A climate migrant escapes its parasites

Running head: Parasite escape in fiddler crabs

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ABSTRACT

When a species colonizes a new range, it can escape enemies found in its original range. Examples of enemy escape abound for invasive species, but are rare for climate migrants, which are populations of a species that colonize a new range due to climate-driven range shifts or expansions. The fiddler crab, *Minuca* (=*Uca*) *pugnax*, is found in the intertidal salt marshes of the east coast of the United States. It recently expanded its range north into the Gulf of Maine due to ocean warming. We tested the hypothesis that *M. pugnax* had escaped its parasite enemies. Parasite richness and trematode intensity were lower in populations in the expanded range than those in the historical range, but infection prevalence did not differ. Although *M. pungax* escaped most of its historical parasites when it migrated northward, it was infected with black-gill lamellae (indicative of *Synophrya hypertrophica*), which was found in the historical range, and by the trematode *Odhneria* cf. *odhneri*, which was not found in the historical range. To our knowledge, this is the first time that *Odhneria* cf. *odhneri* has been reported in fiddler crabs. These results demonstrate that although *M. pugnax* escaped some of its historical parasites when it expanded its range, it appears to have gained a new parasite (*O.* cf. *odhneri*) in the expanded range. Overall, our results demonstrate that climate migrants can escape their enemies despite colonizing habitats adjacent to their enemy-filled historical range.

Keywords

Parasite escape, enemy-release hypothesis, climate change, global change, range expansions, range shift, climate migrant

1. INTRODUCTION

Species across the planet are shifting or expanding their ranges towards greater elevations, latitudes or depths in response to climate change (Parmesan & Yohe 2003, Sorte et al. 2010, Telwala et al. 2013, Johnson 2015, Pershing et al. 2015, Hale et al. 2017). Populations of a species that colonize a new habitat or range as a result of climate-driven range shifts or expansions are climate migrants (Johnson et al. 2019). The successful recruitment of a climate migrant to the expanded range can be attributed to a change in abiotic factors, such as warming temperatures (Pinsky et al. 2013, Pecl et al. 2017). This is logical from a biogeographical point of view as it follows Shelford (1931)'s law of tolerance and Grinnell (1917)'s niche concept which predict that a species' distribution is set by its tolerance for abiotic factors. While changes in abiotic factors such as temperature are the primary drivers of climate-migrant colonization, not all species expand or shift their range as temperatures rise (Sorte et al. 2010, Hale et al. 2017). This may be due, in part, to stochastic factors such as dispersal ability or deterministic factors such as interactions with other species (Pöyry et al. 2009).

Charles Elton hypothesized that some non-native species, specifically invasive species, fail to colonize a new habitat because they "meet resistance" and are rebuffed by enemies, such as predators, parasites, and competitors (Elton 1958). He called this "ecological resistance," though "biotic resistance" is the term more commonly used today (e.g., Kimbro et al. 2013). However, many non-native species successfully establish outside of their original range. For example, the European green crab, *Carcinus maneas*, is an invasive species that has established in coastal habitats worldwide, in part, because it has met little biotic resistance (Torchin et al. 1996, Carlton & Cohen 2003). The enemy-release hypothesis is commonly invoked to explain the

success of non-native species in new ranges (Elton 1958, Keane & Crawley 2002, Colautti et al. 2004). It predicts that a non-native species will successfully colonize a new range if two conditions are met: it escapes enemies found in the original range and that escape benefits its fitness (e.g., body size, fecundity) (Wolfe 2002, Keane & Crawley 2002). This hypothesis has been well-tested for invasive species, but rarely for climate migrants (but see Menéndez et al. 2008, Hopper et al. 2014). Here, we focus on the first condition of the enemy-release hypothesis and test the hypothesis that a climate migrant was able to escape its parasite enemies.

Climate migrants, like invasive species, are non-natives in their expanded ranges. Both climate migrants and invasive species involve the movement of individuals from a source (sometimes called 'donor') community into a recipient one. Following Hopper et al. (2014), we define climate migrants as having an historical (source) range and an expanded (recipient) range, which is analogous to the terminology of native (source) and introduced (recipient) range used for invasive species (Sorte et al. 2010). Climate migrants differ from invasive species in at least two ways. First, invasive species colonize their introduced ranges as a result of direct human transport, whereas, climate migrants expand or shift their range as a result of indirect effects of human activities (i.e., climate change) (Sorte et al. 2010, Hopper et al. 2014). Second, invasive species often colonize areas geographically separated from their source range, whereas, climate migrants colonize areas adjacent to their source range (Sorte et al. 2010, Hopper et al. 2014). Because the expanded range of a climate migrant is adjacent to its historical range, but typically separated by biogeographic barriers, one might predict little chance for enemy-escape as enemies would presumably track climate as well. However, model predictions (Moorcroft et al. 2006) and

empirical evidence (Menéndez et al. 2008, Phillips et al. 2010, Hopper et al. 2014) suggest that some species can escape their enemies as their ranges shift or expand.

Parasites are fundamental members of ecological communities. Yet, they are poorly studied in terms of their ecology relative to their free-living counterparts (Blakeslee et al. 2012, Johnson & Heard 2017). Nonetheless, host-parasite relationships are excellent for testing the enemy-escape hypothesis because of the intimate symbiotic relationship between host and parasite. Furthermore, aspects of their relationship can be used analyze patterns. For example, climate-migrant hosts may escape parasites with indirect life cycles (i.e., have multiple hosts) if other hosts are missing in the expanded range. Similarly, we can look to invasive species for evidence of parasite escape. For example, in a wide-ranging review that included molluscan, fish, crustacean, avian and mammalian hosts, Torchin et al. (2003) found that most invasive species had fewer parasite species in their introduced ranges than conspecifics in their native ranges, suggesting parasite escape.

Cape Cod, Massachusetts, United States is a well-known biogeographic boundary between the Acadian and Virginian provinces and the northern limit for many warm-water marine species (Briggs 1974). North of Cape Cod is the Gulf of Maine, which is much cooler than the ocean south of Cape Cod (Briggs 1974). The Gulf of Maine is warming rapidly (Pershing et al. 2015), and as a result warm-water species are expanding northward (Johnson 2014, Johnson 2015, McDermott & Kraeuter 2015, Wilson & Pohle 2016). One such species is the Atlantic mud fiddler crab *Minuca* (=*Uca*) *pugnax* (Smith 1870) (Figure 1). *Minuca pugnax* is a small crab (up

to 26 mm carapace width) that lives in salt marshes, which are intertidal grasslands, on the east coast of the United States. It is a burrowing crab with strong sexual dimorphism in which males have a single enlarged claw used in defense and courtship displays and a smaller claw used for foraging and burrowing. *Minuca pugnax* is an excellent species to test the parasite-escape hypothesis for climate migrants because it has a clearly defined historical range and expanded range. Historically, *M. pugnax* ranged from northern Florida to Cape Cod, Massachusetts (Williams 1984). It was first detected in the Gulf of Maine in 2003 (Sanford et al. 2006) and has expanded at least to New Hampshire (Johnson 2014). Based on the evidence for parasite escape in invasive hosts, we predicted that the climate migrant, *M. pugnax*, would have lower parasite diversity, prevalence, and intensity in the expanded range (i.e., the Gulf of Maine) than the historical range.

2. METHODS

2.1 Field collections

From 15-25 August 2017, we collected crabs from ten marshes, spanning almost 12° latitude from Sapelo Island, Georgia to Portsmouth, New Hampshire, United States. (Figure 2, Table 1). We refer to their range from Cape Cod, Massachusetts to Florida as 'historical' and their range from Cape Cod, Massachusetts north (i.e., the Gulf of Maine) as 'expanded.' At each site, we haphazardly collected the first 50 adult crabs we encountered by hand on the surface or excavated from burrows they escape into. Crabs were collected within 3 m of the marsh edge in stands of smooth cordgrass, *Spartina alterniflora*. After collection, crabs were kept in 70-L plastic bins containing a thin layer of sediment and water from the collection site and transported

to the laboratory for processing. Crabs were dissected within 5 days of collection. All crabs were alive when dissected.

2.2 Laboratory processing

Prior to dissection, crabs were sexed and measured for size (carapace width) to the nearest 0.1 mm with Vernier calipers. For dissection, the carapace was physically removed, and the body placed in clean, filtered seawater for further dissection under a stereo-microscope. The following tissues were examined for the presence of parasites: branchial chamber, gills, hepatopancreas, thoracic nerve ganglia, brain and associated optic ganglia, sternal and apodemal musculature, epidermis of the dorsal carapace, gonads, antennal glands, midgut, hindgut, and foregut. Egg clutches of ovigerous crabs were also examined for parasites. The clutches were removed from the abdomen and examined with a stereo-microscope.

The number and location of the various parasites and any gross conditions were recorded. Parasites were counted *in situ* and removed to separate well plates for further identification. Metacercarial cysts of trematodes were excysted using gentle warming provided by an electric lamp placed ~15 cm overhead. Those that excysted were identified with a compound microscope by morphological comparisons with trematodes in existing literature (e.g., Hunter & Vernberg 1953, Heard 1966, Heard & Overstreet 1983, Schell 1985, Dunn et al.1990). Nematodes were identified based on their morphology and the tissues in which they were encysted as in Wong, Anderson & Bartlett (1989) and Wong & Anderson (1990). Non-metazoan parasites were identified from primary references (e.g., DeTurk 1940, Tuzet & Manier 1962, McCloskey & Caldwell 1965, Bourdon & Bowman 1970, Mattson 1988) and recorded as present or absent.

2.3 Variables

Except for rarefaction analysis of diversity, we quantified parasite infection at the site-level for each of the ten sites. Prevalence of infection (number of infected crabs/total number of crabs) was estimated for each parasite taxa. For statistical analysis, we used total prevalence (the prevalence of infection by any parasite). Mean intensity (mean number of parasites per infected host per site) was calculated for metazoan parasite (i.e., trematodes, nematodes, crustaceans) but not for non-metazoan parasites. We grouped all trematode infections into one variable because trematodes that use crabs as intermediate hosts can be considered as a guild of similar resource users. Parasite richness (number of parasite taxa) was calculated for all taxa present (metazoans plus non-metazoans). We also estimated diversity in each range with rarefaction analyses on all hosts using Coleman curves in EstimateS, 8.0, (Colwell 2006). Coleman rarefaction curves are a powerful technique to examine differences in diversity between different communities. Crabs were entered randomly into the rarefaction analysis and were grouped collectively by range, not site.

2.4 Statistics

To test the hypothesis that crabs in the expanded range had escaped their historical-range parasites we used generalized linear mixed effects models (GLMM) in the lme4 package (Bates et al. 2012) in R (version 3.6.1, "Action of the Toes," R Core Team 2014). We set range (expanded versus historical) as the fixed factor and site nested within range. We used the following error distributions and their standard link functions for the following dependent variables: total parasite richness (Poisson), total parasite prevalence (binomial), and trematode

intensity (negative binomial). Because trematodes were absent from two sites in the historical range, they were excluded from the intensity analysis. P-values were obtained via stepwise model reduction using likelihood-ratio tests comparing full and reduced models (Crawley 2007).

3. RESULTS

3.1 Overall findings

We dissected 500 fiddler crabs, 50 from each of the 10 sites. We identified 13 different parasite taxa from *M. pugnax* from across the study. For metazoans these included six trematode species (*Odhneria* cf. *odhneri*, *Maritrema* sp., *Gynaecotyla adunca*, *Microphallus* cf. *basodactylophallus*, *Levinseniella* sp., *Maritrema cf. heardi*), two nematode species (*Ancyracanthopsis winegardi*, *Skrjabinoclava inornatae*), and a bopyrid isopod (*Leidya distorta*). *Microphallus* cf. *basodactylophallus* and *Levinseniella* sp. had morphologically similar metacercarial cysts that did not all excyst for identification; hence they were grouped in the analyses. Microbial symbionts included an unidentified bacterial infection, blackened gill lamellae indicative of *Synophyra hypertrophica*, the haplosporidian hyperparasite *Urosporidium crescens* infecting individuals of *Microphallus* cf. *basodactylophallus* and *Leviseniella* sp., commensal peritrich ciliates in the gills, and a species of *Enterobryus*, an endocommensal fungi in the order *Eccrinales* infesting the foregut and hindgut (Table 2). *Urosporidium crescens* is a microparasite that infects individual microphallid trematodes with high intensity infections that are difficult to quantify; therefore, we calculated its mean intensity as the mean intensity of infected trematodes in their crab hosts; its overall prevalence is the percentage of crabs with infected metacercariae in the population.

3.2 Parasite diversity

Parasite richness was significantly greater in the historical range (mean richness = 5.4) than in the expanded range (mean richness = 1.2) ($\chi^2 = 14.45$, df = 1, $p < 0.001$) (Figure 3A). In the expanded range, only one metazoan parasite was found, *Odhneria* cf. *odhneri*. This parasite was not found in crabs from the historical range (Table 2). Black-gill lamellae characteristic of *Synophrya hypertrophica* were found at low prevalence-levels in the expanded range and the historical range. When symbionts were grouped by geographic region in rarefaction analysis, parasite richness reached an asymptote of 13 in the historical range and 2 in the expanded range (Figure 4). With a sample size of 50 randomly selected crabs, richness was estimated at 9.8 species in the historical range and 1.5 species in the expanded range. The mean and maximum richness in the historical range calculated by rarefaction is higher than those calculated by site because it included all the parasites found in the crabs dissected from within the historical range.

3.3 Parasite prevalence

Despite significant differences in parasite richness, there was no difference in total parasite prevalence between the historical (mean = 0.58) and expanded ranges (mean = 0.49) ($\chi^2 = 0.40$, df = 1, $p = 0.53$) (Figure 3B). There were, however, differences in the prevalence patterns for individual symbionts (Appendix Table A1) such as the trematode *Odhneria* cf. *odhneri*, which was only found in crabs from the expanded range. There were also several differences in prevalence levels of individual species of parasites between sites within the historical range. For example, crabs from Stonington, Connecticut, in the historical range had higher prevalence levels of the parasitic isopod *Leidya distorta* compared to the other sites, as well as few other helminths. Most trematode infections occurred in crabs from the southern and central portion of

the historical range, and this was in sharp contrast to the other historical sites that had low levels of these parasites, with the notable exception of the aforementioned *Odhneria* cf. *odhneri* infections in the expanded range (Appendix Table A1).

3.4 Trematode intensity

The mean intensity of trematode infections was more than 4x higher in the historical range (mean = 14) than in the expanded range (mean = 3) (Figure 3C). This difference was significant ($\chi^2 = 4.63$, df = 1, p = 0.03).

4. DISCUSSION

Our study demonstrates that the climate migrant, *Minuca pugnax*, escaped all but one of its historical parasites when it expanded its range. We know of only two other documented examples of parasite escape in climate migrants: Kellet's whelk, *Kelletia kelletii*, on the West Coast of the United States (Hopper et al. 2014) and the brown Argus butterfly, *Aricia agestis*, in Britain (Menéndez et al. 2008). Taken together, climate migrants appear to follow the same parasite-escape pattern found in invasive species: they have fewer parasites in their expanded ranges versus their historical ones (Torchin et al. 2003, Blakeslee et al. 2012, Blakeslee et al. 2013). Thus, climate migrants can escape their enemies despite colonizing habitats that are adjacent to their enemy-filled historical range.

4.1 Mechanisms of parasite escape

At least four mechanisms can be invoked to explain why a climate migrant may escape its parasites. (1) A climate migrant may arrive in the expanded range while in a life stage that is not

infected. In marine systems, non-native species often arrive as planktonic larvae and are likely free of parasites, which typically infect juvenile and adult stages or kill their larval host before metamorphosis (Shields 2012, Shields et al. 2015). This mechanism may apply to *Minuca pugnax* because it disperses as planktonic larvae and has no known parasites that infect its larval and post-larval stages. (2) A climate migrant may expand ahead of intermediate or definitive hosts required to complete the multi-host, indirect life cycles of some parasites (Hopper et al. 2014). It is unlikely that this mechanism explains the parasite escape we see for *M. pugnax* in the expanded range because many of intermediate and definitive hosts used by parasites that infect *M. pugnax* are found in both ranges. For instance, migratory birds, such as Virginia rails (*Rallus limicola*) and saltmarsh sparrows (*Ammodramus caudacutus*), are definitive hosts and move between the expanded (Gulf of Maine) and historical ranges seasonally. Many parasites of *M. pugnax* are trematodes, which use specific gastropods as first intermediate hosts. Several gastropod hosts including the coffee-bean snail, *Melampus bidentatus*, the Atlantic mudsnail, *Tritia* (=*Ilyanassa*) *obsoleta*, and hydrobiid snails are found in marshes in the expanded and historical ranges (Gosner 1978, Johnson et al. 2009, Johnson 2011, Johnson & Short 2013, Johnson & Heard 2017). (3) Phenological mismatch between hosts and parasites may limit *M. pugnax* infection in the expanded range. Crabs and their parasites in the expanded range are at higher latitudes and thus have a shorter growing season. Migratory birds, as definitive hosts, may arrive too late in northern latitudes for certain parasites to develop and successfully overwinter in their snail or fiddler-crab intermediate hosts (Paull & Johnson 2014). For instance, trematodes have well-known seasonal cycles that match the migration patterns of their hosts, which are being disrupted by climate change, leading to phenological mismatch (Galaktionov et al. 2006). (4) *Minuca pugnax* may have escaped parasites due to its small population size in the Gulf of

Maine, which can limit density-dependent transmission (Blakeslee et al. 2012). Crab densities at the leading edge of the expanded range (i.e., northern Massachusetts) are <6 m^{-2} on average (K. Martinez-Soto and D.S. Johnson unpublished data), which is much lower than those found in the historical range (60-120 m^{-2}, Culbertson et al. 2007, Luk & Zajac 2013).

4.2 Acquisition of a novel parasite?

Although *M. pugnax* in the expanded range escaped all metazoan parasites found in the historical range, they may have acquired a new one, the trematode *Odhneria* cf. *odhneri*. To our knowledge, this is the first time *O.* cf. *odhneri* has been reported in *M. pugnax*. This parasite was not found in crabs in the historical range. Moreover, although it was initially reported in *Palaemonetes vulgaris* from the Woods Hole area (Stunkard, 1979), it has not observed in a large collection of this host from Georgia (Pung et al. 2002), nor has it been reported in crustaceans from locations south of Cape Cod, Massachusetts. Notably, *O.* cf. *odhneri* was not found in our collections in the northernmost portion of the historical range, which is less than 8 km away from the area where Stunkard (1979) found it in grass shrimp. Thus, although *O.* cf. *odhneri* infects *M. pugnax* in the expanded range, it does not appear to infect *M. pugnax* in the historical range even though they are found in the same locations.

Invasive species can acquire new parasites in their invaded ranges (Torchin et al. 2003, Kelly et al. 2009). For example, the invasive shrimp, *Palaemon macrodactylus*, was infected by a species of *Odhneria* and a balanid barnacle when it invaded Argentina (Martorelli et al. 2012). In another example, Torchin et al. (2002) found that the invasive European green crab, *Carcinus maenas*, gained novel parasites in its invaded ranges worldwide. Because *O.* cf. *odhneria* appears to be a novel parasite for *M. pugnax*, then, as with invasive species, the crab host was able to

escape its historical parasites in terms of parasite diversity, but in the expanded range it did not escape its vulnerability to host generalists (Torchin et al. 2002, Selechnik et al. 2017).

4.3 Parasite escape or parasite reduction?

Although *M. pugnax* had an average of one parasite per site in the expanded range and an average of five in the historical range, total parasite prevalence was similar between the ranges. These results indicate that *M. pugnax* is equally susceptible to parasite infections in their historical and expanded ranges. Parasite intensity (number of parasites per infected host) can strongly determine a parasite's impact on host fitness (Lafferty & Morris 1996, Shields & Wood 1993, Colautti et al. 2004), though sometimes only one parasite is required to influence host fitness (Lafferty & Kuris 2009). For instance, the trematode *Levinsiniella byrdi* turns its second intermediate host, the amphipod *Orchestia grillus*, orange and negates the photatic response with an average infection intensity of 1 metacecariae per host, presumably making it more susceptible to predators (Johnson & Heard 2017). We found that trematode intensity was significantly lower in crabs in the expanded than in the historical range, further evidence of parasite escape in *M. pugnax*. The lower parasite richness and intensity may benefit *M. pugnax* fitness in the expanded range. In a previous study, we found that male *M. pugnax* are larger and females more fecund in the expanded range relative to the historical range (Johnson et al. 2019). Similarly, the invasive green crab, *Carcinus maenas* is larger in its invaded range than in its native Europe, which Torchin et al. (2001) attribute to parasite escape. These results support the second prediction of the enemy-release hypothesis: a release from parasite enemies will benefit the host's fitness (Keane and Crawley 2002). More work is required to explicitly test this prediction.

4.4 The honeymoon phase

A species that escapes its enemies today may not escape them tomorrow. This may be particularly true for climate migrants whose expanded range is adjacent to an enemy-filled historical range. The honeymoon hypothesis predicts that when a climate migrant or invasive species escapes its enemies those enemies will eventually migrate into the expanded/invaded range from nearby sources (Phillips et al. 2010) or native parasites will colonize the novel host and accumulate over time (Kołodziej-Sobocińska et al. 2018). Again, we can look to invasive species for precedence. For example, in Australia, the invasive cane toad, *Rhinella marina* (formerly, *Bufo marinus*), is expanding westward. Toads at the leading edge of the expansion escape the lungworm parasite, *Rhabdias pseudosphaerocephala*. After 1-3 years, however, lungworms also expand their range and catch-up to infect previously uninfected toads (Phillips et al. 2010). In a marine example, Blakeslee et al. (2012) found that the periwinkle, *Littorina saxitilis*, escaped more parasites than the mud snail, *Tritia obsoleta*, when introduced into San Francisco Bay, United States. They suggest that the differences in parasite escape are driven, in part, to the fact the *L. saxitilis* was introduced more recently than *T. obsoleta*. *Minuca pugnax* was first observed in its expanded range in 2003 (Sanford et al. 2006). Because we found no historical-range metazoan parasites in expanded-range crabs, our results indicate that *M. pugnax* is currently enjoying at least a 14-year honeymoon from their historical metazoan parasites.

4.5 Conclusions

We show that in terms of parasite richness and intensity, *Minuca pugnax* escaped parasites from its historical range as it migrated into its expanded range. If this result is typical of other climate migrants, then it suggests that they follow the same parasite-escape pattern seen in invasive

species: they have fewer parasites in their expanded ranges versus their historical ones (Torchin et al. 2003, Blakeslee et al. 2012, Blakeslee et al. 2013). Thus, our results suggest that climate migrants can escape their parasites despite colonizing habitats that are adjacent to their enemy-filled historical range. However, that escape may only be temporary as parasites catch-up (i.e., honeymoon phase, Phillips et al. 2010, Kołodziej-Sobocińska et al. 2018) or as host-generalist parasites start using expanding populations of a new host (Kelly et al. 2009). Despite the ubiquity of parasites and the growing number of documented climate-migrant hosts (Sorte et al. 2010, Pecl et al. 2017), our study is one of only three that we are aware of to investigate the parasites of climate migrants (Menéndez et al. 2008, Hopper et al. 2014). We advocate exploring host-parasite relationships in the context of climate change to answer fundamental ecological questions.

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Figure 1: A male fiddler crab, *Minuca pugnax*, in Rowley, Massachusetts, which is in the expanded range. Note the blue face of the crab, a characteristic field marking of this species. Photo credit: DS Johnson.

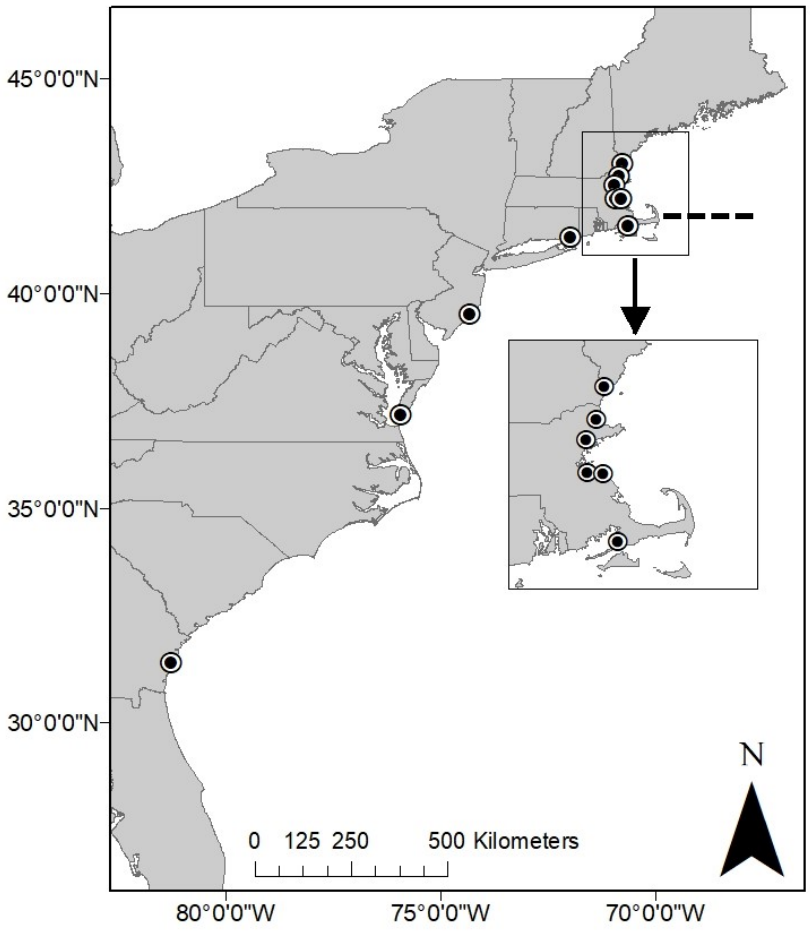
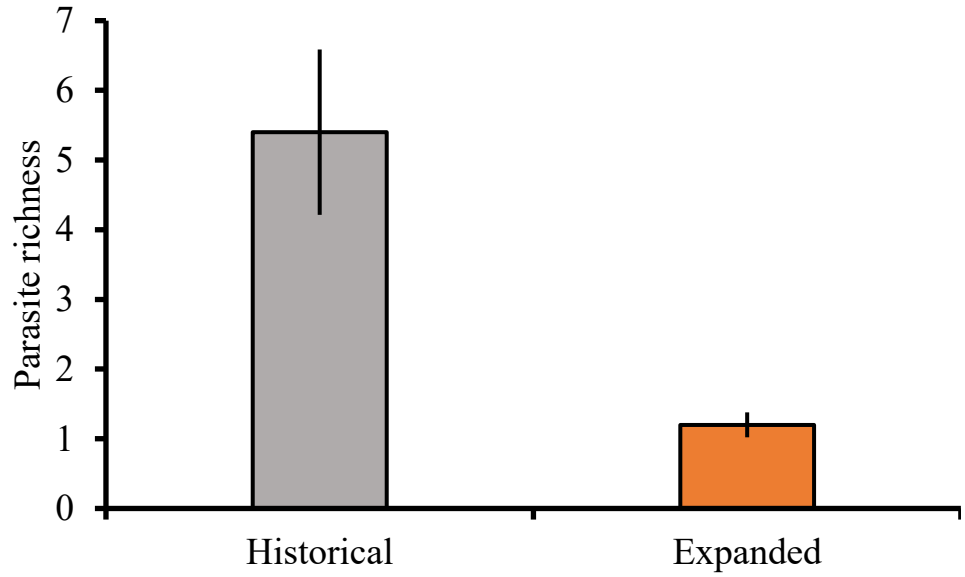
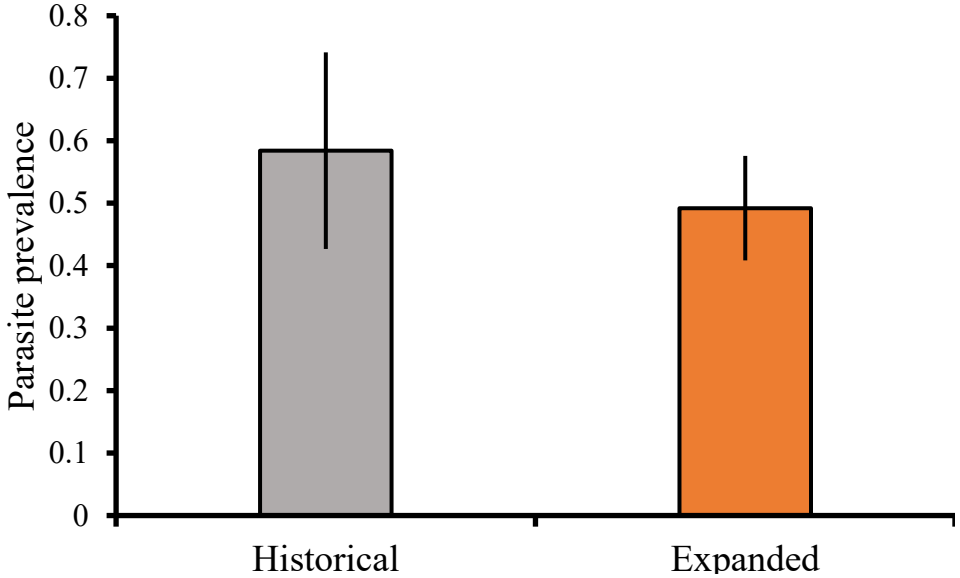


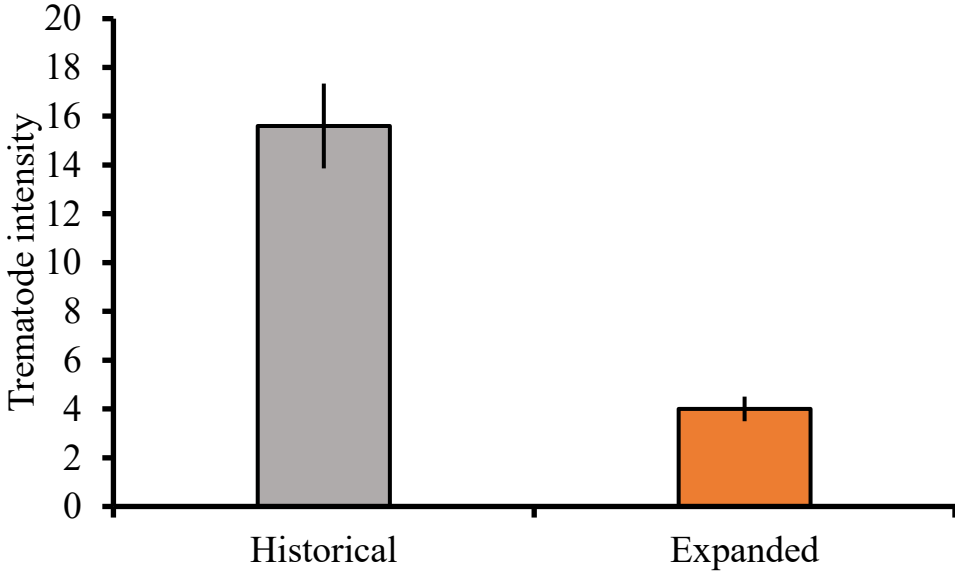
Figure 2: Location of marshes sampled (circles). Dashed line indicates northern limit of historical range.


Parasite richness
7
6
5
4
3
2
1
0
Historical
Expanded

1


Parasite prevalence
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Historical
Expanded

2


Trematode intensity
20
18
16
14
12
10
8
6
4
2
0
Historical
Expanded

3

Figure 3: Mean (±1 SE) A) taxonomic richness of parasites, B) total parasite prevalence (proportion of the population at each site infected with a parasite, regardless of species) and C) trematode intensity (number of parasites per infected crab) found in *Minuca pugnax* in its ranges.

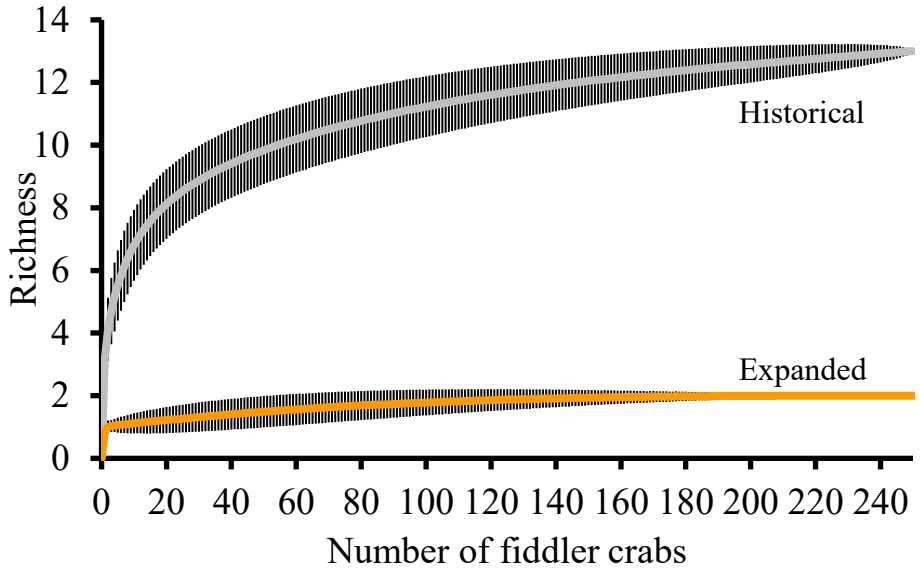


Figure 4: Parasite richness as a function of sample size for fiddler crabs sampled in their historical vs. expanded ranges (Coleman rarefaction curves). Solid line indicates richness estimate, whereas bars are standard deviations.

Table 1: Location of marshes sampled.

Range	Marsh or Estuary	Location	Latitude (N)	Longitude (W)
Expanded	Sagamore Creek	Portsmouth, New Hampshire	43° 3' 3.58"	70° 46' 13.08"
Expanded	Plum Island Estuary	Rowley, Massachusetts	42° 44' 19.63"	70° 50' 23.23"
Expanded	Waters River	Danvers, Massachusetts	42° 32' 47.84"	70° 56' 19.95"
Expanded	Bare Cove	Weymouth, Massachusetts	42° 13' 47.27"	70° 55' 37.26"
Expanded	Musquashcut Brook	Scituate, Massachusetts	42° 13' 34.25"	70° 46' 35.92"
Historical	Great Sippewissett	Falmouth, Massachusetts	41° 35' 0.55"	70° 38' 14.22"
Historical	Mason's Island	Stonington, Connecticut	41° 19' 58.37"	71° 58' 16.98"
Historical	Great Bay Estuary	Little Egg Harbor Township, New Jersey	39° 31' 18.28"	74° 19' 6.32"
Historical	Cushman's Landing	Cape Charles, Virginia	37° 10' 30.94"	75° 56' 32.28"
Historical	Sapelo Island	McIntosh County, Georgia	31° 25' 20.74"	81° 17' 24.25"

Table 2. Prevalence and mean intensity of the parasites and symbionts in *Minuca pugnax* from its native and expanded range.

Parasite	Historical range		Expanded range	
	Prevalence (%)	Mean intensity ± sd	Prevalence (%)	Mean intensity ± sd
Microbial parasites and symbionts				
Bacterial infection	0.4	nd	0.0	
Eccrinales (Fungi)	4.0	nd	0.0	
Peritrich ciliates[a]	±	nd	±	nd
Black gill lamellae cf. *Synophrya hypertrophica*	0.8	nd	0.8	nd
Urosporidium crescens	8.8	2.82 ± 3.07[b]	0.0	
Trematoda				
Odhneria cf. *odhneri*	0.0	0.0	48.4	4.00 ± 5.54
Maritrema sp.	21.6	5.17 ± 5.02	0.0	
Gynaecotyla adunca	18.4	22.24 ± 19.71	0.0	
Microphallus cf. *basodactylophallus & Levinesenilla* sp.	26.0	7.69 ± 8.89	0.0	
Maritrema cf. *heardi*	2.4	3.17± 2.99	0.0	
Nematoda				
Ancyracanthopsis winegardi	16.4	1.32 ± 0.72	0.0	
Skrjabinoclava inornatae	1.6	1.00 ± 0.00	0.0	
Isopoda				
Leidya distorta[c]	7.6	1.37 ± 0.50	0.0	

[a]The peritrich ciliates were only noted when they had high population densities on individuals. They were not included in the analyses.
[b]Because they are hyperparasites and microparasitic on their trematode hosts, the mean intensity for *U. crescens* is the mean number of infected metacercariae in infected crabs. Prevalence is given as proportion of infected crab hosts with trematodes infected by *U. crescens*.
[c]The isopod is a parasitic castrator and the only metazoan parasite using the crab as a definitive host. Mature parasites typically occur in pairs.
nd=no data.

Appendix: Table A1. Parasite prevalence (mean intensity ± sd) of *Minuca pugnax* by location from north to south. Only prevalence is given for bacterial, black gill and *Eccrinales* infections.

Range	Site	Bacterial infection	Black gill	*Eccrinales*	*Urosporidium crescens*[a]	*Odhneria* cf. *odhneri*	*Maritrema sp.*
Expanded	Portsmouth, NH	0	0	0	0	66 (3.85 ± 3.42)	0
Expanded	Rowley, MA	0	0	0	0	26 (1.46 ± 0.66)	0
Expanded	Danvers, MA	0	4	0	0	72 (7.00 ± 8.65)	0
Expanded	Weymouth, MA	0	0	0	0	40 (2.35 ± 1.53)	0
Expanded	Scituate, MA	0	0	0	0	38 (2.26 ± 2.68)	0
Historical	Falmouth, MA	2	0	0	0	0	0
Historical	Stonington, CT	0	0	8	0	0	0
Historical	Little Egg Harbor, NJ	0	0	12	0	0	54 (6.44 ± 6.22)
Historical	Cape Charles, VA	0	4	0	28 (2.07 ± 2.06)	0	20 (4.30 ± 3.56)
Historical	McIntosh County, GA	0	0	0	16 (4.13 ± 4.16)	0	34 (3.65 ± 2.76)

Table A1, continued

Range	Site	*Microphallus* sp. A & *Levinseniella*	*Microphallus* sp. B	*Ancyracanthopsis winegardi*	*Skrjabinonema inornatae*	*Leidya distorta*	Parasite Richness
Expanded	Portsmouth, NH	0	0	0	0	0	1
Expanded	Rowley, MA	0	0	0	0	0	1
Expanded	Danvers, MA	0	0	0	0	0	2
Expanded	Weymouth, MA	0	0	0	0	0	1
Expanded	Scituate, MA	0	0	0	0	0	1
Historical	Falmouth, MA	0	0	0	0	0	1
Historical	Stonington, CT	0	0	2 (3.00 ± 0.00)	0	20 (1.50 ± 0.53)	3
Historical	Little Egg Harbor, NJ	0	0	28 (1.14 ± 0.36)	6 (1.00 ± 0.00)	0	4
Historical	Cape Charles, VA	58 (7.28 ± 6.55)	4 (1.00)	22 (1.64 ± 1.03)	2 (1.00 ± 0.00)	2 (2.00 ± 0.00)	9
Historical	McIntosh County, GA	72 (8.03 ± 10.48)	8 (4.25 ± 3.20)	30 (1.13 ± 0.52)	0	16 (1.13 ± 0.35)	7

[a]Mean intensity of *U. crescens* is the mean intensity of infected metacercariae in the crab population. Prevalence is the percentage of crabs with infected worms.