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ORIGINAL PAPER

Factors influencing variation in reproduction in invasive species: a case study of the Asian shore crab *Hemigrapsus sanguineus*

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Abstract Reproductive success is a strong determinant of invasive species success. It is common for studies on invasive species to assess reproduction by measuring size-specific fecundity and scaling this up using population size or densities. Yet, reproductive success is influenced by numerous factors that are not accounted for in such calculations. We examined the influence of several factors on fecundity (clutch size) and egg size in the Asian shore crab *Hemigrapsus sanguineus*, including body size, spatial variation throughout the invaded range, season, fertilization success, brood loss, and diet. We show that all of these factors influence reproduction simultaneously within the invaded North American range of this species, though the relative importance of these different factors varied across sites or sampling times. Our study demonstrates that numerous factors may influence the reproductive success of invasive species and that studies that rely on fecundity measured at a single place and time, or that ignore factors such as offspring quality or brood loss, may provide a skewed picture of reproduction, and thus of potential invasive success.

Keywords Brood loss · Invasion success · Geographic range · Site-specific reproduction · Reproductive success · Temporal variation

Introduction

Reproductive success is a primary determinant of the success of invasive species. A comparison of native and invasive fish found that invasive species generally had higher fecundity and more life history variation than native species (Liu et al. 2017). Similar patterns have been found in a comparison of native and invasive plants (Moravcova et al. 2010). As a result of such patterns, fecundity is often used as a basis for determining whether a species will become invasive (Keller et al. 2007). Fecundity in invaders can be influenced by a wide variety of factors. Body size is a common predictor of fecundity (larger females often carry larger clutches), and thus has been linked

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to invasion success, across different types of organisms, such as lady beetles (Kajita and Evans 2010), and gall makers (Graziosi and Rieske 2014), with weaker connections to invasion success in vertebrates (Jeschke and Strayer 2006). As a result of size-specific fecundity, reproductive output is often measured as allometric or isometric scaling of fecundity multiplied by the number of clutches produced per year (e.g., Barnes et al. 2008; Bariche et al. 2009; Stephen et al. 2013).

This method of size-dependent scaling assumes that all individuals are identical, apart from differences in body size. In reality, reproductive output can vary for many size-independent reasons, often leading to spatial variation in reproductive output throughout invaded ranges (With 2002). For instance, seed production, germination, and persistence traits in an invasive succulent (*Carpobrotus edulis*) along the coast of Spain differed by as much as 6000% between sites that were separated by as little as 0.5 km (Fenollosa et al. 2021). Similarly, differences in fecundity of the intentionally introduced, but now considered invasive, red king crab (*Paralithodes camtschaticus*) were seen across three fjords in Norway (Hjelset 2012). These differences can be a result of interactions with other species, such as in the invasive houndstongue (*Cynoglossum officinale*) where interactions with an introduced herbivorous beetle decreased flowering size and thus the proportion of plants that were iteroparous (Duncan and Williams 2020). Alternatively, reproduction can differ as a result of environmental conditions, as in the invasive bivalve *Xenostobus securis*, where the timing of gametogenesis in the invaded range, but not in the native range, is triggered by temperature and therefore differs across invaded sites with local temperature variation (Montes et al. 2020). Stressful local conditions can also result in energetic tradeoffs that alter reproductive success of invaders. For instance, the invasive mussel *Mytilus galloprovincialis* invests more in byssal thread production to secure attachment on wave swept shores of the open coast compared to sheltered bays where wave action is reduced, resulting in lower reproductive effort on the open coast than in sheltered bays (Nicastro et al. 2010).

Spatial variation in reproductive effort of invasive species often varies along gradients. Theory predicts that this spatial variation in reproduction should occur as expanding range edges are approached, with evolution leading to increased fecundity at the range edge compared to the range center during periods of range expansion (Thomas et al. 2001; Travis and Dytham 2002; Hughes et al. 2003; Simmons and Thomas 2004; Phillips et al. 2008, 2010; Bartoń et al. 2012; Henry et al. 2013). This theory has been supported by empirical studies in invasive spiny-cheek crayfish (*Orconectes limosus*) (Pârvulescu et al. 2015) and in the round goby (*Neogobius melanostomus*) (Masson et al. 2016). However, this pattern is not always observed, and Courant et al. (2017) found lower reproductive effort at the range edge of an invasive amphibian (*Xenopus laevis*).

In addition to spatial variation, fecundity of invaders may vary seasonally due to environmental conditions (e.g., Barnes et al. 2008; McKenzie et al. 2013; Verhaegen et al. 2021). This seasonal variation may apply consistently throughout the invaded range, or may itself differ across the range (i.e., a site by season interaction). Spatial variation in seasonal differences in fecundity may be expected especially when invasive species span a broad enough latitudinal range that there is considerable variation in seasonality throughout the range.

In addition to changes in fecundity, there can also be changes to other aspects of reproduction across space or time. For instance, egg size differs in the invasive oyster (*Crassostrea gigas*) across latitude in Europe (Cardoso et al. 2007), and it varies in invasive silver carp (*Hypophthalmichthys molitrix*) through time (Lenaerts et al. 2015). Propagule size often increases with the maternal resource allotment and is therefore an indicator of offspring quality (Krist 2011) and can determine establishment success of an invader (Lange and Marshal 2016). Differences in parental diet quality may result in differences in offspring size and number (e.g., Ware et al. 2008; Griffen 2014; Lopez and Hoddle 2014). Reproductive variation may also result from variation in fertilization success (e.g., Barnes et al. 2008) and/or hatching success (Geister et al. 2008). Reproduction may also be influenced by brood loss, defined as the loss of extruded eggs during the period of egg care due to mechanical factors, disease, and egg predators (Kuris 1990), though this has not been examined as a factor limiting invasive reproductive success.

While each of the factors described above are known to influence the reproductive success of invasive species, no study that we are aware of examines each of these factors simultaneously. The relative importance of these various factors, and whether all of them occur simultaneously or individually, therefore remains unclear. Here we examine all of these factors simultaneously in a single invasive species in order to understand the relative importance of each on invasive reproductive success. As a case study, we use the Asian shore crab *Hemigrapsus sanguineus*, in its invasive range along the East Coast of North America. We sampled crabs throughout the entire range of their invasion on the North American coast, and throughout the entire active reproductive season of one year in order to test the null hypotheses that egg number and size do not vary through space or time, that all extruded eggs are fertilized, that brood loss does not occur, and that fecundity is independent of diet. We broadly predicted that reproductive potential would be greatest at the range edges compared to the range center.

Methods

Study system

Hemigrapsus sanguineus was first noted in Cape May, New Jersey in 1988 (Williams and McDermott 1990). Since then, it has spread both north and south along the East Coast of North America, but to different extents. Its southern range limit reached Oregon Inlet on the outer banks of North Carolina by 1995 (McDermott 1998a) and has remained stationary since then. In contrast, the species rapidly expanded the northern edge of its range to midcoast Maine by the early 2000s (Griffen and Delaney 2007), and has continued a slow march northward since then, with recent reports that it has established along the southern shores of Nova Scotia, Canada (Ramey-Balci 2023). Considerable variation in seasonality occurs throughout this range and consequently has impacts on the behavior and physiology of *H. sanguineus* that differ throughout its range, including differences in tissue energetics (Griffen et al. *In review*), temporal and spatial differences in diet (Griffen et al. 2012; Reese et al. 2023), and latitudinal differences in the strategy for financing reproduction (Reese et al. 2024). Shortly after its arrival, the size-fecundity relationship and egg size for this species were determined using animals collected at a single location and time (McDermott 1998b). It remains unclear whether either of these metrics varies through space or time or whether they differ between the range edge and the center of the range. Similarly, little is known about the fertilization dynamics of *H. sanguineus* (Anderson and Epifanio 2010) and therefore what percentage of eggs that are produced become fertilized and viable, or how many eggs are lost from a brood during development.

Sampling

We used *H. sanguineus* samples that had been collected for previous studies (Griffen et al. 2022, 2023; Reese et al. 2024). We collected these samples from five sites spread throughout the range of *H. sanguineus* (Table 1). We collected samples every other month during 2020 (March, May, July, September, November) at each site, with the exception of the site in Connecticut, which we sampled on a monthly basis. We collected 272 gravid females that were used in this study (see Table 1 for sampling dates and sample sizes of gravid females at each individual site). Upon collection, crabs were placed in individual small plastic bags, frozen, and shipped to Brigham Young University in Provo, UT for processing. All crabs were stored at − 80 °C until processed.

Table 1 Sampling state, coordinates, and sample size at each Julian sampling date

Site	Latitude and longitude	Julian sampling dates (sample size)
Maine	43° 43′ 2.7336″ N, − 70° 0′ 11.4624″ W	192(28), 252(21)
New Hampshire	43° 2′ 20″ N, − 70° 42′ 55″ W	194(24), 251(22)
Connecticut	41° 17′ 56.1″ N, − 72° 06′ 44.9″ W	136(30),165(22), 181(16), 226(23)
New Jersey	38° 58′ 3.396″ N, − 74° 57′ 45.9858″ W	131(33), 193(17), 258(13)
North Carolina	35° 46′ 7.33″ N, − 75° 31′ 37.76″ W	75(5), 136(8), 245(1), 259(9)

Egg processing

We processed each crab by thawing them individually in room temperature water. We then measured the carapace width at the widest point using a digital vernier caliper, and counted the number of limbs that were missing and the number that were regenerating based on the presence of limb buds. Next, we removed eggs from the pleopods following methods by Choy (1985), modified based on preliminary sample processing using crabs not collected for this study. Our methods were as follows. We first used scissors to remove each of the pleopods that were carrying eggs. We then submerged each pleopod in 0.6% chloride bleach solution for 90 s, agitating them throughout that time to break down the mucus holding the eggs to the pleopods, thus freeing the eggs. At the end of this time, we immediately added ~ 10 ml of 3% sodium thiosulfate solution to neutralize the bleach and prevent breakdown of the eggs themselves. We then rinsed the eggs thoroughly with DI water using a 53 µm mesh sieve to avoid egg loss. We spread the eggs evenly within a shallow, broad container that we had previously partitioned into eight equal sections, suspending them in 30 PSU saltwater made from Instant Ocean®. We allowed the eggs to sit for at least 30 min to ensure that egg volumes had equilibrated to the same salinity, before removing eggs from one of the eight sections for photographing (i.e., we only analyzed a 1/8 subsample of each clutch of eggs).

We photographed each batch of eggs from a single crab by separating the 1/8 subsample into small containers (white vial caps) so that the eggs were present in a single layer that could all be visualized under the microscope. We then photographed each subsample using a dissecting microscope (Olympus, Model #MVX10) connected to a digital camera (Olympus, Model #DP74) equipped with the cellSens Standard (v. 3.2) imaging program. Following photography, each subsample was recombined with the remaining eggs for that individual crab, rinsed using DI water to avoid salt crystallization, and dried for use in other studies (Griffen et al. 2022, 2023).

We counted the eggs in each photograph using ImageJ (Scheider et al. 2012). To do this, we categorized each egg into one of six stages of development (A–F), following Seneviratna and Taylor (2006). They identified a total of five egg development stages (A–E) and a sixth stage representing hatched zoea (F). Zoea are released from the mother upon hatching, however, we encountered them regularly in our samples. This suggests that these likely came from very late stage E eggs that were ready to be hatched when the mother was captured. The process of egg removal from the pleopods described above therefore likely dissolved the remaining thin shell, releasing these individuals. We therefore included all six stages (A–F) in our assessment of each clutch by counting the number of eggs in each stage and summing these (and multiplied by eight since we only analyzed 1/8 of each clutch) to determine total clutch size. In addition, where possible based on egg development, we used ImageJ to measure the diameter of 10 eggs from each clutch that were in stage A (i.e., new eggs that were still completely full of yolk).

Statistical analyses

We tested the null hypotheses that reproduction was not influenced by body size, collection site, or season using a single analysis. We used a generalized additive model with clutch size as the response variable and carapace width and collection site as predictor variables. We also included the interaction between these terms to determine whether the scaling of clutch size with carapace width changed across sites. Graphical analysis suggested that clutch size varied nonlinearly through time, so we included Julian sampling date (i.e., the linear day of the year) as a smoothed term. Previous work has identified a tradeoff between injury and reproduction in this species (Griffen et al. 2022) and so we also included the number of limbs missing, the number of limbs regenerating, and their interaction as predictor variables. Clutch sizes are count data and were overdispersed, so we used a quasipoisson error structure for our models. We did not analyze temporal changes in clutch size at individual sites (i.e., no interaction between collection site and time) because no site had enough sampling dates with gravid crabs to allow for this test. Therefore, the factor of time in this and all other models described below was modeled with samples pooled across sites.

To examine the influence of body size, collection site, and season on egg size, we used an identical analysis to the one described above, but with average egg size (averaged across the 10 replicate eggs in stage A measured from the same clutch) as the response variable rather than egg number, and using a gaussian error distribution rather than quasipoisson.

To examine the null hypothesis that brood loss (i.e., reduction in clutch size throughout the period of egg care) did not occur, we used a generalized linear model with clutch size as the response variable, and with carapace width and proportion of brood developed as predictor variables. Again, we used a quasipoisson distribution to account for overdisperson of count data. This analysis assumes, consistent with available evidence for *H. sanguineus* (McDermott 1998b; Gamelin 2010), that all eggs in a clutch develop at approximately the same rate, so that reductions in clutch size do not reflect early hatching of some eggs that developed more quickly than others. Proportion of brood developed in this analysis was determined by assigning a proportion to each of the six development stages (stage A = 0, stage B = 0.2, stage C = 0.4, stage D = 0.6, stage E = 0.8, stage F = 1.0). We then multiplied the number of eggs in each stage by these proportion values, summed these products, and divided the sum by the overall clutch size. This yielded a value ranging from 0 to 1 that indicated the relative development of the egg clutch as a whole (i.e., a value of 0 would occur if all eggs had been in stage A, while a value of 1 would occur if all eggs had completed development). Large crustaceans generally suffer less brood loss than smaller crustaceans (Kuris 1990). We therefore conducted two separate analyses, one with crabs < 25 mm and one with crabs ≥ 25 mm carapace width.

To examine the null hypothesis that fertilization success did not influence reproduction differently across sites or through time, we used a generalized linear model with proportion of eggs developing as the response variable (i.e., number of eggs in the clutch not in stage A divided by the overall clutch size) and with collection site and Julian sampling date as predictor variables. We used a binomial error distribution to model these proportional data. This approach assumes that stage A eggs (i.e., those not yet showing any development) were unfertilized. This may have been the case, but it may also be that these eggs were recently produced and would eventually have started to develop if given enough time. We therefore use the term "apparent fertilization" to reflect this uncertainty.

Finally, we examined the null hypothesis that diet did not influence reproduction via altering clutch size or egg size. To do this, we estimated diet quality using residual cardiac stomach size (Reese et al. 2023), because stomach size in crabs, including in *H. sanguineus*, is inversely proportional to diet quality (Griffen and Mosblack 2011). We therefore first used linear regression with stomach width (measured on these same samples as reported in a previous study, Reese et al. 2023) as the response variable and carapace width as the predictor variable. We then used the residuals from this analysis (i.e., stomach size after accounting for differences in body size) as the predictor variable in two separate linear models with either clutch size (quasipoisson error distribution in generalized linear model) or average egg diameter (gaussian distribution) as the response variables.

Results

The baseline site for comparison across sites in statistical models in this study was Connecticut, the central site in the invaded range. Clutch size increased linearly with body size ($t = 9.03$, $P < 0.0001$, Fig. 1), in general increasing by 12.5% for each 1-mm increase in carapace width (assuming all other variables are held constant), and this relationship was similar across four of the sites with two exceptions. We

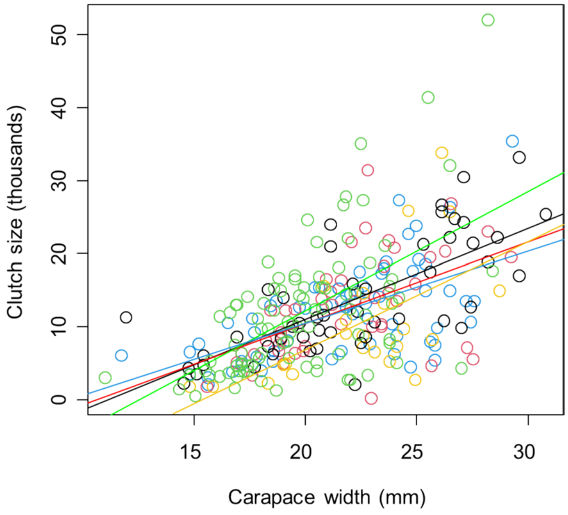

Fig. 1 Relationship between clutch size and carapace width in *Hemigrapsus sanguineus* collected from different sites (black = Maine, red = New Hampshire, green = Connecticut, blue = New Jersey, yellow = North Carolina). Lines are least squares best fits to data from each site individually

found that overall clutch size, after accounting for differences with body size, was 18.6% smaller in North Carolina than in Connecticut ($t = -2.37$, $P = 0.019$, Fig. 2A) and clutch size for crabs from New Hampshire increased 4.9% more slowly with carapace width than for crabs in Connecticut ($t = -2.11$, $P = 0.036$, red vs. green line in Fig. 1). In addition, the interaction between the number of limbs missing and the number of limbs regenerating interacted to influence clutch size ($t = 2.43$, $P = 0.016$), and clutch size varied nonlinearly with Julian sampling date (smoothed term in model, $F = 10.62$, $P < 0.0001$, Fig. 2B). All other relationships were statistically similar ($P > 0.05$).

Average egg size was not influenced by crab carapace width ($t = 0.41$, $P = 0.69$). Egg size differed across some of the sites, being 2% larger in Maine than in Connecticut ($t = 4.78$, $P < 0.0001$, Fig. 3A) and 1.6% larger in New Jersey than in Connecticut ($t = 4.89$, $P < 0.0001$, Fig. 3A). Egg size also varied nonlinearly with Julian sampling date ($F = 6.50$, $P < 0.0001$, Fig. 3B). All other relationships were statistically similar ($P > 0.05$).

We found that clutch size declined by 47.1% throughout larval development in clutches of crabs < 25 mm carapace width ($t = -3.78$, $P = 0.0002$, Fig. 4), even after controlling for the strong impact of carapace width on clutch size ($t = 8.93$, $P < 0.0001$, circle size and color in Fig. 4). However, for crabs ≥ 25 mm carapace width, clutch size was no longer influenced by carapace width ($t = 1.33$, $P < 0.19$,

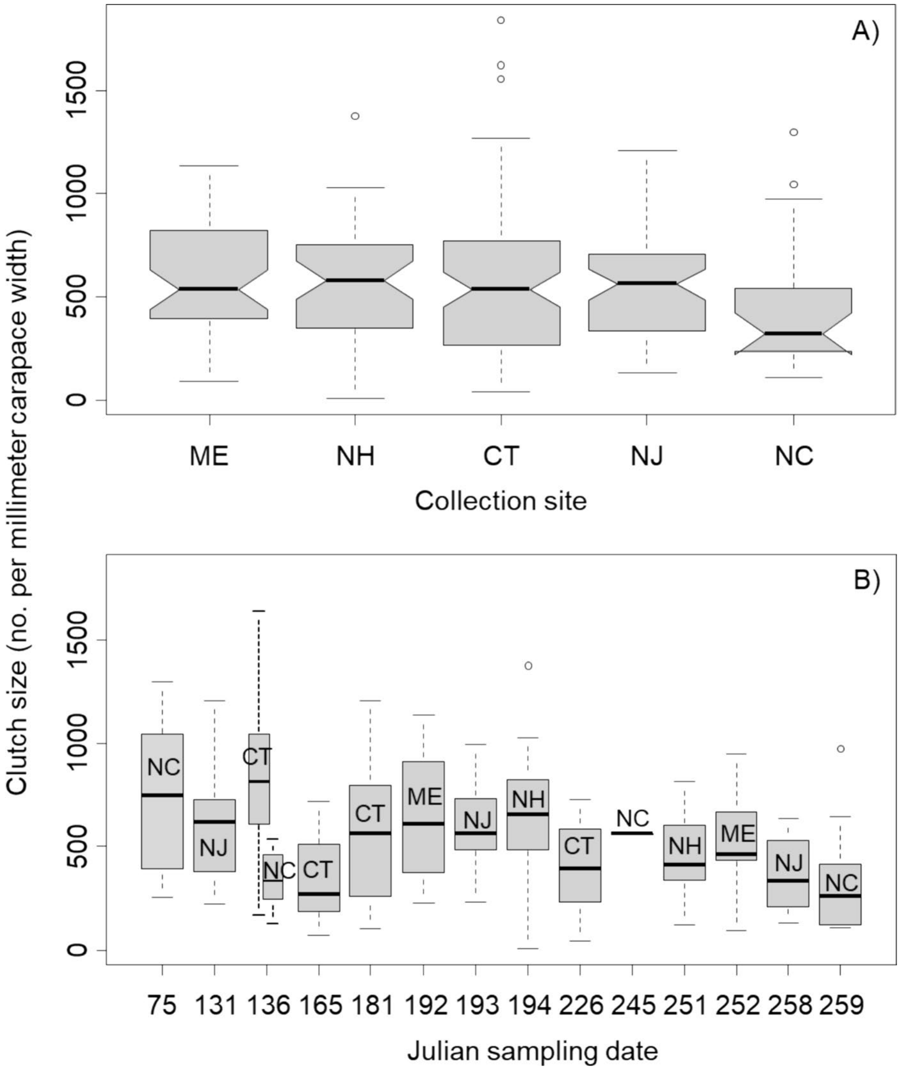

Fig. 2 Standardized clutch size (clutch size/carapace width) of *Hemigrapsus sanguineus* at different sites **A** and collected on different Julian sampling dates **B**. Letters on the x-axis of part A and on the boxplots in part B are state codes (ME = Maine, NH = New Hampshire, CT = Connecticut, NJ = New Jersey, NC = North Carolina). Heavy lines in individual boxplots show median values, boxes encompass the interquartile range, whiskers are 1.5X the interquartile range, circles are data points that fall outside this region, and notches in part A show statistical significance, where notches that do not overlap are significantly different. Two small boxplots are shown on day 136 because both CT and NC were sampled on that date

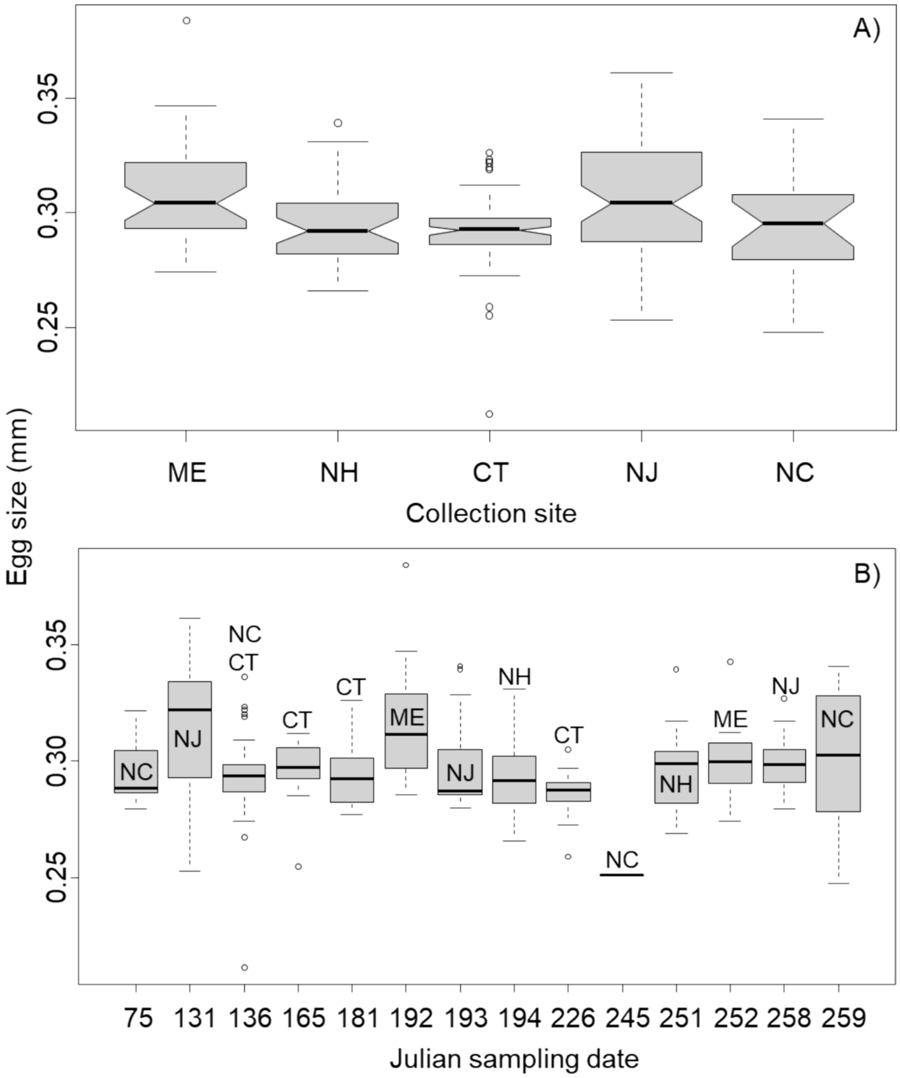

Fig. 3 Average egg diameter of *Hemigrapsus sanguineus* collected from different sites **A** and on different Julian sampling dates **B**. Figure details are as given in the legend for Fig. 2

circle size in Fig. 4) or brood loss ($t = 0.72$, $P = 0.48$, Fig. 4).

We also found that apparent fertilization success increased with Julian sampling date ($z = 4.19$, $P < 0.0001$, Fig. 5A) and also differed across collection sites, with apparent fertilization success being higher in Maine than in New Hampshire ($z = 2.96$, $P = 0.025$, Fig. 5B) or Connecticut ($z = 2.81$, $P = 0.038$, Fig. 5B), and marginally higher in North Carolina than in Connecticut ($z = 2.69$, $P = 0.052$, Fig. 5B).

Finally, we found clutch size was not influenced by diet quality ($t = 1.39$, $P = 0.17$), but that egg size increased as diet quality decreased ($t = 2.33$, $P = 0.021$, Fig. 6). While this relationship was significant, it was weak, with variation in standardized stomach size, used as a proxy for diet quality, explaining just 1.9% of the variation in average egg diameter.

Discussion

We have shown that body size is an important determinant of fecundity, but that this relationship differs across sites throughout the invasive range of *H. sanguineus*. We have also shown that size-specific fecundity was modified by changes in baseline fecundity throughout the reproductive season. These same factors also influenced egg size, a

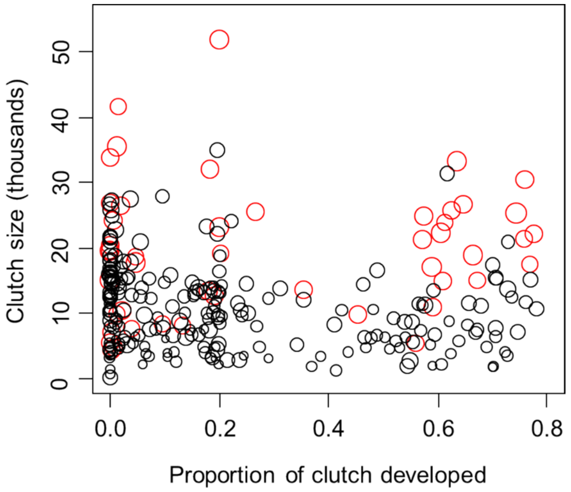

Fig. 4 Clutch size of *Hemigrapsus sanguineus* as a function of the proportion of eggs developed showing a general decline in clutch size through development, consistent with brood loss. Relative circle size shows relative carapace width. Black and red circles are crabs <25 mm and ≥ 25 mm carapace width, respectively

metric that is commonly associated with offspring quality (Krist 2011). We further found that egg size increased as diet quality decreased, though this counterintuitive relationship was weak and only explained a small portion of the variation in egg size. The relationship between egg size and recruitment success is not known for this species, however larval quality in other crab species differs substantially with diet and maternal habitat (Riley and Griffen 2017; Cannizzo et al. 2020).

In addition to the impacts of body size, site, and season, we found that reproductive success was also influenced by three other factors. First, we found a pattern of clutch size consistent with brood loss during the period of egg care. The impacts of brood loss are substantial, and amounted to the loss of several thousand eggs during the period of brood care for crabs <25 mm carapace width. Second, we found that fertilization success appeared to differ throughout the reproductive season and across sites. Third, we found that reproduction was influenced by diet quality, although this relationship was weak. The combination of these factors may drastically reduce the number of viable larvae that are produced and will ultimately influence the population dynamics of *H. sanguineus*.

Putting all these factors together, we can estimate total fecundity by this group of sampled crabs and compare this to expected fecundity following the previously documented size-fecundity relationship for this species. McDermott (1998a, b) sampled crabs from the New Jersey coast (the temporal coverage is unclear for crabs used in measuring fecundity) and determined that fecundity scales with carapace width: fecundity $= -23{,}347 + 1985.1 \times$ carapace width ($R^2 = 0.851$, $N = 50$). The high R^2 gives the impression that there is high fidelity in this relationship, but this breaks down when crabs are collected over space and time, as we have shown. Figure 7 shows expected fecundity for gravid crabs in our study, had they all followed the size-fecundity relationship documented by McDermott (left bar). This is compared to observed combined egg counts for these same crabs, which accounts for variation in fecundity across space and time, as well as brood loss up to the time of capture (middle bar—possibly conservative reduction if additional brood loss is expected before egg development is complete). The right bar accounts for all these same factors as the middle bar, plus it accounts for fertilization success, assuming that all stage A eggs are unfertilized, which may not have been true. For instance, this may underestimate viable eggs if non-developing eggs eventually would have developed (i.e., the clutch was newly produced), but it would overestimate successful reproduction if some of the eggs of different size are of different quality (smaller eggs = less yolk). As with fecundity, McDermott's (1998a, b) single site and time collections found little variation in egg size (stage A eggs were 0.318 ± 0.009 mm diameter). We found considerably more variation in egg size through space and time. Previous work in other crab systems shows that offspring viability after hatching can vary considerably due to variation in yolk (lipid) quality resulting from different habitat-specific maternal diets (Riley and Griffen 2017; Cannizzo et al. 2020).

The primary purpose of this study was to determine whether all the factors examined were important at once or whether any single factor, or subset of factors, had a dominant impact. We were able to examine the impacts of more factors on fecundity than on egg size, and impacts on fecundity were more pronounced than on egg size. That said, even minor impacts on egg quality could translate into substantial consequences for reproductive success (Riley

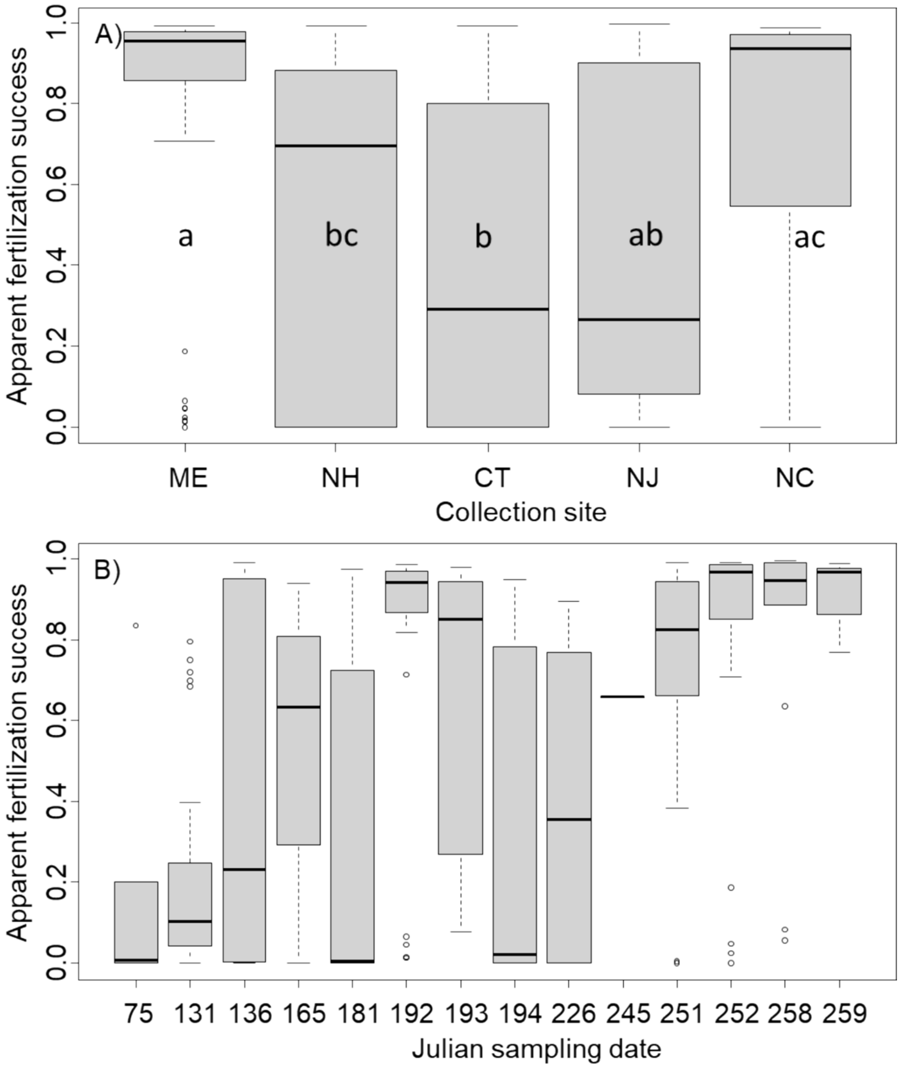

Fig. 5 Apparent fertilization success of female *Hemigrapsus sanguineus* from different sites **A** and collected on different Julian sampling dates **B**. Figure details are as given in the legend for Fig. 2, and where bars with the same lower case letters in part A are not significantly different

and Griffen 2017; Cannizzo et al. 2020). For fecundity, we found that each of the factors examined acted simultaneously to alter reproductive effort, though the relative impacts differed for each. Body size had the largest impact on fecundity, accounting for a five–tenfold increase across the range of mature body sizes. Temporal (seasonal) variation in clutch size and brood loss through development had the next largest impacts, each accounting for an approximately 50% change in clutch size. However, the impacts of brood loss disappeared for the largest individuals (> 25 mm carapace width). Spatial differences across the range had moderate impacts, resulting in 18.5% overall difference in clutch size and 5% difference in change in clutch size with body size. Variation in apparent fertilization success was seemingly very large, though the possibility that these patterns may have been explained by other factors (since we did not directly measure fertilization), especially time since egg extrusion, cannot be overlooked.

Theory predicts increased reproduction should occur towards the expanding edges of invasive species ranges, compared to central regions (Thomas et al. 2001; Travis and Dytham 2002; Hughes et al. 2003; Simmons and Thomas 2004; Phillips et al. 2008, 2010; Bartoń et al. 2012; Henry et al. 2013). We did not find evidence to support this in terms of clutch sizes standardized for crab size, which were relatively constant across the four northernmost sites, but were lower in North Carolina. The

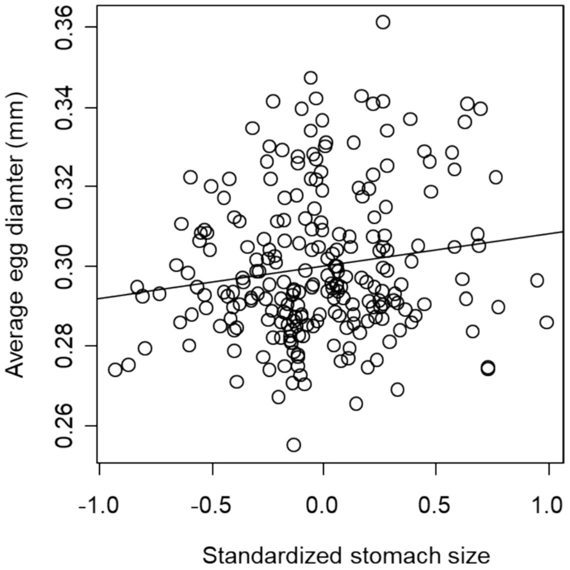

Fig. 6 Average egg diameter as a function of standardized stomach size (a proxy for diet quality), showing that egg diameter increases weakly (i.e., with considerable variation) as diet quality decreases

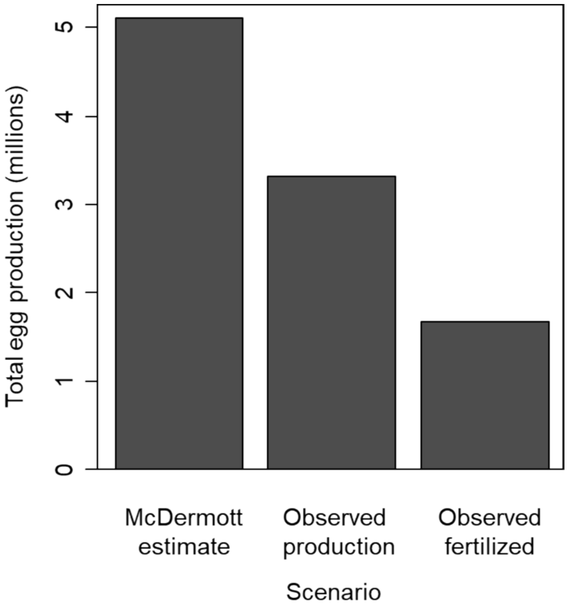

Fig. 7 Projected egg production under different scenarios by all crabs included in this study. The left bar assumes the relationship between carapace width and fecundity when crabs were sampled at a single site and time by McDermott (1998a, b): clutch size = −23,347 + 1985.1× carapace width. The middle bar is the sum of all fecundity observed in the current study. The right bar multiplies the observed fecundity of each crab in this study by the observed proportion of eggs developing, therefore accounting for fertilization success

range edge at North Carolina has been constant since 1995 (McDermott 1998a), consistent with our results that clutch sizes are lower there. However, the northern range edge continues to expand (Ramey-Balci 2023), and we may therefore have expected larger clutch sizes in Maine. While there was no difference in clutch size across sites, we did find the highest apparent fertilization success at the two range edges; however, as explained above, these results could potentially have been confounded by factors that we did not examine, such as time since egg extrusion. Thus, our study does not provide clear support for the predicted increase in reproductive effort at leading edge of the invasion of *H. sanguineus*.

In conclusion, our results suggest that studies examining reproductive success of invaders at a single place or time in their invasion may not provide the full picture of reproductive output. Additionally, studies focusing on individual factors affecting reproductive success may provide an incomplete picture without simultaneously examining other factors that can influence reproduction. Ultimately, as in our system, multiple factors may act simultaneously, and potentially even synergistically to influence reproductive success of invasive populations. While we examined several factors that influence invader reproductive success, other factors not examined here may also be important. These may include human changes to landscapes (Brusa 2016), climate change (Foo and Byrne 2017), pollution (e.g., Jones and Reynolds 1997; Soler et al. 2020), or interactions with native and/or other invasive species (Griffen et al. 2011).

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Data availability All data used in this paper are included as a supplemental file (EggData.csv).

Declarations

Conflict of interest The authors have no conflicts of interest or competing interests to declare.

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