functional Ecology 26:1262–1274.

Epifanio, C. E. 2013. Invasion biology of the Asian shore crab *Hemigrapsus sanguineus*: a review. Journal of Experimental Marine Biology and Ecology 441:33–49.

Fromme, A. E., and M. F. Dybdahl. 2006. Resistance in introduced populations of a freshwater snail to native range parasites. Journal of Evolutionary Biology 19:1948–1955.

Fuji, A., and H. Nomura. 1990. Community structure of the rocky shore macrobenthos in southern Hokkaido, Japan. Marine Biology 107:471–477.

Fukui, Y. 1988. Comparative studies on the life history of the Grapsid crabs (Crustacea, Brachyura) inhabiting intertidal cobble and boulder shores. Publications of the Seto Marine Biological Laboratory 33:121–162.

Graham, A. L., D. M. Shuker, L. C. Pollitt, S. Auld, A. J. Wilson, and T. J. Little. 2011. Fitness consequences of immune responses: strengthening the empirical framework for ecoimmunology. Functional Ecology 25:5–17.

Gribben, P. E., S. I'Ons, N. E. Phillips, S. W. Geange, J. T. Wright, and B. R. Murray. 2013. Biogeographic comparisons of the traits and abundance of an invasive crab throughout its native and invasive ranges. Biological Invasions 15: 1877–1885.

Griffen, B. D., and J. E. Byers. 2009. Community impacts of two invasive crabs: the interactive roles of density, prey recruitment, and indirect effects. Biological Invasions 11:927–940.

Grosholz, E. D., and G. M. Ruiz. 2003. Biological invasions drive size increases in marine and estuarine invertebrates. Ecology Letters 6:700–705.

Hoeg, J. T. 1984. Size and settling behavior in male and female cypris larvae of the parasitic barnacle *Sacculina carcini* Thompson (Crustacea, Cirripedia, Rhizocephala). Journal of Experimental Marine Biology and Ecology 76:145–156.

Konig, C., and P. Schmidhempel. 1995. Foraging activity and immunocompetence in workers of the bumble bee, *Bombus terrestris*. Proceedings of the Royal Society B 260:225–227.

Kraaijeveld, A. R., E. C. Limentani, and H. C. J. Godfray. 2001. Basis of the trade-off between parasitoid resistance and larval competitive ability in *Drosophila melanogaster*. Proceedings of the Royal Society B 268:259–261.

Kuris, A. M., J. H. R. Goddard, M. E. Torchin, N. Murphy, R. Gurney, and K. D. Lafferty. 2007. An experimental evaluation of host specificity: the role of encounter and compatibility filters for a rhizocephalan parasite of crabs. International Journal for Parasitology 37:539–545.

Llewellyn, D., M. B. Thompson, G. P. Brown, B. L. Phillips, and R. Shine. 2012. Reduced investment in immune function in invasion-front populations of the cane toad (*Rhinella marina*) in Australia. Biological Invasions 14:999–1008.

Lohrer, A. M., and R. B. Whitlatch. 2002. Interactions among aliens: apparent replacement of one exotic species by another. Ecology 83:719–732.

Lohrer, A. M., R. B. Whitlach, K. Wada, and Y. Fukui. 2000. Home and away: comparisons of resource utilization by a marine species in native and invaded habitats. Biological Invasions 2:41–57.

McDermott, J. J. 1991. A breeding population of the Western Pacific crab *Hemigrapsus sanguineus* (Crustacea, Decapoda, Grapsidae) established on the Atlantic coast of North America. Biological Bulletin 181:195–198.

McDermott, J. J. 2011. Parasites of shore crabs in the genus *Hemigrapsus* (Decapoda: Brachyura: Varunidae) and their status in crabs geographically displaced: a review. Journal of Natural History 45:2419–2441.

McGaw, I. J., T. C. Edgell, and M. J. Kaiser. 2011. Population demographics of native and newly invasive populations of the green crab *Carcinus maenas*. Marine Ecology Progress Series 430:235–240.

Mitchell, C. E., and A. G. Power. 2003. Release of invasive plants from fungal and viral pathogens. Nature 421:625–627.

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133–142.

O'Connor, N. J. 2014. Invasion dynamics on a temperate rocky shore: from early invasion to establishment of a marine invader. Biological Invasions 16:73–87.

Parker, J. D., et al. 2013. Do invasive species perform better in their new ranges? Ecology 94:985–994.

Perkins, S. E., et al. 2008. Invasion biology and parasitic infections. Pages 179–205 *in* R. S. Ostfeld, F. Keesing, and V. T. Eviner, editors. Infectious disease ecology: effects of ecosystems on disease and of disease on ecosystems. Princeton University Press, Princeton, New Jersey, USA.

R Development Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org

Sheldon, B. C., and S. Verhulst. 1996. Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. Trends in Ecology & Evolution 11:317–321.

Sternberg, E. D., J. C. de Roode, and M. D. Hunter. 2015. Trans-generational parasite protection associated with paternal diet. Journal of Animal Ecology 84:310–321.

Takada, Y. 1999. Influence of shade and number of boulder layers on mobile organisms on a warm temperate boulder shore. Marine Ecology Progress Series 189:171–179.

Takahashi, T., and S. Matsuura. 1994. Laboratory studies on molting and growth of the shore crab, *Hemigrapsus sanguineus* (De Haan), parasitized by a rhizocephalan barnacle. Biological Bulletin 186:300–308.

Torchin, M. E., K. D. Lafferty, A. P. Dobson, V. J. McKenzie, and A. M. Kuris. 2003. Introduced species and their missing parasites. Nature 421:628–630.

White, T. A., and S. E. Perkins. 2012. The ecoimmunology of invasive species. Functional Ecology 26:1313–1323.

Wolfe, L. M., J. A. Elzinga, and A. Biere. 2004. Increased susceptibility to enemies following introduction in the invasive plant *Silene latifolia*. Ecology Letters 7:813–820.

Yamaguchi, T., S. Tokunaga, and H. Aratake. 1994. Contagious infection by the rhizocephalan parasite *Sacculina* sp. in the grapsid crab *Hemigrapsus sanguineus* (De Haan). Crustacean Research 23:89–119.

Yoon, M., S. E. Hong, Y. K. Nam, and D. S. Kim. 2011. Genetic diversity of the Asian shore crab, *Hemigrapsus sanguineas*, in Korea and Japan inferred from mitochondrial cytochrome c oxidase subunit I gene. Animal Cells and Systems 15:243–249.

Zuk, M., and A. M. Stoehr. 2002. Immune defense and host life history. American Naturalist 160:S9–S22.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.1953/suppinfo