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ORIGINAL PAPER

# Potential impacts of invasive crabs on one life history strategy of native rock crabs in the Gulf of Maine

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**Abstract** Organismal life history strategies are continually being strained by increasing environmental change, including exposure to invasive species. The rock crab *Cancer irroratus* is a commercially harvested species in the Northeastern US and Canada where previous studies have reported it uses subtidal habitats as a juvenile and then undergoes a habitat shift into deeper offshore waters to mature and reproduce. We demonstrate that in intertidal habitats of the Gulf of Maine, this species reaches reproductive maturity, and does so at a smaller size than has previously been recognized. Our goal here is to identify potential mechanisms by which the presence of invasive European green crabs (*Carcinus maenas*) and Asian shore crabs (*Hemigrapsus sanguineus*) may influence the success of this intertidal life history strategy of rock crabs based on the ecology and reproductive requirements of these young intertidal crabs. We experimentally demonstrate that the reproductive success of small rock crabs in intertidal habitats depends on a carnivorous lifestyle. Further, we demonstrate that juvenile rock crabs are more susceptible to predation by both invasive species than they are to cannibalism. Finally, using a numerical model to calculate lifetime rock crab fecundity, we demonstrate that this intertidal strategy is only beneficial when crabs experience reduced predation risk intertidally relative to in subtidal habitats. Together, our results demonstrate that invasive European green crabs and Asian shore crabs have the potential to greatly reduce the reproductive benefit of intertidal habitat use by young rock crabs.

**Keywords** *Cancer irroratus* · *Carcinus maenas* · Fecundity · *Hemigrapsus sanguineus* · Invasive species · Life-history strategy

## Introduction

Invasive species have the potential to alter numerous biological and ecological aspects of invaded systems. By altering habitat, species abundance, or interactions between native species, invaders have the potential to cause local or global extinctions (Clavero and García-Berthou 2005) and to alter the evolutionary trajectory of native species (Mooney and Cleland 2001). One key biological aspect of native species that invaders may potentially alter, one with far reaching consequences, is life history strategy. Life history strategies have long been recognized as important determinants of population success (Cole 1954). However, life history is not a static feature of organisms and can vary both

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temporally (e.g., Sæther and Bakke 2000) and spatially (e.g., Leggett and Carscadden 1978) in response to environmental gradients or changes in environmental conditions. Thus, continuing environmental challenges caused by humans, including the continued introduction of novel species into habitats, may conflict with existing life history strategies to negatively impact native species success.

One potential example of this may be occurring in the rock crab *Cancer irroratus* that can be found along the North American east coast from Newfoundland to Florida (Stehlik et al. 1991). Rock crabs are an important species both ecologically as important prey for lobsters (Gendron et al. 2001), and economically as a commercially fished species in Canadian waters since 2004 (Robichaud and Frail 2006) and as a retained "bycatch" species in the American lobster fishery since at least 1990 (ASMFC 2013). Rock crabs display spatial variation in life history and habitat utilization across their range. In general, larvae recruit to shallow waters where the first 2 years of life are spent (Bigford 1979); older individuals then move into deeper water (Haefner 1976). In southern areas of the mid-Atlantic juveniles are found subtidally in shallow water that is generally <20 m depth (Bigford 1979), whereas in more northern areas within the Gulf of Maine juveniles are found abundantly in intertidal areas (density estimates are not available, but Krouse 1976 reports capturing crabs <60 mm CW in intertidal areas at an average rate of 55 crabs per hour during monthly sampling by hand of a single stretch of beach over a 4-year interval). Size at maturity for female crabs in northern parts of its range has previously been reported to be in year 3 when crabs are between 50 and 60 mm CW (Krouse 1972; Scarratt and Lowe 1972; Haefner 1976). However, much smaller reproductively mature females (14–40 mm CW) have been documented in shallow waters within the mid-Atlantic (Haefner 1976), with approximately 20 % of crabs <50 mm CW carrying eggs in Rhode Island waters (Reilly and Saila 1978). Bigford (1979) summarized previous studies and concluded that rock crabs in southern areas of its range mature at about 30 mm CW (likely year 2 rather than year 3). No instance of early reproductive maturity has previously been reported for crabs within the Gulf of Maine, and it was previously assumed that all intertidal individuals were in fact juveniles that had not yet reached sexual maturity (Krouse 1976).

Use of intertidal habitats by young rock crabs likely provides two main benefits. First, the risk of predation is likely much lower in intertidal areas. Mortality due to predation by fish and skates in particular is high in subtidal areas during the first 2 years of life (75–85 % mortality annually, Reilly and Saila 1978). Juvenile rock crabs prefer boulder habitat (Scarratt and Lowe 1972), presumably because it provides predation refuge, and intertidal areas where rock crabs occur in the Gulf of Maine are dominated by boulders. Second, there is an abundance of food (both plant and animal material) available in intertidal areas that supports the rapid growth that occurs during early stages of life. Rock crabs generally molt numerous times within the first 15 months after settlement (Krouse 1976; Reilly and Saila 1978) and consume a wide range of animal foods to support this rapid growth (Scarratt and Lowe 1972). However, not all juvenile rock crabs settle intertidally (Scarratt and Lowe 1972), and uses of intertidal and subtidal habitats during early life stages therefore represent alternative strategies. Any anthropogenic changes that compromise the two intertidal benefits of reduced mortality risk and abundant food resources may reduce the reproductive profitability of this intertidal strategy relative to the subtidal alternative.

The success of these life history strategies may be influenced and potentially compromised by the continued range expansion of two species of invasive crab, the European green crab *Carcinus maenas* and the Asian shore crab *Hemigrapsus sanguineus*. The European green crab invaded the North American east coast in the early 1800s (Say 1817). Its northward spread has been slow, taking nearly two centuries to spread throughout New England and into Canada; it continues to spread throughout Canadian waters where rock crabs are captured commercially (Audet et al. 2003). The Asian shore crab was introduced in New Jersey in the late 1980s (Williams and McDermott 1990), then rapidly spread from central Maine to North Carolina (McDermott 1998). On the shores of mid-Atlantic states, this new invader quickly became the dominant consumer in intertidal areas by consuming the majority of animal prey (Lohrer and Whitlatch 2002a; Kraemer et al. 2007; Griffen et al. 2015) and eliminating other brachyuran crabs within <5 years of its arrival (Lohrer and Whitlatch 2002b; Kraemer et al. 2007). The impacts of this new invader have occurred more slowly in the Gulf of Maine, possibly due to the prevalence of complex boulder habitats and more abundant hard bottom substrate that may reduce species interactions. However, despite the slower trajectory of impacts, southern areas of the Gulf of Maine are now dominated by the Asian shore crab where its effects are strong, and it appears to be migrating northward (Griffen et al. 2011).

These two invaders could negatively influence young rock crabs in the intertidal via two mechanisms that are not mutually exclusive. First, they could reduce the availability of animal prey for rock crabs via exploitative competition. Although subtidal rock crabs are known to be primarily carnivorous (Scarratt and Lowe 1972), the diet of young crabs in intertidal areas has not been examined previously. Second, invasive crabs may directly consume juvenile rock crabs as they do with juveniles of other crab species (Lohrer and Whitlatch 2002b; Moksnes 2004), thus eliminating the refuge from predation risk that rock crabs likely experience by taking up intertidal residence.

Here we examine the potential impacts of these two invasive species on the life history strategy of young intertidal rock crabs using a multi-pronged approach. We first examine the diet of young intertidal rock crabs using gut content analysis to determine the importance of animal prey that are commonly depleted by these invaders. Second, we examine the sexual maturity of intertidal rock crabs, challenging the assumption that intertidal crabs in the Gulf of Maine are immature. Third, we experimentally examine the impacts on reproductive effort that would occur if young, mature intertidal individuals should reduce their animal dietary intake due to exploitative competition. Fourth, we examine the potential for European green crabs and Asian shore crabs to consume juvenile rock crabs relative to consumption of rock crabs by cannibalism. And lastly, we use a numerical model to examine how lifetime reproductive success of rock crabs may be influenced by both the reproductive consequences of diet changes and increased mortality risk in intertidal areas. We show that the European green crab and the Asian shore crab have the potential to substantially reduce the benefits for young rock crabs of using intertidal habitats in the Gulf of Maine.

## Methods

### Diet of intertidal individuals

We collected 40 rock crabs of a range of sizes (11.9–65.4 mm CW, mean = 30.6, SD = 11.6) of both sexes (14 male, 26 female) on a single day from intertidal areas at Nubble Lighthouse, ME (43°9′56.29″N, 70°35′31.27″W) in May of 2010. These were dissected, and their gut contents were removed and examined using a dissecting microscope. We separated the different food types (plant and animal species) into grid cells on a Petri dish and determined the proportional contribution of each of the different food types from the number of grid cells (or proportions of grid cells) that each occupied (Griffen and Mosblack 2011).

### Proportion of intertidal females that are reproductive

We collected 40 female rock crabs (26.1–52.1 mm CW) from Nubble Lighthouse in November of 2012 and dissected them to determine their reproductive state. For each crab we categorized ovary development into one of five stages reflecting the relative stage of egg production and vitellogenesis (following Campbell and Eagles 1983), as follows: 1 = ovaries undeveloped and not detectable without microscope; 2 = ovaries threadlike, colorless or white, no oocytes; 3 = ovaries half the volume of hepatopancreas, white to orange color, oocytes present; 4 = ovary and hepatopancreas approximately equal volume, ovaries light orange to orange, oocytes present; 5 = ovary larger than hepatopancreas, orange to red color, oocytes present. We then examined whether ovary development stage was size-dependent using a generalized linear model with ovary developmental stage as a Poisson-distributed response variable (since intermediate stages were not possible) and carapace width as a continuous predictor variable.

### Effects of diet on reproductive success of small intertidal individuals

Depletion of animal prey by invasive crabs in the Gulf of Maine, similar to what has been documented further south (see reference in “Introduction” section), would force young intertidal rock crabs to alter their diet and consume plant material instead of their preferred animal prey. In order to examine the reproductive consequences of this potential diet shift, we conducted a diet experiment that varied the total amount of food present and the proportion of that food that was animal or algal tissue in the diet. We maintained crabs on the same diet for 8 weeks, after which we quantified their reproductive effort and physiological condition. The experiment was conducted as follows.

We collected 40 female crabs (36.1 ± 5.8 mm CW) from Nubble Lighthouse, ME in September 2012 and returned them alive to the University of South Carolina. There, they were maintained in a recirculating aquarium in conditions that reflected those of their collection site in the fall (temperature: 13 °C and salinity: 33–34 ppt). Each crab was maintained in an individual experimental chamber that was submerged in the recirculating aquarium. Experimental chambers were individually plumbed so that each had a constant flow of water.

Crabs were initially weighed and these initial weights were used to determine the amount of food that they would receive. Crabs were randomly assigned to food treatments which crossed four levels of food amount (1, 2, 4, 8 % of body weight per day) and five levels of proportion of that food that was animal tissue or algae (all animal, 0.25 animal and 0.75 plant, 0.5 of each, 0.75 animal and 0.25 plant, all animal). The red alga *Chondrus crispus*, the most abundant algal food source at the crab collection site, was the plant material offered to crabs in this experiment. Although the most common animal food consumed by intertidal crabs at this site was mussel (see "Results" section), large nonconsumptive losses of mussel tissue in preliminary experiments prompted us to offer crabs fish (tilapia) tissue in this study, as mussels and tilapia represent similar food sources energetically and nutritionally (Griffen 2014). The four levels of diet amount and five levels of diet type were crossed orthogonally, yielding 20 different diets, with two crabs receiving each of these diets. However, the metric of interest in this experiment was the exact diet consumed, not the diet offered. The offered diet therefore served only to constrain consumption within certain bounds, and the actual amount consumed by two crabs offered the same diet treatment may not have been the same. Thus, while two crabs were provided with each of the 20 diet treatments, these should not be considered as replicates, and our statistical analyses (described below) reflect this experimental design.

Crabs were fed twice per week (Monday and Thursday), and uneaten food was removed after 48 h, dried at 70 °C for 48 h, and weighed. No-crab controls were also used to assess any nonconsumptive changes in food mass that occurred during each feeding period. The amount of food consumed ($C$) by each crab during each feeding period was determined for animal and plant tissue separately as:

$$C = F_I \times (1 - W) - F_F \quad (1)$$

where $F_I$ is the initial wet weight of animal or plant tissue offered, $W$ is the proportion water in that food, and $F_F$ is the final dry weight of nonconsumed food.

At the conclusion of the experiment we dissected each crab and removed the ovaries and the hepatopancreas. We used the gonadosomatic index (GSI), or the proportion of body weight allocated to the ovaries, as an estimate of reproductive effort (Kyomo 1988). The hepatopancreas is a digestive organ that stores energy as lipids for future growth and reproduction in crustaceans (Vonk 1960). We therefore used the hepatosomatic index (HSI), or the proportion of body weight allocated to the hepatopancreas, as an estimate of physiological condition (Kyomo 1988). We examined changes in reproductive effort with diet using a linear model with GSI as the response variable and the mass-specific daily animal consumption and mass-specific daily algal consumption as the predictor variables. Seven crabs released eggs during the experiment and five crabs molted during the experiment (diet amounts of molted crabs were adjusted following molting to reflect their new body weight). We therefore also incorporated egg release and molting occurrence as additional binary predictor variables in the analysis. During exploratory data analysis it became evident that crabs reduced their mass-specific consumption rate as mass increased. We therefore also included crab mass as a predictor variable in the analysis. Finally, we conducted a similar analysis to examine energy storage during the experiment with HSI as the response variable. Explanatory variables were identical except that GSI (continuous variable) was used rather than whether or not a crab had reproduced during the experiment to account for energy allocated to reproduction rather than stored. Three crabs died during the experiment and so were not included in the analyses.

### Relative predation risk from invasives for juvenile rock crabs

We examined the potential for consumption of juvenile rock crabs by European green crabs and Asian shore crabs, relative to the potential risk from cannibalism. We used a simple experiment in May 2014 in which juvenile rock crabs (18.5 ± 5.1 mm CW) were paired with larger individuals of each of the three potential predators (CW for *C. maenas*: 34.8 ± 4.2 mm; for *H. sanguineus*: 25.5 ± 2.7 mm; for *C. irroratus*: 28.0 ± 3.5 mm). Large and small crabs were paired for 24 h in 0.5 L plastic circular containers with mesh lids that were placed together into a large cage constructed of lobster wire and suspended from a dock at the University of New Hampshire Coastal Marine Research Complex in New Castle, NH, after which consumption was assessed. The number of replicates were not equal across the three species pairs because of the paucity of large (predator sized) *C. maenas* and *C. irroratus*. As a result, there were 10 replicates with *C. maenas* as the predator, 18 with *H. sanguineus* as the predator, and 12 with *C. irroratus* as the predator. We determined whether consumption by heterospecific predators was more likely than cannibalism using a logistic regression (consumed or not as the response variable) with predator species treated as a fixed factor (*C. irroratus* was set as the baseline for the analysis so that results compare predation by the other two species relative to cannibalism) and the size difference between the pair of crabs was treated as a continuous predictor variable. This experiment assumes that confining crabs in these small containers influenced the propensity for consumption equally for each of these species, and similarly, that the relative consumption rates by these three species under these simplified conditions would remain the same under field conditions with natural refuge habitat.

## Modeling potential changes to probable lifetime reproductive success

We developed a simple numerical model that calculated the potential impacts on lifetime reproductive success of an intertidal life history strategy. We started with a reference model that represented a completely subtidal life history where crabs mature at 50 mm CW after moving to deeper water offshore (Bigford 1979). We used this model as the baseline for comparison with two modified models for intertidal life histories, one that included early maturity in the intertidal and assumed no food competition from invasive crabs, and the other that assumed that food competition eliminated early reproduction in the intertidal and simultaneously caused reduced growth rates (as implied by the results of the lab experiment reported here). Calculations were made as follows.

### *Reference subtidal model*

We included size-dependent fecundity (*f*) following the equation given by Campbell and Eagles (1983):

$$log_{10}f = 0.5827 + 2.559log_{10}CW. \quad (2)$$

Carapace width (CW) values for use in Eq. 2 were obtained from the relationship between molt instar and size given by Reilly and Saila (1978) for mature female rock crabs:

$$CW = 12.571 + 0.953x, \quad (3)$$

where $x$ is the pre-molt carapace width. Size-specific mortality of rock crabs in subtidal habitats primarily reflects predation by fish and skates and is estimated at 75–85 % during the first 2 years of life and 65–68 % in the third year (Reilly and Saila 1978). Mortality rates of older crabs are not known, but are presumed to decrease with age as crabs attain a size refuge from predation (Reilly and Saila 1978). We therefore used survival rates ($s$) of 0.2 in years 1 and 2 and 0.35 in year 3. We then assumed that survival rates increased in years 4–8 at the same rate that they increased between years 2 and 3:

$$s_{y+1} = \left(1 - s_y\right)\left(\frac{1 - s_2}{1 - s_3}\right). \quad (4)$$

We therefore calculated the average lifetime fecundity ($F_s$) as the size-dependent fecundity (*f*) at each year ($y$), multiplied by the probability of surviving to that year class ($s$), summed across years:

$$F_s = \sum_{y}^{0-8} f_y \times s_y. \quad (5)$$

### *Intertidal with no food competition*

We next calculated the lifetime fecundity of crabs using an intertidal strategy during early life using Eqs. 2–5, but with the following three modifications reflecting this intertidal strategy. First, we assumed early reproduction during the second year (instar 7, 31.1 CW, see calculations below), consistent with results reported here. This was a conservative estimate of the onset of intertidal reproduction, as we found many intertidal females that were vitelogenic at much smaller sizes (<20 mm CW), suggesting that reproduction may have started as early as instar 5 or 6. Second, we incorporated decreased growth rates due to early reproduction. Growth rates of immature males and females are the same, but diverge once mature females start investing in egg development at the expense of growth (Krouse 1976). This tradeoff becomes progressively more expensive with size, so that the differences in growth rates between males and females become progressively and linearly larger with size (Reilly and Saila 1978). The end result of this is that crabs that begin reproduction early are smaller at each instar than crabs that begin reproducing later. We used the size at each instar for males and females given by Reilly and Saila (1978) to calculate the percent decrease in carapace width for females relative to males, and found that this percent difference increased linearly between instars 8–13 (female size as percent of male size = $-0.079 \times$ instar + 1.497, $R^2 = 0.99$). We then used this linear relationship to extrapolate back to the size at onset of maturity for female crabs employing an intertidal life history strategy assuming that they had begun reproducing at instar 7 rather than instar 8. This yielded a size of 31.1 mm CW for the size at first reproduction, which falls well within the range of sizes observed in our sampling. We then carried this decreased size forward across future instars using Eq. (3). Third, we assumed survival differed in intertidal habitats relative to survival reported by Reilly and Saila (1978) for subtidal habitats due to the complex nature of the intertidal habitat and the lack of prominent subtidal predators. The actual survival benefit of intertidal relative to subtidal habitats is unknown. We therefore examined changes in survival from −10 to +50 % during these first 2 years of life.

### *Intertidal with food competition*

Lastly, we made a third fecundity calculation that included exploitative food competition due to food depletion by invasive crabs. Our sampling and experimental results indicated that intertidal rock crabs primarily consume animal prey and that animal consumption is necessary for successful reproduction and storage of the energy and nutrients required for growth (see "Results" section). However, a consistent impact of high densities of the invasive Asian shore crab is reduced abundance of animals normally consumed by rock crabs, including mussels, barnacles, and crustaceans (Lohrer and Whitlatch 2002a, b; Kraemer et al. 2007; Griffen and Byers 2009). This third model therefore assumed that rock crabs occurred intertidally during the first 2 years of life prior to moving offshore, did not reproduce early, but still experienced reduced growth because of food limitation equivalent to that which occurs with early reproduction. We calculated lifetime fecundity over the same range of survival values (−10 to +50 %) as used for the previous model.

### *Model analysis*

For each of the two intertidal strategy models, we calculated the percent change in lifetime fecundity relative to crabs employing the subtidal strategy over the entire range of survival values given above. For each of the two models, we then statistically examined the percent change in lifetime fecundity across different survival values intertidally using the following nonlinear model:

$$\%\,Change\ in\ F_s = aM^b. \qquad (6)$$

where $a$ and $b$ are coefficients and $M$ is the percent change in annual survival rate in intertidal areas relative to subtidal survival rates.

## Results

### Diet of intertidal individuals

Of the 40 crabs collected, only 8 male and 17 female had food in their guts. Similar to what has been reported for larger subtidal adults, we found that smaller intertidal rock crabs are primarily carnivorous, consuming principally mussels, barnacles, and other crustaceans (Fig. 1).

### Proportion of intertidal females that are reproductive

Contrary to what has been previously assumed, we found that rock crabs become sexually mature intertidally and at much smaller sizes than previously expected in the Gulf of Maine. Specifically, we found that 37 of the 40 crabs showed some level of ovary development, and that the majority of crabs were near the final stages of ovary development associated with egg production (Fig. 2). Ovary developmental stage was not influenced by crab size (GLM, z = $-0.535$, $P = 0.59$).

## Effects of diet on reproductive success of small intertidal individuals

The relative values of the parameter estimates in the following analyses indicate the relative magnitude of the influence of each explanatory variable on the response. The mass-specific investment into reproductive effort (i.e., the GSI) increased strongly with animal consumption (parameter estimate = 0.95, $P = 0.007$, Fig. 3a) and increased very weakly with crab mass (parameter estimate = 0.02, $P = 0.035$), but was not influenced by algal consumption ($P = 0.98$). GSI also decreased weakly both for crabs that produced eggs during the experiment (parameter estimate = $-0.068$, $P = 0.016$) and for crabs that molted during the experiment (parameter estimate = $-0.109$, $P = 0.001$).

Similar results were observed for energy storage (i.e., the HSI). Specifically, mass-specific energy

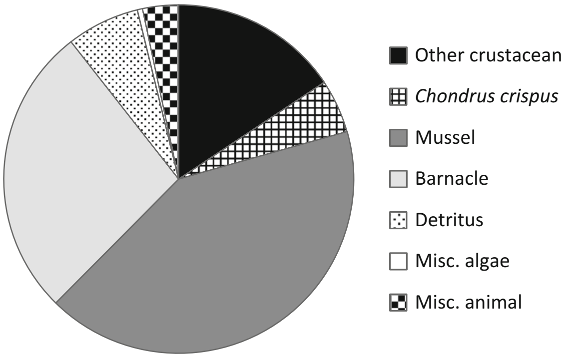

**Fig. 1** Relative contribution of different items to the diet of intertidal rock crabs *C. irroratus* at Nubble Lighthouse (n = 25). Food items encountered that made up <2 % of the gut contents are grouped together as miscellaneous alage or animals

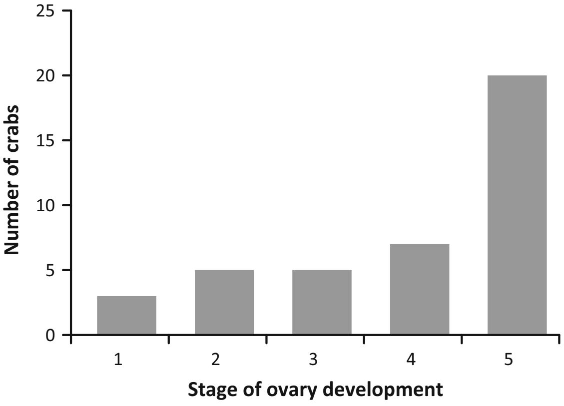

**Fig. 2** Number of rock crabs *C. irroratus* collected intertidally from Nubble Lighthouse, ME at different stages of ovary development, where *1* is undeveloped, *2* is slight development, *3* is moderate development, *4* is developed, and *5* is well developed (see Campbell and Eagles 1983 for descriptions of ovaries and eggs in each of these 5 stages for this species)

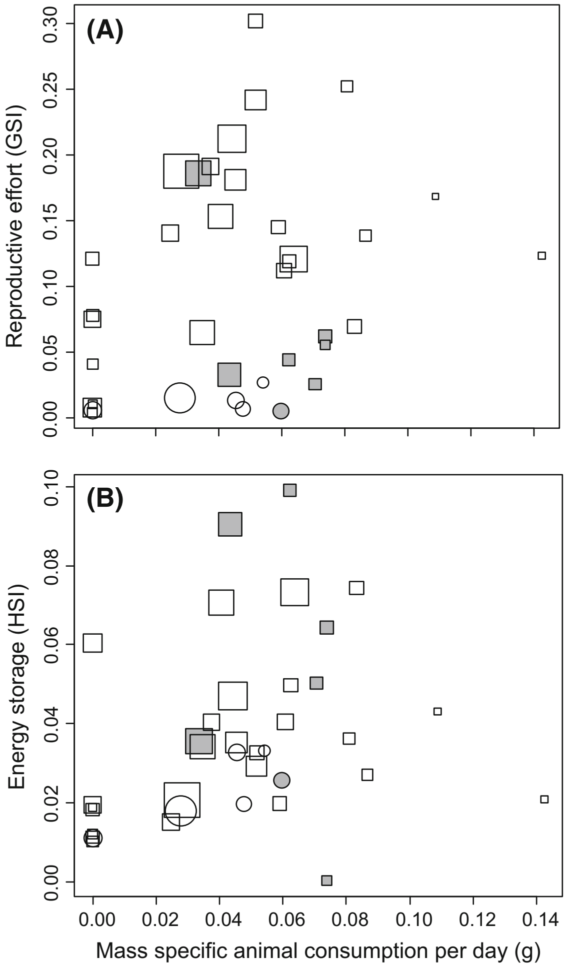

**Fig. 3** **a** Gonadosomatic index (GSI) and **b** hepatosomatic index (HSI) of experimental crabs as a function of diet, crab size, and whether crabs molted or reproduced during the experiment. *Size of symbol* indicates relative mass of the crab, *gray symbols* are crabs that released eggs during the experiment, *circles* are crabs that molted during the course of the experiment

storage increased most strongly with animal consumption (parameter estimate $= 0.341$, $P = 0.005$, Fig. 3b), increased weakly with the mass of the crab (parameter estimate $= 0.008$, $P = 0.05$), and was not influenced by algal consumption ($P = 0.31$). At the same time, energy storage declined with allocation to reproduction (parameter estimate for GSI $= -0.12$, $P = 0.036$), and declined weakly for crabs that molted during the experiment (parameter estimate $= -0.02$, $P = 0.05$).

### Relative predation risk from invasives for juvenile rock crabs

We found that small rock crabs were more likely to be consumed when paired with either of the invasive species than when paired with a larger conspecific. Specifically, proportional mortality of small rock crabs in conspecific pairs was 0.167, but increased to 0.8 when paired with European green crabs ($z = 1.95$, $P = 0.05$) and to 0.5 when paired with Asian shore crabs ($z = 2.99$, $P = 0.003$).

### Modeling potential changes to probable lifetime reproductive success

Both alternative intertidal models demonstrate that lifetime fecundity increases with survival rates (parameter values for both models, $P \ll 0.0001$, Fig. 4).

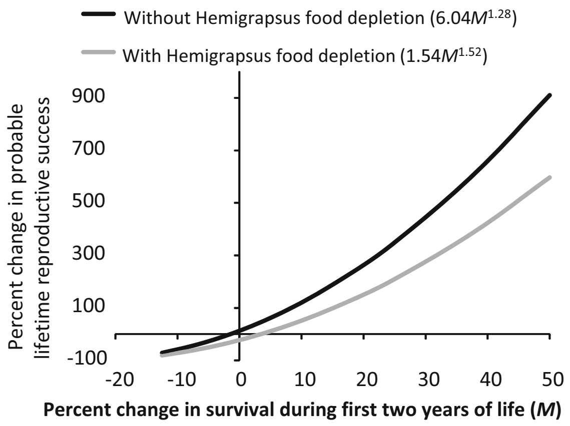

**Fig. 4** Model results showing percent change in potential lifetime fecundity for rock crabs that use an intertidal lifestyle early in life relative to those that live subtidally throughout their lives. *X-axis* shows percent change in survival during first 2 years of life intertidally relative to in subtidal habitats. Model results include crabs that reproduce early (*black line*) and those that do not reproduce early and that experience food shortage due to exploitative competition from invasive crabs (*gray line*)

This increase in survival is the dominant benefit of intertidal existence, increasing overall lifetime fecundity by up to 600 and 900 % for the models with and without food competition, respectively, when survival increases by 50 % relative to subtidal habitats. As increases in survival (relative to subtidal crabs) become more modest, the fecundity benefits drop off quickly. For crabs that experience food depletion from these invasive competitors, survival rates must increase by 3 % relative to survival in subtidal habitats in order for an intertidal life history strategy to be more beneficial reproductively. However, for crabs that do not experience food depletion from competitors, this intertidal strategy always results in superior lifetime reproduction as long as survival in intertidal areas is not lower than in subtidal areas.

## Discussion

We demonstrated that carnivory is the primary dietary strategy of intertidal rock crabs, and that this carnivory is essential for reproductive success and for energy storage that enables future growth and reproduction. We further demonstrated that a large percentage of young intertidal rock crabs in the Gulf of Maine are in fact reproductively mature and are in the process of producing eggs, contrary to previous assumptions that intertidal rock crabs are reproductively immature. Our results also show that rock crabs are more vulnerable to predation by European green crabs and the Asian shore crabs than they are to cannibalism. Finally, our numerical model demonstrated that spending the first 2 years of life in intertidal habitats can greatly enhance lifetime reproductive success if mortality risk during this time is lower intertidally than subtidally, even under conditions of food depletion that are associated with the presence of the Asian shore crab.

Consistent with our findings for intertidal rock crabs, studies in shallow subtidal areas have also shown that rock crabs >25 mm CW have a primarily carnivorous diet (Drummond-Davis et al. 1982; Scarratt and Lowe 1972). These findings are also consistent with a previous study that examined gut morphology of brachyuran crabs and showed first, that gut size increases with percent herbivory in the diet, and second, that intertidal rock crabs have very small guts, consistent with a carnivorous diet (Griffen and Mosblack 2011). The different food items encountered in gut contents here are common at the site where crabs were collected and it is possible that the relative abundance of different animal prey reported here simply reflected the relative availability rather than selective feeding. However, drift algae, particularly *C. crispus*, is abundant at this site (though it was not quantified on the specific day that crabs were collected for gut content analysis). The dominance of animal tissue (95 % of gut contents) relative to plant material, combined with results of studies reported above, suggests that a generally carnivorous diet reflects a preference and active selection of animal rather than plant foods by rock crabs. We should note that diet and reproductive data came from a limited number of crabs (25 for diet analyses and 40 for reproduction) collected at a single time from a single site. Broader temporal/spatial sampling will help to corroborate the extent to which these results from Nubble Lighthouse represent broader patterns.

Previous studies have shown that juvenile rock crabs settle in intertidal areas, but have presumed that rock crabs move subtidally before becoming sexually mature (Krouse 1976). This presumption likely resulted from the lack of berried individuals intertidally and the fact that Krouse (1976) did not dissect crabs to examine sexual maturity. We also have not observed any gravid females intertidally, but our results clearly demonstrate that a large portion of rock crabs become sexually mature intertidally and begin investing in egg production prior to moving offshore. It remains unclear what proportion of rock crabs use this intertidal strategy as opposed to initially settling in deeper waters. However, both the European green crab (Hunter and Naylor 1993) and the Asian shore crab (Gilman and Grace 2009) are found in shallow subtidal waters and the results found here may also be applicable to rock crabs in these areas.

We found that European green crabs were more likely than Asian shore crabs to consume juvenile rock crabs (though this result is tenuous given the small sample size in our predation experiment), but that both represent an increased mortality risk relative to cannibalism. Lower rates of cannibalism than predation by the European green crab have previously been reported for rock crabs in a long term laboratory experiment (Breen and Metaxas 2009). A previous study conducted on the Canadian coast also documented the presence of rock crabs in gut contents of European green crabs (Elner 1981). However, as is commonly true for crabs, interactions between rock crabs and European green crabs are size specific. Rock crabs will readily consume smaller European green crabs with positive effects on resulting rock crab growth rates (Breen and Metaxas 2009). Interactions between these European green crabs and Asian shore crabs are highly agonistic, and Asian shore crabs have eliminated or greatly depressed the numbers of European green crabs in many areas (Lohrer and Whitlatch 2002b; Griffen et al. 2011; Griffen 2014). The lower per capita threat from Asian shore crabs would initially suggest that this should reduce predation risk for rock crabs; however, this may not be the case given the much greater population densities of Asian shore crabs (Griffen and Delaney 2007).

Results of our numerical model indicate that potential impacts of exploitative competition on lifetime reproductive potential are likely much lower than those of increased mortality risk in intertidal habitats. Any effects of reduced animal consumption due to exploitative competition from either invader are also likely temporally and spatially variable. For instance, during our 2012 sampling at Nubble Lighthouse we observed relatively few barnacles and no mussels intertidally. In contrast, at the same site in 2014, recent barnacle and mussel recruits covered nearly every conceivable hard surface, while at another site (Odiorne Point, NH) just a few miles down the road recruitment of these prey species were much lower (Griffen, pers. obs.). Densities of both invasive crab species can also vary spatially and temporally (Griffen and Delaney 2007; Griffen et al. 2011). Both the competition and predation effects of these predators on intertidal rock crabs will likely be highest at places and times when the invasive crab densities are high and recruitment of preferred prey items (mussels and barnacles) are low.

## Life history variation

Given the prevalence of environmental variability, having a diversity of life history strategies within a single species can provide a form of bet hedging that can buffer a species from the effects of spatial and temporal variation (Stearns 1992; Wilbur and Rudolf 2006). For brachyuran crabs in general, life histories have evolved to maximize lifetime egg production (Hartnoll and Gould 1988). Previous evidence suggested that the life history strategy of rock crabs varied with latitude (Shields 1991; Stehlik et al. 1991), with individuals in southern latitudes becoming mature at smaller sizes and in shallower waters than individuals at northern latitudes (Bigford 1979). Our results indicate instead that rock crabs in northern areas within the Gulf of Maine also reach sexual maturity at small sizes and in coastal waters.

Our numerical model results demonstrate that the lifetime reproductive success of crabs employing this intertidal strategy increase quickly relative to a permanent subtidal strategy when mortality risk is reduced in intertidal habitats. Fish and skates are the primary predators in subtidal habitats (Reilly and Saila 1978), and predation risk from these species is surely reduced in intertidal habitats. Cannibalism appears to be low in rock crabs (results presented here and Scarratt and Lowe 1972), and is therefore unlikely to present a mortality risk in intertidal habitats that matches that from fish and skates in subtidal habitats. However, our results suggest that this intertidal life history strategy may become less tenable with the continually expanding ranges of European green crabs and Asian shore crabs if these predators decrease survival rates of rock crabs as they are known to do for other crab species (Lohrer and Whitlatch 2002b; Kraemer et al. 2007). In this case, continued reliance of rock crabs on this strategy would represent an ecological trap (Schlaepfer et al. 2002) that would decrease rock crab population growth rates in proportion to the increase in their own mortality rates in intertidal habitats.

### Implications for the rock crab fishery

The impacts of European green crabs and Asian shore crabs on the rock crab population will likely depend on what proportion of the population recruits intertidally (or at least to nearshore habitats) as opposed to subtidal, deeper water habitats. This is currently unknown for any region. Some hypotheses can, however, be formed by comparing rock crab strategies in the Gulf of Maine to those in areas further south. While small rock crabs are found in shallow waters in mid-Atlantic regions, there are no reports of rock crabs found intertidally south of the Gulf of Maine. This may reflect latitudinal differences in intertidal temperature regimes or in the abundance of intertidal refuge habitat. In either case, it is possible that an entirely subtidal life cycle in southern areas presents a much greater predation risk that results ultimately in lower average lifetime reproductive success. In contrast, as we have shown, the reduction of mortality risk during early life through the use of intertidal habitat would greatly increase lifetime reproductive success. Thus, it may be that northern rock crab populations are large enough to sustain commercial fisheries because of the higher average lifetime reproductive success attributable to this intertidal habitat use in northern regions and the fact that these shallow water individuals do not experience fishing pressure until they stray into deeper water, whereas the smaller population sizes (insufficient to sustain fisheries) in southern regions reflect lower average lifetime fecundity due to greater mortality of smaller individuals in subtidal habitats. This hypothesis would require additional information to test.

If the above hypothesis is true, or if the premise on which it is based is true (that intertidal habitats afford young crabs greater protection relative to subtidal habitats and that this in turn increases the average lifetime fecundity), then the continued spread of the European green crab and the Asian shore crab within the Gulf of Maine may have negative consequences on the rock crab population size, and thus on the nascent rock crab fishery. And while northward expansions of the Asian shore crab may stop short of northern areas where rock crabs are commercially fished (Byers and Pringle 2006), the European green crab continues to expand its invasive range throughout important fishery grounds (Audet et al. 2003; DFO 2013).

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