

Energetic effects of diet choice by invasive Asian shore crabs: implications for persistence when prey are scarce

Blaine D. Griffen^{1,2,*}, Margaret Vogel², Lacey Goulding², Rachel Hartman²

¹Department of Biological Sciences, and ²Marine Science Program, University of South Carolina, Columbia, SC 29208, USA

ABSTRACT: Invasive consumers often achieve very high abundances and consequently have large consumptive impacts on invaded habitats. Consumptive impacts that strongly reduce the abundance of native prey cause invasive species to subsequently make less favorable prey choices. Here we examine the energetic implications of diet choice in the invasive Asian shore crab *Hemigrapsus sanguineus*, an omnivorous consumer that has strongly reduced its favored prey species across much of its invaded range. In the first of 2 long-term feeding experiments, we examined the energetic implications of animal versus algal consumption when this invader has the choice between its most commonly consumed foods. In the second experiment we compare the energetic payoff of consuming several alternative algal and animal foods that are available on beaches where this invader has already strongly depressed or depleted its preferred prey items. We show that despite the primarily herbivorous nature of the Asian shore crab, animal consumption yields the greatest energetic payoff. We also demonstrate that on beaches where its preferred foods have been depleted, cannibalism presents the best choice energetically. However, in a third experiment we demonstrate that the propensity for cannibalism in this species is weak. Our results may help explain recently described declines in Asian shore crabs on beaches where it has dominated for ~20 yr since its invasion. Further, extension of our results provides a general hypothesized framework to understand self-limitation of invasive species in habitats that they have strongly altered.

KEY WORDS: Cannibalism · Energetics · Invasive species · Self-regulation

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INTRODUCTION

Invasive species have become a ubiquitous part of ecological communities and are important drivers of ecological change (Didham et al. 2005). This change occurs both through direct and indirect effects that modify the biological and physical environments in ways that can make these environments less suitable for the survival of native species. As a result of these strong impacts on invaded habitats, invasive species can even be a substantial cause of extinction (Gurevitch & Padilla 2004, Clavero & García-Berthou 2005).

Biological impacts of invaders may be especially strong when these invaders are consumers. Numerous examples exist of strong consumptive effects of invaders that reduce the abundance of native prey species. For instance, consumption by invasive lionfish in the western Atlantic greatly reduces the abundance of native coral-reef fish (Albins & Hixon 2008). Also, consumption by invasive European green crabs has caused large declines in numerous prey species on the California coast (Grosholz et al. 2000). Similarly, consumption by invasive crayfish in Mediterranean lakes strongly depresses abundances of native snails, fish, and plants (Gherardi & Acquis-

*Corresponding author: bgriffen@biol.sc.edu

tapace 2007). And as a final example, consumption by invasive rats on invaded islands strongly depresses the populations of both seabird and turtle prey (Caut et al. 2008). Impacts of invasive consumers can be particularly strong when their own abundances reach very high levels due to enemy release in their new habitat, allowing them to proliferate unchecked by competitors, consumers, or parasites that limited their numbers and impacts within their native range.

One such case is the Asian shore crab *Hemigrapsus sanguineus*. This omnivorous consumer was introduced to the east coast of North America in the late 1980s (Williams & McDermott 1990). It then spread rapidly, reaching remarkably high densities that commonly meet or exceed 100 ind. m⁻² (Lohrer & Whitlatch 2002a, Brousseau et al. 2003, Griffen & Delaney 2007, O'Connor 2014), much higher than densities achieved in its native Japan (Lohrer et al. 2000). Very high densities in invaded areas may be attributable to enemy release from predators (reviewed by Epifanio 2013), competitors (Lohrer et al. 2000) and parasites (Blakeslee et al. 2009), all of which help limit its proliferation in its native range. This omnivore naturally consumes primarily plant material (McDermott 1998a, Lohrer et al. 2000, Ledesma & O'Connor 2001, Griffen & Mosblack 2011, Griffen et al. 2012), but prefers to consume animal material when it is available (Brousseau & Baglivo 2005, Griffen 2011) and will include a substantial amount of animal material in its diet, particularly during the summer reproductive months (Griffen et al. 2012). As a result of its consumptive activities, native prey species often decline in both abundance and diversity following the arrival of this invader on a beach (Lohrer & Whitlatch 2002a, Kraemer et al. 2007, Griffen & Byers 2009). Specifically, previous experimental and observational work has demonstrated that, despite the Asian shore crab's primary reliance on plant material, consumption by this species greatly depletes mussels and other crustaceans (Lohrer & Whitlatch 2002a,b, Kraemer et al. 2007), and depresses but does not eliminate barnacles (Brousseau & Goldberg 2007) and snails (Kraemer et al. 2007). Despite strong consumptive impacts and the resulting decreases in prey availability, the Asian shore crab has been able to persist at high densities throughout much of its invaded range (Griffen et al. 2011, O'Connor 2014). However, in some areas, high initial abundances have given way to much lower densities over time (Schab et al. 2013).

Previous work has demonstrated the importance of animal consumption for meeting metabolic nitrogen

demands in herbivores in general (White 1993, Mattson 1980), and in primarily herbivorous crabs in particular (Kennish 1996, Riley et al. 2014). These demands can be met by the consumption of hetero-specific prey (White 1985) or by cannibalism (White 1993). It should therefore be expected that inclusion of animal material in the diet by Asian shore crabs would similarly have metabolic benefits. However, the relative benefits of the most preferred animal and algal foods remain unclear. It is also unclear what strategy offers the most benefit to Asian shore crabs at times or in places where consumption by this invader has depressed or depleted preferred animal and algal food items.

Here we take an energetic approach and examine the energetic consequences of diet choice by the Asian shore crab. We conducted 2 experiments that examined energy storage in the hepatopancreas of female crabs that can later be used for growth and/or reproduction (Vonk 1960, O'Connor & Gilbert 1968, Anilkumar 1980). The first experiment examined diet selection when the most commonly consumed or preferred animal prey and the most commonly consumed alga were offered in different abundances, and tested the hypothesis that absorption and energy storage would vary with diet. Based on similar experiments with other crab species (Griffen 2014, Riley et al. 2014), we hypothesized that energy storage would increase with increasing animal consumption, but would not be influenced by plant consumption. The second experiment focused on energetic consequences of qualitative changes in diet that may at times be forced upon Asian crabs when their own consumptive effects (or when lack of prey recruitment) may have eliminated their preferred food sources. For this experiment, we tested 2 hypotheses. First, that energy storage would be greatest when crabs consumed the 3 most abundant animal foods as compared to the 3 most abundant algal food sources available at a single site less than 15 yr after the invasion of the Asian shore crab. Second, that cannibalism would reflect the most energetically favorable diet option. Finally, we conducted a third, simple field experiment to test the hypothesis that cannibalism by the Asian shore crab is weak.

MATERIALS AND METHODS

Omnivory Expt 1: Diet type and amount

We conducted an experiment to determine the effect of food type (algae vs. animal) and amount of

food consumed on the energetic state of the Asian shore crab. We chose to use the most commonly consumed and preferred food types in invaded habitats. For animals, this is the mussel *Mytilus edulis* (Lohrer & Whitlatch 2002b, Griffen & Byers 2009), and for algae it is the abundant red alga *Chondrus crispus* (Griffen et al. 2008). Other species of algae, particularly green algae, are preferred by this consumer in laboratory preference trials (Bourdeau & O'Connor 2003); however, these are rarely found in the gut contents of wild-caught crabs (Griffen et al. 2008).

We collected female crabs (21.3 ± 2.3 mm carapace width [CW]) from Odiorne Point, NH, USA in early May 2011. To standardize reproductive state of experimental crabs as far as possible, we only collected gravid females. Crabs were taken immediately to the University of South Carolina where they were held at elevated temperatures (20°C , which falls within the range of natural summer temperatures for seawater at the site where these crabs were collected, but is higher than temperatures that commonly occur, B. D. Griffen unpubl. data) for 5 d to stimulate egg hatching. All crabs used in the experiment had therefore recently produced and released a clutch of eggs. This species produces multiple clutches per reproductive season (McDermott 1998b). The experiment was conducted in a closed, recirculating aquarium (salinity 34 psu) at water temperatures that mimicked summer temperatures on the New Hampshire coast (15°C), and with a 18 h light:6h dark cycle. Each crab was housed in its own experimental chamber (1 l volume). Each chamber was supplied with water so that flow occurred through each chamber within the recirculating system. Chambers were designed to capture all feces and unconsumed food particles (crabs generally shred their food and create large amounts of food waste) so that these could be precisely quantified for each crab. Algae fed to crabs during the experiment were collected at the same time and place as crabs. However, given the scarcity of mussels at the site at the time of collection, we purchased live mussels from Cape Cod Shellfish & Seafood (Boston, MA) and froze them until they were used in the experiment. Only mussel mantle tissue was used. No crabs died or molted during the 10 wk experiment.

Feeding and consumption

Each crab was fed a constant diet 3 times per week throughout the experiment. These experimental diets differed in the total amount of food offered at

each feeding (0.1, 0.2, 0.4, 0.8 g wet weight) and the percent of that food that was mussel or algae (ratios used were 0:100, 25:75, 50:50, 75:25, 100:0), yielding a total of 20 different quantitative \times qualitative diet combinations. Our experiment used 40 crabs. We therefore fed each of the 20 diet combinations to 2 different crabs. These 2 crabs should not, however, be considered experimental replicates. The experimental treatment of interest was the amount and type of food consumed rather than the specific diet that was offered. The diet offered served only to constrain the possible consumption within certain bounds, and each of the 40 crabs therefore had a unique dietary intake over the course of the experiment that reflected their daily individual diet choices within the constraints of what was offered to them. As a result, true experimental replication was not possible, a fact that is reflected in our statistical analyses described below.

Crabs were fed on Monday, Wednesday, and Friday throughout the 10 wk experiment and were given 24 h to consume the provided food before any uneaten food was removed, dried at 70°C for 48 h, and weighed (mussel and algae separately) to determine the precise amount of each food type remaining. Initial dry weight of food offered was calculated from measured wet weights using the percent water content of each of the different food types (mussel: $82.5 \pm 1.6\%$; algae: $70.0 \pm 0.3\%$; mean \pm SD), determined independently using the mean difference in mass of wet and dry replicate samples ($n = 30$) of each food type. Additionally, a nonconsumption control (mussel tissue and algae submerged within the experimental chamber, but not accessible to a crab) was included on each feeding day to determine any nonconsumptive changes in food mass. However, this nonconsumptive control may have missed some of the dissolving/leaching of mussel tissue if this nonconsumptive loss increased as crabs handled mussel tissue. If so, then consumption and absorption rates of mussel tissue reported here will be over- and underestimates, respectively. We examined the relationship between amount of food provided and amount of food eaten (averaged across all feeding periods) for each food type separately (but with both food types offered included as predictor variables) using linear models.

Absorption

After removing uneaten food in each feeding cycle, crabs were then given 24 h for gut clearance before

being fed again (except on weekends where food was removed on Saturday and feeding did not occur again until Monday). Experimental chambers were designed with a mesh subfloor so that feces fell through to a collection chamber where they were isolated from the crab to prevent reingestion. Feces were collected by filtration onto a Whatman Qualitative No. 1 filter, and were weighed after drying for 24 h at 70°C. We used the ratio of the dry weight of feces produced and the dry weight of food consumed as the absorption efficiency (*AE*). This provides an estimate of total absorption efficiency, but does not indicate whether consumed mussel or algae were absorbed differently. Given the messy nature of crab eating, small uneaten food particles were often collected with the feces. These particles were removed prior to drying and weighing the feces and were added to the uneaten food for weighing as described in the preceding paragraph.

AE appeared to change nonlinearly with food consumption. We used an information theoretic approach (Burnham & Anderson 2009) to verify this and to determine how *AE* changed with consumption amount and with food composition. We used total average daily consumption (*C*, measured as described in the previous subsection) and the proportion of consumed food that was mussel tissue (*P*) because we could not differentiate absorption of consumed mussel and absorption of consumed algae and had to therefore make the assumption that both foods were absorbed equally. We fit the following models (k_1 to k_4 in these models were constants determined by fitting the models to the data). These models were chosen to reflect increasing phenomenological complexity in the way that absorption efficiency changed with *C* and *P*. We then used Akaike's information criterion (AIC) to select the most parsimonious model. We used the following models: Model 1, *AE* increases linearly with both *C* and *P*:

$$AE = C + P \quad (1)$$

Model 2, *AE* increases exponentially with *C*, but linearly with *P*:

$$AE = P e^{(k_1 C)} \quad (2)$$

Model 3, *AE* increases exponentially with *P*, but linearly with *C*:

$$AE = C e^{(k_1 P)} \quad (3)$$

Model 4, *AE* increases exponentially with both *P* and *C*, but not independently:

$$AE = k_1 e^{(k_2 C + k_3 P)} \quad (4)$$

Model 5, *AE* increases independently and exponentially with both *P* and *C*:

$$AE = k_1 e^{(k_2 C)} + k_3 e^{(k_4 P)} \quad (5)$$

Metabolic rate

In the 9th week of the experiment we also measured the metabolic rate of each crab to determine whether diet-induced differences in metabolic rate could be responsible for any differences in physiological condition seen at the end of the experiment. Rates were measured using a YSI dissolved oxygen meter (model no. 52CE) in a closed volume chamber. Measurements were made after the gut clearance period (so at least 24 h after crabs had eaten). Crabs were placed into a closed chamber filled with water at the same salinity and temperature as the experimental water. They were allowed 15 min after introduction into the respirometry chamber to acclimate before the initial oxygen reading was taken. It is possible that this acclimation period was insufficient to eliminate all stresses induced by the change in environments, but this procedure was consistent across all crabs and so should not influence the relationship between diet and metabolic rate tested here. The final reading was then taken 15 min later and the metabolic rate was calculated as mg O₂ consumed per gram dry weight of crab per hour. Following the metabolic rate measurement, the crab was then returned to its experimental chamber and the regular feeding schedule continued as described above. Metabolic rate was regressed against crab dry weight and the residual from this relationship was determined for each crab. These residuals were then used as the response variable in a linear model with mean daily mussel and algal consumption treated as predictor variables to examine the effects of food consumption on metabolic rate independently of differences due to body size.

Physiological condition

At the conclusion of the experiment, each crab was dissected and the hepatopancreas was removed. The hepatopancreas and the rest of the crab were then each dried for 72 h at 70°C and weighed. We calculated the hepatosomatic index, a size-independent measure of physiological condition in crabs (Kyomo 1988), as the mass of the hepatopancreas divided by the remaining mass of the crab. As a second estimate

of physiological condition, we measured the percent lipid of the hepatopancreas tissue. Bulk lipids were extracted using a modified Folch method (Folch et al. 1957) where chloroform is replaced with hexanes (Hara & Radin 1978). We verified that these 2 metrics provide a redundant estimate of physiological condition using a linear model with the hepatosomatic index as response variable and percent lipid of the hepatopancreas as a predictor variable.

We statistically examined how the physiological condition of crabs was influenced by their dietary intake using linear models with the hepatosomatic index and percent lipid as response variables in separate analyses and daily mass of mussel and algal tissue consumed per gram of crab (i.e. the mass-specific consumption rates) as predictor variables in both analyses.

Omnivory Expt 2: Qualitative diet experiment

Asian shore crabs often eliminate or strongly depress the abundance of native prey on invaded shores (see references given in 'Introduction'). We therefore conducted an experiment to determine the ability of the Asian shore crab to build energy reserves when consuming non-preferred diets in habitats that they have invaded. We chose to use the most abundant food items available at Odiorne State Park, NH, USA, a site that has been influenced by Asian shore crab consumption for nearly 15 yr (Tyrrell & Harris 2000). Our sampling of ten 0.5 m² quadrats randomly dispersed along a transect 1.0 m above mean lower low water found only 2 attached types of algae: *Ascophyllum nodosum* covered 31% of the sampled area and *Fucus* spp. covered 18% of the area. In addition, while not attached, there was a considerable amount of red drift algae comprised mainly of *Mastocarpus stellatus* and *Chondrus crispus*. The abundances of potential animal prey were as follows: 1076 ± 1371 *Semibalanus balanoides*, 130 ± 60 *Littorina littorea*, 7 ± 3.5 *Hemigrapsus sanguineus*, 1.5 ± 1.5 *Carcinus maenas*, and 0.5 ± 0.75 *Nucella lapillus*. Also present at low abundances at the site, but not in our sampling quadrats, were *Mytilus edulis* and *Gammarus* spp. These relative species abundances indicate a predominance of species that are non-preferred prey items of Asian shore crabs (Bourdeau & O'Connor 2003, Brousseau & Baglivo 2005, Griffen 2011) and are consistent with experiments documenting the long-term consumptive impacts of this species (Kraemer et al. 2007, Griffen & Byers 2009). Based on these sampled abun-

dances, we chose to use *A. nodosum*, *F. vesiculosus*, and *M. stellatus* as algal foods in our experiment, and the barnacle *S. balanoides*, the snail *L. littorea*, and conspecifics (i.e. cannibalism on juvenile *Hemigrapsus sanguineus*) as animal prey.

We collected 63 female Asian shore crabs (18.7 ± 2.2 mm CW) from Odiorne Point, NH in July 2013 and took them to the University of South Carolina, where we conducted this experiment using the same experimental conditions as described for the previous experiment. At the same time, we also collected from Odiorne Point sufficient large snails (>1 cm shell length), several small rocks bearing live barnacles, juvenile Asian shore crabs (<13 mm CW), and all 3 species of algae. These were frozen until required for use in feeding.

Feeding and consumption

Each crab was fed on Monday, Wednesday and Friday. For each diet type, we provided sufficient food so that it was generally not all consumed in 48 h. Any uneaten food was removed at the next feeding (except for uneaten food from the Friday feedings, which was removed on Sunday in order to maintain a 48 h feeding period) and the presence of feces was noted as evidence that consumption had occurred. Snail shells were cracked, barnacles were scraped from rocks, and the carapace of juvenile crabs was opened prior to giving these food items to crabs, essentially eliminating differences in handling effort across food types. The experiment included 9 diet treatments, each replicated 7 times: (1 to 3) each of the 3 animal foods separately, (4 to 6) each of the 3 plant foods separately, (7) the 3 animal foods fed on a rotating basis at each feeding so that each diet item was received once per week, (8) the 3 alga types were fed on a rotating basis at each feeding so that each was received once per week, and (9) all 3 animal and all 3 plants fed on a rotating basis so that each diet item was received once every 2 wk. The experiment continued for 7 wk (i.e. 21 feeding periods). No crabs died or molted during the experiment. We used a generalized linear model (GLM) with a Poisson distribution to determine whether the number of days with feces present depended on diet treatment. We set the treatment where all 6 foods were rotated through the diet as the baseline for comparison, and the model then compared each of the other diets to this single diet to see if they differed in the number of feeding periods with feces present.

Physiological condition

At the conclusion of the experiment, each crab was dissected and the hepatopancreas was removed. The hepatopancreas and the rest of the crab were then each dried for 72 h at 70°C and weighed. We then calculated the hepatosomatic index as described for Omnivory Expt 1. We statistically compared physiological conditions between feeding treatments using a 1-way ANOVA with the hepatosomatic index as the response variable. This was followed by a series of 5 *a priori* linear contrasts to compare the mean of all the food items independently to the treatment in which all 6 foods were rotated (Diets 1 to 6 vs. Diet 9), the mean of the 3 animal diets independently to the treatment with all 3 animal foods rotated (Diets 1 to 3 vs. Diet 7), the mean of the 3 plant diets independently to the treatment with all 3 plant foods rotated (Diets 4 to 6 vs. Diet 8), the effect of a broad carnivorous diet to the effect of a broad herbivorous diet (Diets 7 vs. Diet 8), and cannibalism to the mean of the other 2 animal diets (Diet 1 vs. Diets 2 and 3). We controlled for the probability of a Type I error in these multiple comparisons by adjusting the critical value of p using a Bonferroni correction (corrected $\alpha = 0.01$).

Cannibalism experiment

Cannibalism generally includes killing and eating conspecifics, whereas our experiment described above examined consumption of conspecifics that were already dead (equivalent to scavenging). We conducted a simple field experiment to quantify the prevalence of cannibalism amongst Asian shore crabs to test the hypothesis that cannibalism in this species is weak. We collected 20 adult male crabs (25.7 ± 2.4 mm CW) and 20 juvenile crabs of the most common size observed at this site during much of the year (11.7 ± 1.7 mm CW) from Odiorne Point, NH in May 2014. Male adult crabs were conservatively used because they are more aggressive than females (B. D. Griffen pers. obs.), and we reasoned that they would therefore be more likely to cannibalize smaller individuals. We starved the adult crabs for 24 h to standardize hunger. We then placed a single adult together with a single juvenile crab into individual small plastic chambers with holes punched in the sides to allow water flow. These chambers were then placed in a large mesh cage that was suspended off a dock at the University of New Hampshire Marine Research Complex. After 24 h crabs were removed and we assessed

mortality of juveniles. We analyzed cannibalism using a GLM with binomial distribution and with the difference in size between the adult and the paired juvenile as the predictor variable.

RESULTS

Omnivory Expt 1: Diet type and amount

Feeding and consumption

Nearly all mussel tissue provided was consumed. Mean daily mussel tissue consumption increased by 0.89 ± 0.02 g with every 1.0 g increase in amount of mussel tissue offered ($p < 0.0001$, $R^2 = 0.99$), but was not influenced by the amount of algae offered ($p = 0.38$). In contrast to this, mean daily algal consumption increased by 0.27 ± 0.01 g with every 1.0 g increase in the amount of algae offered ($p < 0.0001$, $R^2 = 0.92$), but decreased by 0.18 ± 0.05 g with every 1.0 g increase in the amount of animal tissue provided ($p = 0.002$) as crabs preferentially elected to consume mussel tissue instead of algae.

Absorption

AIC model selection indicated that Model 5 best fit the data (Δ AIC values: Model 1 = 9.21, Model 2 = 74.40, Model 3 = 86.35, Model 4 = 5.58, Model 5 = 0), indicating that mean daily absorption efficiency declined exponentially and independently with both mean total daily food consumption ($k_1 = 0.68 \pm 0.11$, $p < 0.0001$; $k_2 = -58.77 \pm 13.82$, $p = 0.0001$, Fig. 1A) and the proportion of that consumed food that was mussel tissue ($k_3 = -4.25 \pm 2.05$, $p = 0.045$; $k_4 = 0.28 \pm 0.04$, $p < 0.0001$, Fig. 1B).

Metabolic rate

Metabolic rate ($\text{mg O}_2 \text{ g}^{-1} \text{ dry wt h}^{-1}$) increased by 0.05 ± 0.01 with each mm increase in crab CW ($p = 0.001$, $R^2 = 0.22$). Using the residual metabolic rate from this analysis to control for effects of crab size, residual metabolic rate increased by 3.88 ± 1.78 with every 1.0 g increase in the mean daily mass of mussel tissue consumed due to the increased cost of digestion ($p = 0.036$, $R^2 = 0.07$), but was not influenced by algal consumption ($p = 0.56$). Thus, while metabolic rates were influenced by crab size and diet, the low R^2 values in these analyses indicate that the influ-

ence of crab size and diet were weak and did not explain much of the variance in metabolic rate.

Physiological condition

Energy storage in the hepatopancreas as determined by the hepatosomatic index increased by 1.68 ± 0.22 with the mass-specific consumption of mussel tissue (i.e. for every 0.01 g of mussel tissue consumed per gram of crab) ($p < 0.0001$, $R^2 = 0.63$,

Fig. 2A), but was not influenced by algal consumption ($p = 0.38$, Fig. 2B). Similarly, we found that the percent of the hepatopancreas tissue comprised of lipids increased by 6.49% with mass-specific consumption of mussel tissue ($p < 0.0001$, $R^2 = 0.47$, Fig. 3), but was not influenced by algal consumption ($p = 0.63$). These 2 metrics of physiological condition were positively correlated (hepatosomatic index increases by 0.16 for every 1% increase in percent lipid in the hepatopancreas $p < 0.0001$, $R^2 = 0.55$, Fig. 4).

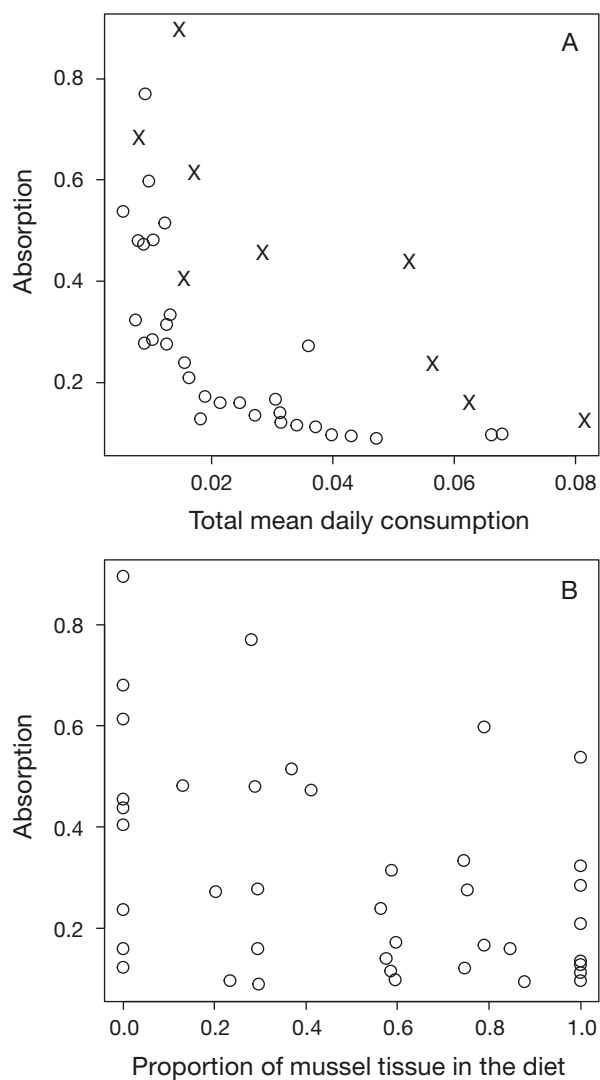


Fig. 1. Absorption efficiency of Asian shore crabs *Hemigrapsus sanguineus* in Expt 1. Absorption efficiency decreased exponentially with both (A) the mean daily total amount of food consumed and (B) the proportion of mussel (*Mytilus edulis*) tissue in the diet. (X) Crabs that only ate algae *Chondrus crispus* and no animal material (8 of these are crabs that were given only algae and one is a crab that was given animal material, but chose to eat only algae)

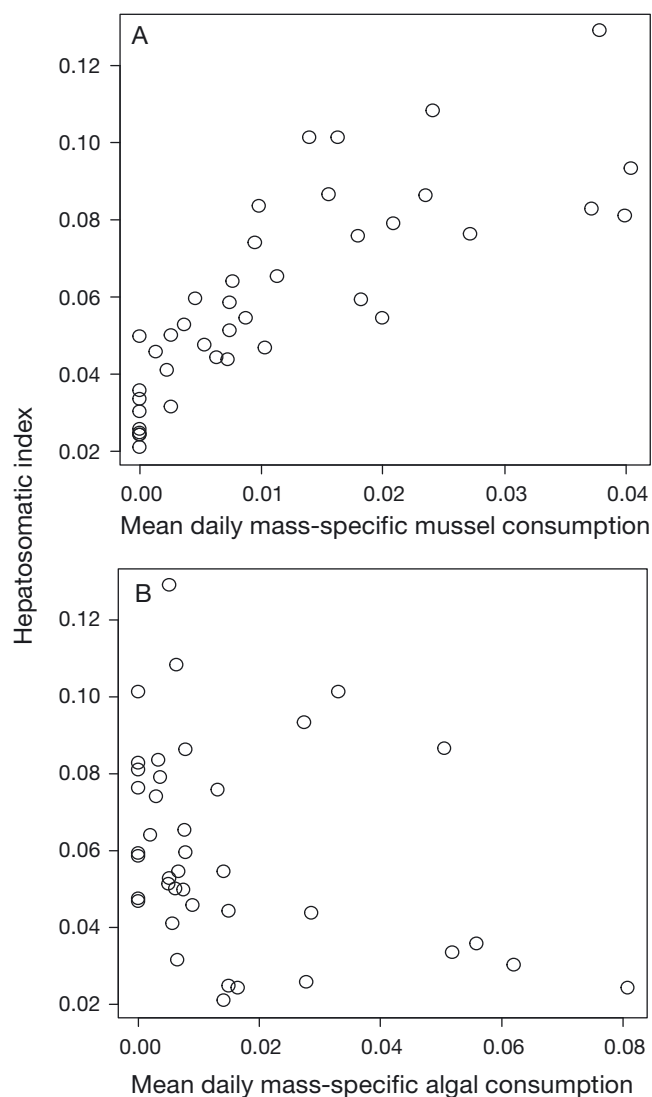


Fig. 2. Energy storage of Asian shore crabs *Hemigrapsus sanguineus* in Expt 1 as measured by the hepatosomatic index. Energy storage (A) increased with the mean daily mass of mussel (*Mytilus edulis*) tissue consumed per gram of crab, but (B) was not influenced by the mean daily mass of algae *Chondrus crispus* consumed per gram of crab

Omnivory Expt 2: Qualitative diet experiment

Feeding and consumption

The number of days on which crabs fed, as indicated by the number of days when feces were observed, ranged from 14 to 21 of the 21 total feeding

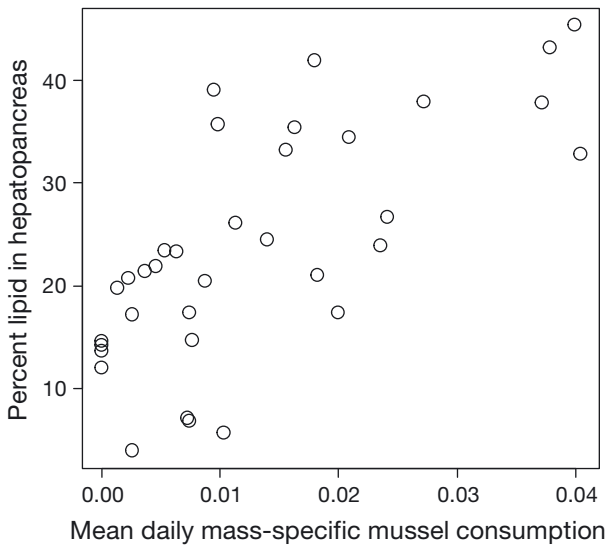


Fig. 3. Energy storage of Asian shore crabs *Hemigrapsus sanguineus* in Expt 1, as measured by the percent of hepatopancreas tissue that was comprised of lipids, increased with the mean daily mass of mussel (*Mytilus edulis*) tissue consumed per gram of crab

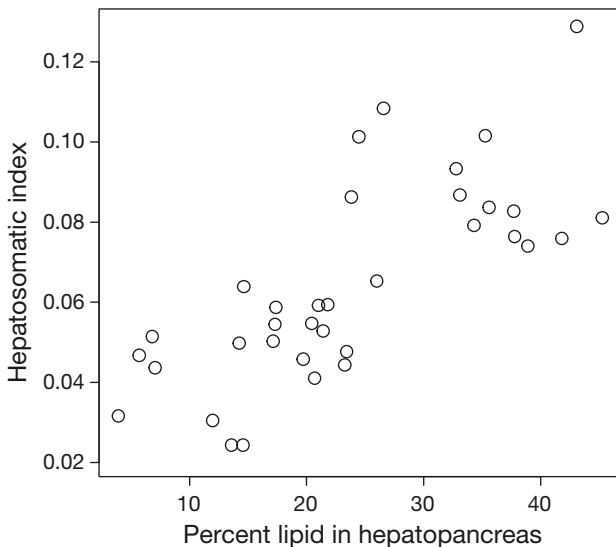


Fig. 4. Relationship between hepatosomatic index and the percent lipid content of the hepatopancreas, indicating that changes in the hepatopancreas mass of experimental crabs *Hemigrapsus sanguineus* were due largely to the accumulation of lipids

periods (mean = 19.6 ± 1.6) and did not vary by diet treatment (GLM, range of p = 0.39 to 0.91 for the comparison of each of the other 8 diet treatments to the treatment with all 6 foods rotated).

Physiological condition

The 6 foods differed substantially in their impacts on energy storage (ANOVA, $F_{8,54} = 9.98$, $p < 0.0001$, Fig. 5). Specifically, we found that diet mixing by rotating through all 6 food sources over sequential feeding periods led to a greater hepatosomatic index than the average of each of the 6 food sources provided continuously (linear contrast, $p = 0.0002$). Mixing the 3 animal diets by rotating through these over sequential feeding periods yielded a hepatosomatic index that was no different from the average of each of the 3 animal foods provided alone (linear contrast, $p = 0.39$). Similarly, mixing the 3 plant diets by rotating through these over sequential feeding periods

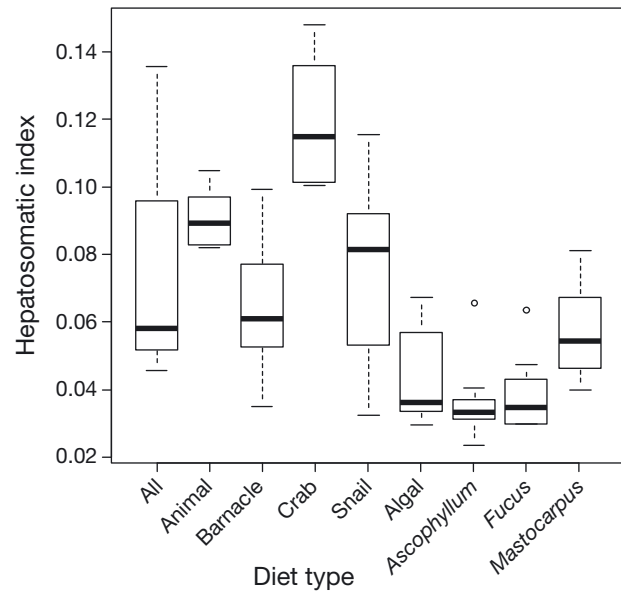


Fig. 5. Energy storage of Asian shore crabs *Hemigrapsus sanguineus* for the 9 different diet treatments in Expt 2 as measured by the hepatosomatic index. 'All' refers to all 6 diet choices rotated, 'Animal' and 'Algal' refer to the 3 animal species (the barnacle *Semibalanus balanoides*, the snail *Littorina littorea*, and conspecific juvenile *Hemigrapsus sanguineus*) or 3 algal species (*Ascophyllum nodosum*, *Fucus vesiculosus*, and *Mastocarpus stellatus*) rotated, respectively. The figure demonstrates that energy storage was greatest on a cannibalistic diet, but was greater in general for an animal diet than for algal diets. Heavy black lines are medians; the box encompasses the upper and lower quartiles of the data; the error bars encompass the whole range of data, except statistical outliers; the circles are statistical outliers

yielded an identical hepatosomatic index to the average of each of the 3 plant foods provided separately (linear contrast, $p = 0.98$). Cannibalism resulted in a greater hepatosomatic index than the average of the other 2 animal foods (linear contrast, $p < 0.0001$). And finally, combining all 3 animal foods resulted in a greater hepatosomatic index than combining all 3 plant foods (linear contrast, $p = 0.0002$).

Cannibalism experiment

Only 3 of the 20 juvenile Asian shore crabs were cannibalized in our experiment, and this cannibalism was not influenced by the size difference between the pair of adult and juvenile crabs (GLM, $p = 0.2$).

DISCUSSION

We have demonstrated that energy storage, via lipids in the hepatopancreas, in the Asian shore crab *Hemigrapsus sanguineus* is greatest on a diet of animal material. This benefit of animal consumption comes despite the fact that this dietary strategy carries elevated metabolic costs through both increased resting metabolic rates (i.e. a weak effect of specific dynamic action associated with digestion, McCue 2006) and reduced absorption efficiency for animal tissue as compared to an algal diet. Further, we have shown that, of the foods most abundantly available to the Asian shore crab on beaches where it has already had an impact on prey density, cannibalism represents the best option energetically. Energy stored in the hepatopancreas is subsequently used for future growth and reproduction, and our results therefore have important implications for the population dynamics and persistence of Asian shore crabs in invaded habitats, as well as having broader implications.

Implications for the Asian shore crab

The high abundances of both snails and barnacles at this site, relative to other potential prey such as mussels and other crustaceans, following nearly 15 yr of predation pressure from the new invader are consistent with previous studies that predict relatively minor impacts on barnacles (Brousseau & Goldberg 2007) and that demonstrate that the Asian shore crab generally does not prefer *Littorina littorea* (Bourdeau & O'Connor 2003, Griffen 2011). The paucity of other potential prey species is also generally consistent

with consumptive impacts of this species reported in other areas (Lohrer & Whitlatch 2002a,b, Kraemer et al. 2007). Snails and barnacles in this region have similar energy, fat, and protein content to more preferred prey such as mussels (McKinney et al. 2004), and preferences against snails and barnacles may therefore reflect relatively high handling costs of opening and consuming these prey relative to other foods. However, in our experiment we removed these differences in handling time by opening prey items prior to giving them to crabs. Lower energy storage in crabs provided with barnacles and snails relative to those fed conspecifics in our experiment may therefore reflect differences in absorption of these different food types.

Larval recruitment of preferred prey items is temporally and spatially variable (Griffen & Byers 2009). When the rate of recruitment of preferred prey is insufficient to keep up with consumptive effects of Asian shore crabs, prey depletion will ensue, leading to food limitation that could limit further increases in consumer population size and could also force this invader to consume less preferred prey species. Previously documented depletion of preferred prey from shores where the Asian shore crab is abundant (Lohrer & Whitlatch 2002a,b, Kraemer et al. 2007) suggests that such food limitation may often be the case.

Cannibalism as a general strategy

When depletion of preferred foods occurs due to high densities of Asian shore crabs, our results indicate that cannibalism would appear to be the best option energetically. Cannibalism is a common practice in natural populations (Fox 1975) and is especially common amongst primarily herbivorous species as a means of supplementing nitrogen intake (White 1993). It is commonly high among crabs in particular (Moksnes et al. 1997, Moksnes 2004) and can be a nutritionally superior strategy given the stoichiometric/nutritional similarity of consumer and conspecific prey (e.g. Snyder et al. 2000). This may explain the high energy storage we observed in crabs fed a cannibalistic diet. However, despite its theoretical benefits, cannibalism appears to be low amongst Asian shore crabs (our results here and Griffen & Byers 2009). This conclusion should, however, be viewed tentatively, because cannibalism should be expected to become stronger as the density of Asian shore crabs increases and the abundance of preferred prey decreases. No studies to our knowledge have examined cannibalism

rates of Asian shore crabs under these conditions. Our cannibalism experiment was conducted in a similar manner to a previous experiment that paired large Asian shore crabs with small European green crabs *Carcinus maenas* and found that predation on these smaller crabs was intense and increased rapidly as the size difference between the paired individuals increased from 0 to 10 mm CW (Lohrer & Whitlatch 2002a). Similarly, a recent study examining predation by Asian shore crabs on juvenile rock crabs *Cancer irroratus* found a relatively strong predation risk for rock crabs that increased as the size difference between paired individuals became larger (B. D. Griffen & M. E. Riley unpubl.). Thus, cannibalism by the Asian shore crab appears to be much weaker than predation by this species on heterospecific crabs. Yet even if cannibalism does play a nutritional role in this species, the imperfect transfer of energy in trophic interactions (Karasov & Martínez del Rio 2007) means that it is unlikely that the Asian crab is able to persist indefinitely on a diet to which cannibalism makes a substantial contribution. Rather, if cannibalism plays a role in population persistence at all, it would likely only occur episodically between periods of larval recruitment, which can be highly variable in areas invaded by this species (reviewed in Bertness et al. 2014).

Self-limitation of invasive species

The results of this study lead to an interesting hypothesis that deserves further attention by invasion ecologists: that invasive species may limit their own success via impacts on the invaded habitat. In our study system, Asian shore crabs deplete or strongly depress preferred prey (Lohrer & Whitlatch 2002a,b, Kraemer et al. 2007), leaving only prey that are consumed less readily (Bourdeau & O'Connor 2003, Griffen 2011) and that yield a lower return on investment based on our energy storage results. This may lead to energetic stress that can decrease individual survival and reproductive success. Such a series of steps may be a contributing factor to the recent decline in abundance of Asian shore crabs in some areas where they were previously very abundant (Schab et al. 2013).

Similar self-limiting processes could also occur in other systems where invasive species have large impacts. Large physical (e.g. Mytinger & Williamson 1987, Shi et al. 2000) and biological (Wilde et al. 2005) impacts of invasive species are common. Habitat- or community-modifying impacts of invaders can be beneficial to the invading species, speeding their

ability to expand into areas that, without modification, would be inhospitable to the new species (Cuddington & Hastings 2004). However, these habitat- or community-modifying impacts of invaders could also have detrimental impacts on the invader itself if the elicited changes, for example, remove essential resources. Multiple instances have been documented of invasive species declining in the absence of human intervention for unknown causes (reviewed by Simberloff 2013). One mechanism contributing to these unexplained declines could be self-regulating negative feedbacks initiated by habitat changes brought on by the invasive species itself. The idea of self-regulation via a habitat carrying capacity is a fundamental concept of ecological theory (Case 2000), whether populations are native or nonnative. Self-regulation in invasive populations may be more important than in native populations if enemy release has removed external population controls that normally exist for native species (parasites, predators, competitors), allowing the invasive species to achieve larger population sizes than it does in its native range.

In summary, animal consumption leads to greater energy storage than algal consumption in invasive Asian shore crabs. Cannibalism represents a particularly efficient energetic option when more preferred foods are depleted, but available evidence does not support strong cannibalism in this species. Finally, our results suggest that impacts of invasive species (specifically reduced food availability in our system) may potentially lead to a self-regulating mechanism for invaders that could contribute to previously unexplained declines in once-abundant invasive species.

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