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Effects of season and latitude on the diet quality of the invasive Asian shore crab *Hemigrapsus sanguineus*

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ABSTRACT: Invasive species alter invaded ecosystems via direct impacts such as consumption. In turn, an invasive species' ability to thrive in new habitats depends on its ability to exploit available resources, which may change over time and space. Diet quality and quantity are indicators of a consumer's consumptive effects and can be strongly influenced by season and latitude. We examined the effects of season and latitude on the diet quality and quantity of the invasive Asian shore crab *Hemigrapsus sanguineus* throughout a non-winter sampling year at 5 different sites spanning 8° of latitude across its invaded United States range. We found that diet quality, averaged through time, largely follows an expected latitudinal cline, being higher in the center of its range and lower toward the southern and northern edges. We also found that while some sites show similar patterns of diet quality variation with season, no pattern is consistent across all latitudes. Finally, we found that crabs at sites with low diet quality during summer reproductive months did not compensate by increasing total consumption. Because the Asian shore crab is an important consumer in its invaded ecosystems, understanding how its diet quality and quantity vary with season and latitude can help us better understand how this species influences trophic interactions and community structure, how it has been able to establish across a wide ecological and environmental range, and where future range expansion is most likely to occur.

KEY WORDS: Gut size · Energetics · Diet quality · Energy content · Residual gut mass · Invasive species

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1. INTRODUCTION

Invasive species have broad impacts on invaded ecosystems and on native species (Gallardo et al. 2016), including causing changes in community structure and threatening populations of native species, sometimes leading to their local extinction (Cuddington & Hastings 2004, Molnar et al. 2008). These effects can be especially extensive when the invader is a generalist consumer because generalist consumers have direct consumptive connections to multiple trophic levels and can persist through un-

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favorable conditions and changes in prey availability (Schmitt et al. 2019). For example, invasive lionfish *Pterois* spp. have become damaging generalist consumers throughout the Caribbean, causing the decline of ecologically important native fish populations of multiple species that occupy different trophic levels (Hixon et al. 2016). Similarly, invasive blue catfish *Ictalurus furcatus* have become harmful consumers in the Chesapeake Bay ecosystems by consuming and competing with a variety of native species (Fabrizio et al. 2021).

Diet quality and quantity are useful indicators of an invader's consumptive effects (Calizza et al. 2021). These metrics, when sampled over time and space, can yield insights into the invasive population's dietary patterns and tendencies, as well as its possible geographic range expansion or compression. This is because population growth is limited by, among other things, the availability of energy, which is itself affected by the average diet quality and intake amount across a population (Norris et al. 2007). For example, in harbor porpoises *Phocoena phocoena*, recent modeling work showed that decreases in prey size caused reduced energy availability and storage, which ultimately led to population declines (Gallagher et al. 2022). Population level dynamics are necessarily driven by processes occurring at the individual level (Stillman et al. 2015). For instance, when individual energy intake is insufficient, individuals are forced to put less energy toward reproduction and to instead prioritize essential bodily functions. When this occurs throughout a population, population growth slows and can even begin to decline. Thus, diet quality and quantity have important effects on the energetics of populations and on population stability throughout their ranges. Further, season (time) and latitude (space) are known to strongly influence the diet quality and intake amount of many species, leading to variation in these metrics across the range of a single species (Karachle & Stergiou 2008, Storms et al. 2008, Ely & Raveling 2011).

Temporal variation in diet occurs due to seasonal fluctuations in prey abundance and composition (e.g. Schafer et al. 2002), seasonal changes in prey nutritional quality (Scheirs et al. 2002), and life history-related energetic requirements of the consumer (such as seasonally dependent reproduction [Thometz et al. 2014] and molting [Mantelatto & Christofoletti 2001]). Spatial variation in diet occurs for similar reasons, including changes in prey species composition and distribution (Gibson et al. 2007), latitudinal clines in prey nutritional quality (Pennings et al. 2001), and latitudinal variation in temperature-driven energy requirements of the consumer (Clausen et al. 2014). For example, the palatability of a range of salt marsh plants increases with latitude (Pennings et al. 2001), suggesting that omnivores at lower latitudes should consume less salt marsh plant material and more animal tissue, resulting in increased top-down control over animal prey and impacts on community composition at these lower latitudes (Freestone et al. 2011). Because seasonal and latitudinal influences on diet can vary simultaneously, understanding their individual and combined influences is important for assessing the consumptive impacts of invasive species across their invaded ranges and the role that diet quality and quantity plays in influencing the geographic range expansion of invasive species.

We examined seasonal and latitudinal variation in the diet quality and diet quantity of the Asian shore crab *Hemigrapsus sanguineus*, an invasive species that has significant impacts on its invaded ecosystems. Native to the east coast of Asia, the Asian shore crab was first observed in New Jersey, USA, in 1988 (Williams & McDermott 1990). This species rapidly expanded its invaded range and established populations can now be found on the US east coast from North Carolina to Maine (Epifanio 2013). A combination of a high reproductive rate (McDermott 1998b), broad salinity tolerance (Hudson et al. 2018), low parasite load and diversity (Blakeslee et al. 2013, Kroft & Blakeslee 2016), and an opportunistic omnivorous diet (Griffen et al. 2012) has allowed the Asian shore crab to outcompete some species, such as the long-established invasive European green crab *Carcinus maenas* (Katsanevakis et al. 2014), and deplete other species, such as the native blue mussel *Mytilus edulis* (Bloch et al. 2015). Though the Asian shore crab is primarily herbivorous, it demonstrates a preference for animal tissue when available (Brousseau & Baglivo 2005). This is likely because consumption of animal material leads to superior body conditions compared to a diet of algae alone (Griffen et al. 2012, 2015). Across many species, including the Asian shore crab, a higher quality diet yields greater energy storage (Fearman et al. 2009, Griffen et al. 2015); thus, a diet composed of considerable amounts of animal material yields the greatest energetic benefit to the Asian shore crab. In addition, a higher-quality diet increases fecundity and thus population growth and may also influence other co-occurring species via exploitative competition for preferred food items (Griffen & Byers 2006, Dauvin et al. 2009).

The composition and quality of an animal's diet can be difficult to determine without continuous observation, which is impractical for most species under natural field conditions. However, reliable proxies that correlate with diet quality have been identified for many species. One such proxy is gut size, which varies with diet composition and quality across a broad range of taxa, including birds (Miller 1975), mammals (Milton 1981, Lee & Houston 1993), fish (Wagner et al. 2009), and crabs, including the Asian shore crab (Griffen & Mosblack 2011, Quezada-Villa et al. unpubl.). The crab gut is shaped approximately like a tetrahedron, so gut size can be assessed reliably using the width of the anterior dorsal margin (Griffen & Mosblack 2011). In crabs, a larger gut width to carapace width ratio (hereafter 'standardized gut size') corresponds to a lower-quality, often primarily herbivorous diet, which yields less energetic benefit than a high-quality, often primarily carnivorous diet (Griffen & Mosblack 2011, Quezada-Villa et al. unpubl.). A larger gut allows for consumption of a larger volume of a lower-quality diet (i.e. compensatory feeding) in order to meet nutrient, particularly nitrogen, requirements (Wolcott & O'Connor 1992). Standardized gut size is a useful metric for the quality of a crab's overall diet because it is integrated over periods extending from weeks to months (Griffen et al. 2012). Thus, determining the relative distributions of the standardized gut size of populations can yield valuable insights into the diet quality, composition, and quantity of those populations over time.

Studies on multiple species demonstrate that gut size is a valid proxy for the diet composition and diet quality of individual crabs. For example, Cannizzo et al. (2018) showed that mangrove tree crabs *Aratus pisonii* that eat a higher-quality diet have smaller guts than those that eat a lower-quality diet. Griffen & Mosblack (2011) used field experiments to determine that Asian shore crabs — the same species examined in this study — that choose to eat a higher-quality diet have smaller guts. Studies also demonstrate that diet composition and diet quality can influence population growth by affecting reproduction and other processes. Gül & Griffen (2020) found that ghost crabs *Ocypode quadrata* at sites heavily impacted by humans eat a lower-quality diet of algae and thus have larger guts and the reduced diet quality hampered the crabs' reproductive performance. This finding was supported by Griffen et al. (2020), who showed that Asian shore crabs at sites with lower diet quality have larger guts and reduced reproductive performance compared to crabs at sites with higher diet quality. Finally, Cannizzo et al. (2020) also showed that mangrove tree crabs that subsist on higher-quality diets produce higher-quality larvae that have enhanced survival.

Previous work, also using gut size as a metric for diet quality, documented a pattern of increased diet quality in summer months for Asian shore crabs on the New Hampshire coast (Griffen et al. 2012). This likely reflected increased availability of animal material and changes in prey selection throughout the summer reproductive season. However, we are not aware of any studies that have investigated whether a similar pattern exists at other sites across the Asian shore crab's invaded geographic range. We hypothesized that this seasonal pattern of a higher-quality diet in the summer would persist throughout the Asian shore crab's range, regardless of latitude. We tested this hypothesis by measuring standardized gut size and gut mass-specific gut energy content (hereafter 'gut energy content') — a more precise indicator of the quality of a crab's last meal — of crabs collected from sites throughout their invaded United States range. We also hypothesized that mean diet quality would decrease with increasing latitude based on the knowledge that plant nutritional quality increases with increasing latitude (Pennings et al. 2001), and that higher-latitude sites with abundant Asian shore crab populations tend to have more algae present than lower latitude sites (B. D. Griffen pers. obs.). We also expected that diet quality may be highest towards the center of the Asian shore crab's range, since conditions in the center of a species' range are expected to be most conducive to success. Finally, we hypothesized that if diet quality at some sites/latitudes was low during summer (reproductive) months, crabs would compensate by increasing total consumption at those sites in order to meet nutrient requirements for reproduction. We tested this hypothesis by measuring residual gut mass — an estimate of the amount of food consumed during the crab's final meal.

2. MATERIALS AND METHODS

2.1. Crab sampling

From March 1 to November 11, 2020, we hand-collected 799 mature female Asian shore crabs from 5 sites along a latitudinal gradient on the East Coast of the United States. We only collected mature female crabs (maturity was based on 12 mm carapace width, McDermott 1998b) to remove the influence of sex and maturity on the results. We collected crabs during morning low tides because crabs eat most actively at night, thus increasing the likelihood that their guts would be full when collected (Depledge

1984, Saigusa & Kawagoye 1997). After collection, crabs were frozen, shipped on dry ice to Brigham Young University in Provo, Utah, and stored at −80°C until they could be dissected.

2.2. Sampling sites

Our 5 sampling sites included Bailey Island in Harpswell, Maine (ME); Rye, New Hampshire (NH); Goshen Point at Harkness Memorial State Park in Waterford, Connecticut (CT); Cape May Ferry, North Cape May, New Jersey (NJ); and Oregon Inlet, North Carolina (NC) (Table 1).

2.2.1. ME. We collected crabs from the intertidal zone at the southern end of Bailey Island in Harpswell, ME, a site characterized by a large tidal range (mean = 2.7 m) and composed of large rocks and cobble over exposed bedrock, gravel, and coarse sand. Crabs were primarily collected from underneath large rocks situated on gravel/sand in the lower intertidal zone. This site was selected because it is close to the northern edge of this species' geographic range while still having a large enough population to collect a sufficient sample size for this study (with the exception of March sampling when Asian shore crabs were especially difficult to find at this site). However, this site had a relatively low density of Asian shore crabs throughout the collection period compared to other sites.

2.2.2. NH. The site at Rye, NH, just south of Odiorne Point State Park, is characterized by a rocky shelf and mid-to-large rocks with a large tidal range (~2 to 4 m). With the exception of March sampling, Asian shore crabs were abundant and readily found by flipping rocks by hand. See Griffen et al. (2021), who examined Asian shore crabs at this same site, for a more detailed report of the biological and physical characteristics of this area.

2.2.3. CT. The Goshen Point site at Harkness Memorial State Park in Waterford, CT, sits roughly at the center of the Asian shore crab's invaded range. This site was sampled more frequently (monthly) than other sites (every other month) to resolve temporal changes in diet quality at a finer scale. This site contains a relatively small stretch of intertidal boulders within Long Island Sound, situated between stretches of sandy shore. Crabs were easily found by overturning boulders.

2.2.4. NJ. The site at Cape May Ferry, North Cape May, NJ, represents the area of first colonization by Asian shore crabs in North America, prior to their spreading north and south along the East Coast. While natural rocky intertidal habitat is not available in this region, the Asian shore crab has established populations in areas of anthropogenic hard substrate such as riprap, jetties, and breakwaters that also support natural oyster reefs. Crabs were sampled from a breakwater adjacent to the Cape May Ferry Terminal, near the mouth of Delaware Bay. Crabs were readily found under rocks and boulders throughout the sampling season, with peak densities occurring in the summer months (May, July, and September). Samples from this site were only available through September (i.e. 4 sampling periods) since samples collected in November were significantly degraded upon delivery due to shipping delays.

2.2.5. NC. The site at Oregon Inlet, NC, lies at the southern end of this species' invaded US range. Oregon Inlet is located on the Outer Banks of North Carolina, which is characterized by multiple barrier islands. This inlet represents a direct connection from the Atlantic Ocean to North Carolina sounds and estuaries. Many of the areas within these sounds and es-

Table 1. Information about the Asian shore crabs *Hemigrapsus sanguineus* collected at each of the 5 sampling sites in the US. DOY: day of year

Site	Latitude, longitude	Sampling DOY (sampling size)	Gut width range (mm)	Carapace width range (mm)
Maine	43° 43′ 2.7″ N, 70° 0′ 11.5″ W	75 (20), 133 (30), 192 (41), 252 (34), 314 (32)	4.4–13.8	10.1–35.1
New Hampshire	43° 2′ 20″ N, 70° 42′ 55″ W	61 (24), 133 (32), 194 (33), 251 (36), 313 (32)	5.0–13.0	10.6–31.2
Connecticut	41° 17′ 56.1″ N, 72° 06′ 44.9″ W	63 (21), 75 (27), 93 (33), 136 (30), 165 (30), 181 (30), 194 (3), 226 (30), 256 (28), 285 (26), 316 (30)	4.3–13.3	11.0–31.9
New Jersey	38° 58′ 3.4″ N, 74° 57′ 46″ W	66 (18), 131 (35), 193 (35), 258 (33)	3.2–13.3	9.3–33.0
North Carolina	35° 46′ 7.3″ N, 75° 31′ 37.8″ W	75 (27), 136 (30), 197 (5), 259 (14)	4.9–13.9	11.2–33.6

tuaries are soft sediment, with structure created by oyster reefs and anthropogenic riprap. The sampling site at Oregon Inlet is characterized by a rock/boulder fishing jetty with various sized boulders covered in oysters adjacent to the jetty. Crabs were found under these rocks and within crevices of the jetty. Over the course of the sampling period, crabs were sometimes difficult to locate and capture (given the nature of the habitat), which resulted in variable sample sizes across the sampling months (see Table 1). As with NJ, samples from this site were only available through September since November samples were degraded upon delivery.

2.3. Standardized gut size

To measure standardized gut size, we thawed frozen crabs in water to room temperature, measured each crab's carapace width to the nearest 0.1 mm using a vernier caliper, and dissected the crab using dorsal carapace removal. The gut was then extracted and its width at the anterior dorsal margin was measured to the nearest 0.1 mm under a dissecting microscope. We were particularly careful not to rupture the gut during extraction, as gut fullness was subsequently visually judged and recorded on a scale from 0 to 4, where 0 is completely empty and 4 is completely full (Griffen et al. 2012). We determined the standardized gut size for each crab as the unitless ratio of the gut width to the carapace width. Following these measurements, we placed the dissected body and the gut into separate aluminum weigh boats and dried them to constant weight at 60°C (e.g. Hostert et al. 2019). Dried body and gut were then weighed using a XS205DU Mettler Toledo semi-micro balance.

2.4. Gut energy content

After each crab was dissected and its gut size measured, we performed bomb calorimetry to measure the energy content of the gut using a Parr 6725 semi-micro oxygen bomb calorimeter connected to a Parr 6772 Calorimetric Thermometer. While the gut wall itself has some caloric content, its overall mass is much less than the minimum mass that can be measured calorimetrically, and we therefore assumed the caloric value of the gut itself to be negligible. The energy content of the gut provides a snapshot of the energetic value of that crab's last meal; therefore, while these values are not particularly useful on their own due to normal sampling variation, aggregating many gut energy values yields insights into the diet quality of that population at that point in time. Due to the requirements of the calorimeter, only guts that weighed 0.019 g or more ($N = 612$) were measured.

2.5. Residual gut mass

We investigated whether season and/or latitude affected the amount of food an individual consumed by measuring residual gut mass, which is a metric of the amount of food a crab ate during its last meal (minus any digestion that has occurred). This metric was obtained for each crab by measuring the weight of the dried gut. To account for body size differences across crabs, we determined the residual gut mass from the regression of log gut mass on log total crab mass, using the dried gut and body masses described above. Pooling many residual gut mass values from a sampling site provides a snapshot of consumption amounts at that site.

2.6. Analyses

We used a similar approach to analyze each of the 3 metrics examined here (standardized gut size, gut mass-specific gut energy content, and residual gut mass). We verified that the data met the assumptions of parametric statistics (normality and homogeneity) using residual plots and visual inspection of the data. We used an alpha level of 0.05 for all statistical tests. For each of these 3 metrics, we first conducted preliminary analyses to examine the effect of gut fullness and to test linearity in the relationships between variables. Specifically, we used a linear model with carapace width and gut fullness as predictor variables and gut width as the response variable to verify that gut width increased linearly with carapace width and was not influenced by gut fullness. Next, we used a linear model with gut fullness as the predictor variable and gut energy content as the response variable to confirm that gut energy content was not influenced by gut fullness. Finally, we used a linear model with carapace width and gut fullness as predictor variables and residual gut mass as the response variable to test whether residual gut mass was influenced by carapace width or gut fullness.

We also compared the overall differences in standardized gut size among sampling sites and determined whether a latitudinal cline in diet quality exists using an ANOVA followed by a Tukey's HSD test to compare standardized gut size (i.e. time integrated diet quality) across the 5 sampling sites. We did not use gut energy content to test for a latitudinal cline in diet quality because gut energy content is an indicator of the quality of only the crab's most recent meal and is thus more susceptible to the effects of random variation.

Visual inspection of standardized gut size, gut energy content, and residual gut mass showed that all 3 of these response variables changed nonlinearly with time and that the pattern of nonlinearity differed somewhat across sampling sites. We therefore used polynomial models (using sampling day of the year and sampling day of the year squared to account for nonlinearity) to separately explore each of these response variables through time at each site individually. It should be noted that different numbers of sampling dates across the 5 sites yielded site-specific abilities to detect nonlinear changes in gut energy content through time. Our preliminary analyses indicated that carapace width and gut fullness were important determinants of residual gut mass. We therefore also included these as predictor variables in our models that examined residual gut mass.

Lastly, in addition to examining changes in each of these variables through time, we also examined relationships between the response variables themselves. Specifically, we used site-specific linear models to determine whether diet quality affected consumption amount at any site. To do this, we used standardized gut size and gut energy content as predictor variables, and residual gut mass as the response variable. These models used only data collected during summer reproductive months (May 10 to September 16 or sampling day of the year 130 to 259; McDermott 1998a, Epifanio 2013), allowing us to examine the effect of diet quality on the amount of food consumed during the energetically expensive reproductive period. We used R v. 4.1.2 (R Core Team 2021, tidyverse package: Wickham et al. 2019) for all analyses.

3. RESULTS

Averaged through time, standardized gut size was significantly different among sampling sites ($F_{4,794}$ = 5.045, p = 0.001, Fig. 1) and largely followed an expected latitudinal cline, with the exception of the NJ site. Consistent with our predictions, diet quality was higher in the center of this species' range and appeared to be somewhat higher at the southern edge of the range than at the northern edge of the range (Fig. 1).

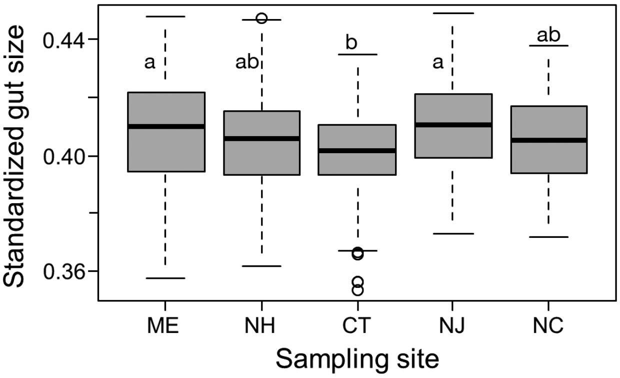

Fig. 1. Distribution of standardized gut size of Asian shore crab *Hemigrapsus sanguineus* at each of the 5 sampling sites in the US (ME: Maine; NH: New Hampshire; CT: Connecticut; NJ: New Jersey; NC: North Carolina). Thick black lines are medians and each box contains the upper and lower quartiles of the data. Whiskers include the most extreme data point that is no more than 1.5 times the IQR. Hollow circles are statistical outliers. Note that a larger standardized gut size corresponds to a lower-quality diet. Lowercase letters above boxplots indicate sampling sites where standardized gut sizes did not differ significantly from one another based on Tukey's HSD test at the $p \leq 0.05$ level

3.1. Standardized gut size

We found that gut width increased linearly with carapace width at all 5 sampling sites (t = 87.542, $p <$ 0.001) and was not influenced by gut fullness (t = 1.126, p = 0.260), confirming that our data met the expectations for standardized gut size as a proxy for longer-term diet quality. At the ME, NH, and NC sites, standardized gut size did not change throughout the sampling year (ME: linear term: t = 1.259, p = 0.210, Fig. 2A; NH: linear term: t = –1.455, p = 0.148, Fig. 2B; NC: linear term: t = –1.390, p = 0.169, Fig. 2E). At the CT site, standardized gut size decreased from March to July (linear term: t = –3.357, p = 0.001) and then increased throughout the rest of the year (second order term: t = 3.286, p = 0.001, Fig. 2C). At the NJ site, standardized gut size increased from March to May (linear term: t = 2.203, p = 0.030) and then decreased throughout the rest of the year (second order term: t = –2.266, p = 0.025, Fig. 2D).

3.2. Gut energy content

We found that gut energy content was not influenced by gut fullness (t = –0.955, p = 0.340), allowing us to leave out gut fullness as a predictor variable in the linear models of gut energy content. At the ME and NC sites, gut energy content did not change throughout the sampling year (ME: linear term: t = 0.891, p = 0.377, Fig. 3A; NC: linear term: t = 1.463, p = 0.150, Fig. 3E). At the 3 central sites, gut energy content showed similar temporal trends by increasing until early- to mid-summer and then decreasing throughout the rest of the sampling year (NH: linear term t = 3.545, p = 0.001, second order term t = –3.751, p < 0.001, Fig. 3B; CT: linear term t = 2.218, p = 0.028, second order term t = –2.135, p = 0.034, Fig. 3C; NJ: linear term t = 2.075, p = 0.041, second order term t = –2.477, p = 0.015, Fig. 3D).

3.3. Residual gut mass

We found that residual gut mass was influenced by both carapace width (t = 5.197, p < 0.001) and gut fullness (t = 13.689, p < 0.001) and so these were included in the linear model for each site. At the ME site, residual gut mass increased linearly with carapace width (t = 2.662, p = 0.009) and gut fullness (t = 5.364, p < 0.001). However, residual gut mass did not change throughout the sampling year at this site (linear term: t = 0.297, p = 0.767, Fig. 4A). At the NH site, residual gut mass increased linearly with carapace width (t = 3.070, p = 0.003) and gut fullness (t = 7.687, p < 0.001). Residual gut mass decreased until midsummer (linear term: t = –3.487, p = 0.001) and then increased throughout the rest of the sampling year at this site (second order term: t = 3.471, p = 0.001, Fig. 4B). At the CT site, residual gut mass increased linearly with gut fullness (t = 10.707, p < 0.001) but did not change with carapace width (t = 0.753, p = 0.452). Residual gut mass decreased until the start of summer (linear term: t = -3.054, p = 0.003) and then increased throughout the rest of the sampling year at this site (second order term: t = 3.794, p < 0.001, Fig. 4C). At the NJ site, residual gut mass increased linearly with both carapace width (t = 2.482, p = 0.015) and gut fullness (t = 3.735, p < 0.001). However, residual gut mass did not change throughout the sampling year at this site (linear term: t = 0.165, p = 0.870, Fig. 4D). At the NC site, residual gut mass increased linearly with gut fullness (t = 3.539, p = 0.001) but was not influenced by carapace width (t = 1.735, p = 0.088), nor did it change throughout the sampling year (linear term: t = –1.401, p = 0.166, Fig. 4E).

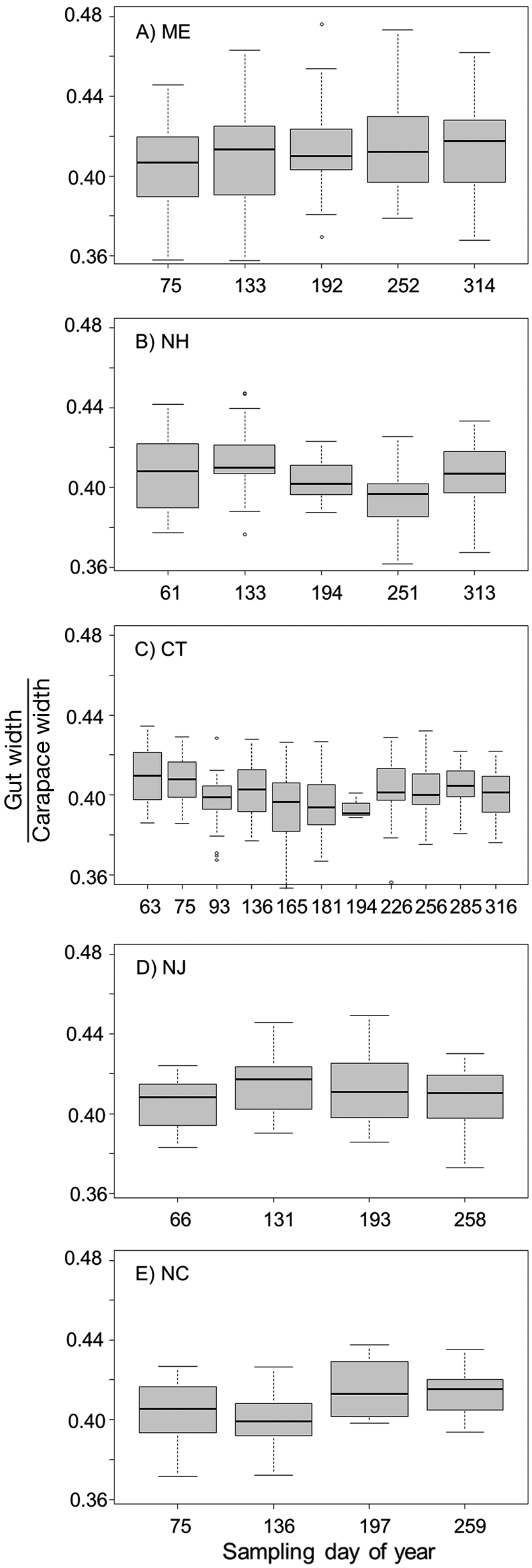

Fig. 2. Standardized gut size variation through time at each sampling site (Section 2.2). Boxplots and abbreviations are as described in Fig. 1

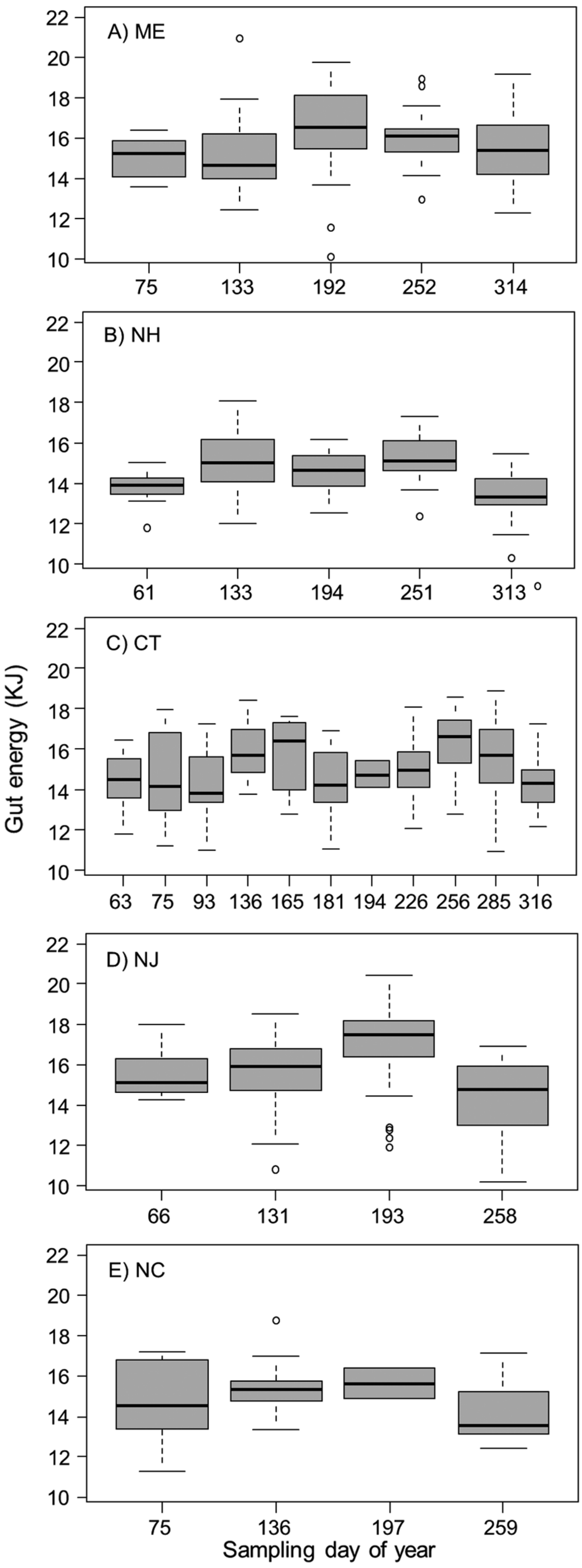

Fig. 3. Gut energy content variation through time at each sampling site (Section 2.2). Boxplots and abbreviations are as described in Fig. 1

There was no significant correlation between residual gut mass and standardized gut size at any site during summer reproductive months ($p > 0.050$ for all analyses). However, there was a significant negative correlation between residual gut mass and gut energy content at 2 sites during summer reproductive months (CT: $t = -2.122$, $p = 0.037$; and NC: $t = -2.121$, $p = 0.042$), but not at the other sites ($p > 0.050$).

4. DISCUSSION AND CONCLUSIONS

We have shown that seasonal patterns of diet quality in the invasive Asian shore crab vary across its latitudinal distribution along the east coast of the United States. Additionally, diet quality largely follows an expected latitudinal cline, with higher diet quality in the center of its range and lower diet quality especially toward the northern edge of its range. We have also shown that the amount of food consumed by crabs changes idiosyncratically through time at each site. Below, we discuss these patterns and their implications in more detail.

4.1. Latitudinal cline in diet quality

Our results suggesting a predictable latitudinal cline in diet quality in this species have important implications for this species' possible future range expansion. Higher diet quality often leads to greater energy intake and storage (van Gils et al. 2008), and thus individuals in populations with higher diet quality often have more energy to grow and reproduce, which are essential processes in establishing a new population (Keller et al. 2011). This reasoning suggests that diet quality (due to its connection with energy intake and storage) may be a limiting factor in the range expansion of this species. We found that diet quality was lowest at northern sites, which could be a contributing factor to the slower population growth observed by Lord & Williams (2017) near the northern limit of the Asian shore crab range compared to that at the center of its range. Poor diet quality can be expected to continue to inhibit the Asian shore crab's northward range expansion unless the crabs begin consuming more food. However, it should be noted that diet quality, while important, is only one of multiple factors likely acting on this species' range limits and range expansion. Cold water and air temperatures in northern areas (Stephenson et al. 2009, Lord & Williams 2017), combined with mean southward current flows (Byers & Pringle 2006), have also been described as important constraints on this species' distribution, though increasing temperatures due to climate change (Karmalkar & Horton 2021) may eventually weaken these physical constraints. In other crab species, reduced diet quality in reproducing females leads to lower-quality offspring that have reduced longevity (Cannizzo et al. 2020). If similar relationships exist between maternal diet quality and larval quality in this species, then reduced diet quality at the northern edge of the range may interact with these previously documented physical constraints to limit the northward range expansion of the Asian shore crab.

It is unclear from our data whether diet quality could provide the same constraints on range expansion at the southern edge of the Asian shore crab's range. However, other factors, such as a lack of suitable rocky intertidal habitat and ocean currents that hinder southward larval transport may make large-scale southward range expansion improbable (Epifanio 2013). Finally, it is important to note that the NJ sampling site had lower mean diet quality than expected given the observed latitudinal cline. We are unsure of the reasons for this, though it is possible that influences such as low wave action (B. D. Griffen pers. obs.), the prevalence of anthropogenic substrate rather than natural rocky shores, increased competition for animal prey, or consumption of large amounts of microalgae or sediment play a role in this site's lower diet quality. Further research is needed to explain this outlier of the latitudinal cline in diet quality.

4.2. Seasonal patterns of diet quality

Contrary to our hypothesis, we did not find a seasonal pattern of increased diet quality in the summer at all latitudes. Specifically, using standardized gut size as a proxy for diet quality, we did not observe this seasonal pattern at the highest-latitude site (ME site). We suggest that this may be due to the rela-

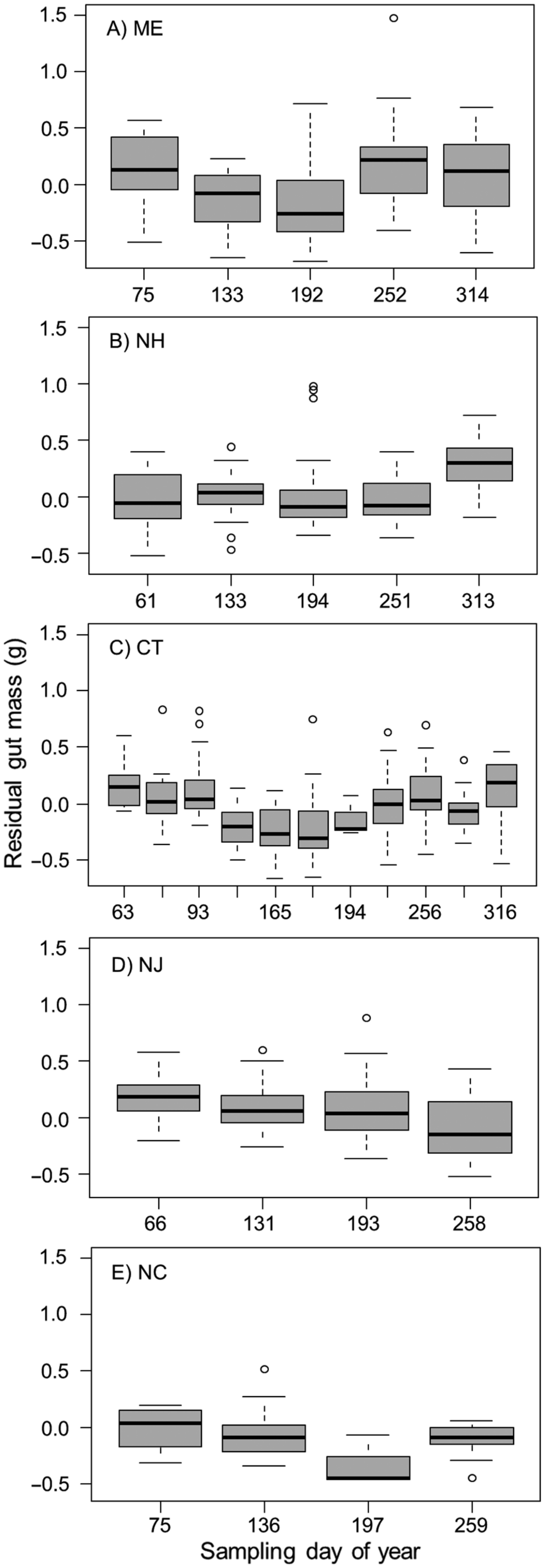

Fig. 4. Residual gut mass variation through time at each sampling site (Section 2.2). Boxplots and abbreviations are as described in Fig. 1

tively low density of crabs present at the ME sampling site. It is possible that the crab population at this site is not dense enough to deplete preferred food sources (animal prey) at any time during the year, thus allowing diet quality to remain relatively constant through time. We also did not detect this seasonal pattern at the NH site, in contrast with a previous study at this same site (Griffen et al. 2012). In contrast to the patterns at this site, at the CT site diet quality increased throughout the year after midsummer, as expected. This trend was likely a result of the increased energetic demands of summer reproduction in this species (Kennish 1996, Griffen et al. 2012). Higher-resolution temporal sampling at this site may have made this seasonal pattern more detectable. Diet quality decreased over the summer at the lower-latitude NJ site and did not change throughout the year at the NC site, which was the lowest-latitude sampling site.

These departures from our expectations are likely due to both site- and latitude-specific factors, such as prey availability and assemblages, seasonal temperature variation (which is reduced at southern sites compared to northern sites), habitat type and quality, and intensity of interspecific competition with native/well-established species, especially at northern sites where the European green crab is abundant (Gibson et al. 2007, Compton et al. 2010). Lower palatability of algae at lower latitudes (Bolser & Hay 1996) could also be playing an important role in these observed patterns of diet quality by driving crabs to eat more animal material, though this has not been extensively explored in crabs or in the Asian shore crab's rocky intertidal habitat (but see Pennings et al. 2001 and Demko et al. 2017). Our findings are consistent with those of Brodie et al. (2017), who demonstrated a complex interaction of season and latitude in the energy reserves of mud fiddler crabs *Uca pugnax*. Future research should continue to examine the influence of these site- and latitude-specific factors on the diet quality of Asian shore crabs, as this could inform our understanding of the timing and intensity of this species' consumptive effects on its prey species as well as the energy dynamics that influence this species' possible range expansion. Habitats with more energy-rich prey available are more likely to be able to support substantial Asian shore crab populations, and could therefore represent source sites to further spur the invasion.

We also did not observe a seasonal pattern of increased diet quality in the summer at all sites using gut energy content as a proxy for diet quality. Further, our 2 proxies for diet quality (standardized gut size and gut energy content) did not yield the same seasonal patterns at each site, contrary to our expectations. We suggest that this is because gut energy content analyses necessarily used a smaller sample size (612 crabs) due to the limitations of the bomb calorimeter which may have weakened our ability to detect useful patterns and trends. Further, because the gut energy content trends through time were analyzed for each site separately, it is likely that some sampling dates at specific sites did not have enough data to show a clear or statistically significant trend. The NH site is an example of this — the graph using standardized gut size as the proxy for diet quality visually shows the same seasonal pattern as the data using gut energy content as the proxy, but the data using gut energy content were too sparse at this site to generate a statistically significant trend. Thus, we favored using the diet quality proxy of standardized gut size to draw longer-term inferences and conclusions.

We also found that gut fullness did not correlate with gut energy content. This finding is in accordance with previous work in this species that demonstrates increased consumption amount when diet quality is reduced (Griffen et al. 2020), consistent with compensatory feeding. These results are also likely influenced by changes in diet quality across season and latitude in the present study.

4.3. Seasonal patterns of food consumption

We also found that residual gut mass — a measure of the amount of food consumed during a crab's final meal — differed across latitude, likely due to differences in prey availability and/or varying degrees of inter-/intra-specific competition. However, the lack of a significant negative correlation between residual gut mass (consumption amount) and standardized gut size (diet quality) at any sampling site refutes our hypothesis that crabs at sites with low diet quality during summer months would compensate by increasing total consumption in order to meet nutrient requirements for reproduction. This could be due to limited food availability, competition, and/or differences in digestion time for different diets (Karasov et al. 2011).

4.4. Ecological implications

Due to the relationship between diet quality, energy intake and storage, and population density, habitats with more available animal prey may be able to support higher Asian shore crab population densities (Forbes et al. 2014). However, this expectation may be complicated by other factors, such as differences in planktonic larval settlement (O'Connor 1993) or increased predation on smaller conspecifics with increased recruitment (Crane & O'Connor 2021). Regardless, a decline in diet quality during the reproductive season at certain locations could be a contributing factor to recent decreases in Asian shore crab population densities, such as those reported at sites in Massachusetts (O'Connor 2018, Bloch et al. 2019). In contrast, an improvement in diet quality during the reproductive season at a location could play a role in increasing Asian shore crab population density in that region, which could increase the chances of that population expanding its range. We also acknowledge the importance of other range-limiting factors previously discussed. A higher Asian shore crab density at a location could also negatively affect other co-occurring species through exploitative competition for higher-quality food items or space (Griffen & Byers 2006, Dauvin et al. 2009). However, our findings that diet quality did not increase during the reproductive season at either the northernmost (ME) or southernmost (NC) site suggest that this species may be energetically limited in its ability to expand its geographic range. This idea is supported by the conceptual understanding that diet quality should be highest in the center of a species' range and poorer toward the edges (as our data largely show for the Asian shore crab, see Fig. 1). However, understanding the influence of diet quality across the range may be complicated by the interaction of 2 potentially competing trends: (1) the latitudinal trend in diet quality and (2) the tendency for diet quality to be highest in the center of a species' range. This understanding may also be complicated by the fact that the range of a recently invaded species can be heavily influenced by the initial point of introduction and subsequent dispersal pathways (Arim et al. 2006, Gallien et al. 2015), potentially causing a mismatch between the center of that species' current range and the peak of its diet quality distribution.

4.5. Conclusions

In summary, the diet quality of Asian shore crab populations is affected by both seasonal and latitudinal factors, and these factors interact to produce a largely predictable latitudinal cline in diet quality, with higher diet quality in the center of its range and lower diet quality toward the southern and northern edges. At some sites, this species' diet quality is highest in the summer, its reproductive season, which has important ecological implications for population growth and for the impacts of this invader on other species in its communities. Finally, the amount of food an Asian shore crab consumes differs across latitude. These results provide a foundation for understanding the consumptive impacts of this widespread invader through time and space and invite further study into the factors affecting this invader's ecological and environmental range.

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LITERATURE CITED

Arim M, Abades SR, Neill PE, Lima M, Marquet PA (2006) Spread dynamics of invasive species. Proc Natl Acad Sci USA 103:374–378

Blakeslee AMH, Fowler AE, Keogh CL (2013) Marine invasions and parasite escape: updates and new perspectives. Adv Mar Biol 66:87–169

Bloch CP, Curry KD, Jahoda JC (2015) Long-term effects of an invasive shore crab on Cape Cod, Massachusetts. North-East Nat 22:178–191

Bloch CP, Curry KD, Fisher-Reid MC, Surasinghe TD (2019) Population decline of the invasive Asian shore crab (*Hemigrapsus sanguineus*) and dynamics of associated intertidal invertebrates on Cape Cod, Massachusetts. Northeast Nat 26:772–784

Bolser RC, Hay ME (1996) Are tropical plants better defended? Palatability and defenses of temperate vs. tropical seaweeds. Ecology 77:2269–2286

Brodie R, Roberts B, Espinosa J, Heilman K, Borgianini S, Welch J, Reinsel K (2017) Seasonal and latitudinal variations in the energy reserves of the mud fiddler crab *Uca pugnax*: implications for the response to climate change. Aquat Biol 26:113–123

Brousseau DJ, Baglivo JA (2005) Laboratory investigations of food selection by the Asian shore crab, *Hemigrapsus sanguineus*: algal versus animal preference. J Crustac Biol 25:130–134

Byers JE, Pringle JM (2006) Going against the flow: retention, range limits and invasions in advective environments. Mar Ecol Prog Ser 313:27–41

Calizza E, Rossi L, Careddu G, Sporta Caputi S, Costantini ML (2021) A novel approach to quantifying trophic interaction strengths and impact of invasive species in food webs. Biol Invasions 23:2093–2107

Cannizzo ZJ, Dizon SR, Griffen BD (2018) An anthropogentic habitat within a suboptimal colonized ecosystem provides improved conditions for a range-shifting species. Ecol Evol 8:1521–1533

Cannizzo ZJ, Lang SQ, Benitez-Nelson B, Griffen BD (2020) An artificial habitat increases the reproductive fitness of a range-shifting species within a newly colonized ecosystem. Sci Rep 10:554

Clausen KK, Krause-Jensen D, Olesen B, Marbà N (2014) Seasonality of eelgrass biomass across gradients in temperature and latitude. Mar Ecol Prog Ser 506:71–85

Compton TJ, Leathwick JR, Inglis GJ (2010) Thermogeography predicts the potential global range of the invasive European green crab (*Carcinus maenas*). Divers Distrib 16:243–255

Crane LC, O'Connor NJ (2021) Cannibalism as a potential factor affecting recruitment of the invasive Asian shore crab *Hemigrapsus sanguineus.* Mar Biol 168:46

Cuddington K, Hastings A (2004) Invasive engineers. Ecol Modell 178:335–347

Dauvin JC, Tous Rius A, Ruellet T (2009) Recent expansion of two invasive crabs species *Hemigrapsus sanguineus* (de Haan, 1835) and *H. takanoi* Asakura and Watanabe 2005 along the Opal Coast, France. Aquat Invasions 4:451–465

Demko AM, Amsler CD, Hay ME, Long JD, McClintock JB, Paul VJ, Sotka EE (2017) Declines in plant palatability from polar to tropical latitudes depend on herbivore and plant identity. Ecology 98:2312–2321

Depledge MH (1984) Cardiac activity in the intertidal crab *Hemigrapsus sanguineus* (de Haan). Asian Mar Biol 1: 115–123

Ely CR, Raveling DG (2011) Seasonal variation in nutritional characteristics of the diet of greater white-fronted geese. J Wildl Manag 75:78–91

Epifanio CE (2013) Invasion biology of the Asian shore crab *Hemigrapsus sanguineus*: a review. J Exp Mar Biol Ecol 441:33–49

Fabrizio MC, Nepal V, Tuckey TD (2021) Invasive blue catfish in the Chesapeake Bay Region: a case study of competing management objectives. N Am J Fish Manage 41: S156–S166

Fearman JA, Bolch CJS, Moltschaniwskyj NA (2009) Energy storage and reproduction in mussels, *Mytilus galloprovincialis*: the influence of diet quality. J Shellfish Res 28:305–312

Forbes KM, Stuart P, Mappes T, Hoset KS, Henttonen H, Huitu O (2014) Diet quality limits summer growth of field vole populations. PLOS ONE 9:e91113

Freestone AL, Osman RW, Ruiz GM, Torchin ME (2011) Stronger predation in the tropics shapes species richness patterns in marine communities. Ecology 92:983–993

Gallagher CA, Chimienti M, Grimm V, Nabe-Nielsen J (2022) Energy-mediated responses to changing prey size and distribution in marine top predator movements and population dynamics. J Anim Ecol 91:241–254

Gallardo B, Clavero M, Sánchez MI, Vilà M (2016) Global ecological impacts of invasive species in aquatic ecosystems. Glob Change Biol 22:151–163

Gallien L, Mazel F, Lavergne S, Renaud J, Douzet R, Thuiller W (2015) Contrasting the effects of environment, dispersal and biotic interactions to explain the distribution of invasive plants in alpine communities. Biol Invasions 17:1407–1423

Gibson RN, Atkinson RJA, Gordon JDM (2007) Oceanography and marine biology: an annual review, Vol 45. CRC Press, Boca Raton, FL

Griffen BD, Byers JE (2006) Partitioning mechanisms of predator interference in different habitats. Oecologia 146:608–614

Griffen BD, Mosblack H (2011) Predicting diet and consumption rate differences between and within species using gut ecomorphology. J Anim Ecol 80:854–863

Griffen BD, Altman I, Bess BM, Hurley J, Penfield A (2012) The role of foraging in the success of invasive Asian shore crabs in New England. Biol Invasions 14:2545–2558

Griffen BD, Vogel M, Goulding L, Hartman R (2015) Energetic effects of diet choice by invasive Asian shore crabs: implications for persistence when prey are scarce. Mar Ecol Prog Ser 522:181–192

Griffen BD, Bailey J, Carver J, Vernier A and others (2020) Mechanisms of possible self-limitation in the invasive Asian shore crab *Hemigrapsus sanguineus.* Sci Rep 10: 16908

Griffen BD, van den Akker D, DiNuzzo ER, Anderson L, Vernier A (2021) Comparing methods for predicting the impacts of invasive species. Biol Invasions 23:491–505

Gül MR, Griffen BD (2020) Diet, energy storage, and reproductive condition in a bioindicator species across beaches with different levels of human disturbance. Ecol Indic 117:106636

Hixon MA, Green SJ, Albins MA, Akins JL, Morris JA (2016) Lionfish: a major marine invasion. Mar Ecol Prog Ser 558: 161–165

Hostert LE, Pintor LM, Byers JE (2019) Sex, size, and prey caloric value affect diet specialization and consumption of an invasive prey by a native predator. Curr Zool 65: 499–507

Hudson DM, Sexton DJ, Wint D, Capizzano C, Crivello JF (2018) Physiological and behavioral response of the Asian shore crab, *Hemigrapsus sanguineus*, to salinity: implications for estuarine distribution and invasion. PeerJ 6:e5446

Karachle PK, Stergiou KI (2008) The effect of season and sex on trophic levels of marine fishes. J Fish Biol 72: 1463–1487

Karasov WH, Martínez del Rio C, Caviedes-Vidal E (2011) Ecological physiology of diet and digestive systems. Annu Rev Physiol 73:69–93

Karmalkar AV, Horton RM (2021) Drivers of exceptional coastal warming in the northeastern United States. Nat Clim Chang 11:854–860

Katsanevakis S, Wallentinus I, Zenetos A, Leppäkoski E and others (2014) Impacts of invasive alien marine species on ecosystem services and biodiversity: a pan-European review. Aquat Invasions 9:391–423

Keller RP, Geist J, Jeschke JM, Kühn I (2011) Invasive species in Europe: ecology, status, and policy. Environ Sci Eur 23: 23

Kennish R (1996) Diet composition influences the fitness of the herbivorous crab *Grapsus albolineatus.* Oecologia 105:22–29

Kroft K, Blakeslee A (2016) Comparison of parasite diversity in native panopeid mud crabs and the invasive Asian shore crab in estuaries of northeast North America. Aquat Invasions 11:287–301

Lee WB, Houston DC (1993) The effect of diet quality on gut anatomy in British voles (Microtinae). J Comp Physiol B 163:337–339

Lord JP, Williams LM (2017) Increase in density of genetically diverse invasive Asian shore crab (*Hemigrapsus sanguineus*) populations in the Gulf of Maine. Biol Invasions 19:1153–1168

Mantelatto FLM, Christofoletti RA (2001) Natural feeding activity of the crab *Callinectes ornatus* (Portunidae) in Ubatuba Bay (São Paulo, Brazil): influence of season, sex, size and molt stage. Mar Biol 138:585–594

McDermott JJ (1998a) The western Pacific brachyuran (*Hemigrapsus sanguineus*: Grapsidae), in its new habitat along the Atlantic Coast of the United States: geographic distribution and ecology. ICES J Mar Sci 55:289–298

McDermott JJ (1998b) The western Pacific brachyuran *Hemigrapsus sanguineus* (Grapsidae) in its new habitat along the Atlantic Coast of the United States: reproduction. J Crustac Biol 18:308–316

Miller MR (1975) Gut morphology of mallards in relation to diet quality. J Wildl Manag 39:168–173

Milton K (1981) Food choice and digestive strategies of two sympatric primate species. Am Nat 117:496–505

Molnar JL, Gamboa RL, Revenga C, Spalding MD (2008) Assessing the global threat of invasive species to marine biodiversity. Front Ecol Environ 6:485–492

Norris DR, Arcese P, Preikshot D, Bertram DF, Kyser TK (2007) Diet reconstruction and historic population dynamics in a threatened seabird. J Appl Ecol 44:875–884

O'Connor NJ (1993) Settlement and recruitment of the fiddler crabs *Uca pugnax* and *U. pugilator* in a North Carolina, USA, salt marsh. Mar Ecol Prog Ser 93:227–234

O'Connor NJ (2018) Changes in population sizes of *Hemigrapsus sanguineus* (Asian shore crab) and resident crab species in southeastern New England (2010–2016). Northeast Nat 25:197–201

Pennings SC, Siska EL, Bertness MD (2001) Latitudinal differences in plant palatability in Atlantic Coast salt marshes. Ecology 82:1344–1359

R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Saigusa M, Kawagoye O (1997) Circatidal rhythm of an intertidal crab, *Hemigrapsus sanguineus*: synchrony with unequal tide height and involvement of a light-response mechanism. Mar Biol 129:87–96

Schafer LN, Platell ME, Valesini FJ, Potter IC (2002) Comparisons between the influence of habitat type, season and body size on the dietary compositions of fish species in nearshore marine waters. J Exp Mar Biol Ecol 278: 67–92

Scheirs J, Bruyn LD, Verhagen R (2002) Seasonal changes in leaf nutritional quality influence grass miner performance. Ecol Entomol 27:84–93

Schmitt JD, Peoples BK, Castello L, Orth DJ (2019) Feeding ecology of generalist consumers: a case study of invasive blue catfish *Ictalurus furcatus* in Chesapeake Bay, Virginia, USA. Environ Biol Fishes 102:443–465

Stephenson EH, Steneck RS, Seeley RH (2009) Possible temperature limits to range expansion of non-native Asian shore crabs in Maine. J Exp Mar Biol Ecol 375:21–31

Stillman RA, Railsback SF, Giske J, Berger U, Grimm V (2015) Making predictions in a changing world: the benefits of individual-based ecology. Bioscience 65:140–150

Storms D, Aubry P, Hamann JL, Saïd S, Fritz H, Saint-Andrieux C, Klein F (2008) Seasonal variation in diet composition and similarity of sympatric red deer *Cervus elaphus* and roe deer *Capreolus capreolus.* Wildl Biol 14: 237–250

Thometz NM, Tinker MT, Staedler MM, Mayer KA, Williams TM (2014) Energetic demands of immature sea otters from birth to weaning: implications for maternal costs, reproductive behavior and population-level trends. J Exp Biol 217:2053–2061

van Gils JA, Beekman JH, Coehoorn P, Corporaal E and others (2008) Longer guts and higher food quality increase energy intake in migratory swans. J Anim Ecol 77: 1234–1241

Wagner CE, McIntyre PB, Buels KS, Gilbert DM, Michel E (2009) Diet predicts intestine length in Lake Tanganyika's cichlid fishes. Funct Ecol 23:1122–1131

Wickham H, Averick M, Bryan J, Chang W and others (2019) Welcome to the tidyverse. J Open Source Softw 4: 1686

Williams AB, McDermott JJ (1990) An eastern United States record for the Western Indo-Pacific crab, *Hemigrapsus sanguineus* (Crustacea: Decapoda: Grapsidae). Proc Biol Soc Wash 103:108–109

Wolcott DL, O'Connor NJ (1992) Herbivory in crabs: adaptations and ecological considerations. Am Zool 32:370–381

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