

# Predicting diet and consumption rate differences between and within species using gut ecomorphology

Blaine D. Griffen<sup>1,2\*</sup> and Hallie Mosblack<sup>2</sup>

<sup>1</sup>Department of Biological Sciences, University of South Carolina, Columbia, SC 29208, USA; and <sup>2</sup>Marine Science Program, University of South Carolina, Columbia, SC 29208, USA

## Summary

**1.** Rapid environmental changes and pressing human needs to forecast the consequences of environmental change are increasingly driving ecology to become a predictive science. The need for effective prediction requires both the development of new tools and the refocusing of existing tools that may have previously been used primarily for purposes other than prediction. One such tool that historically has been more descriptive in nature is ecomorphology (the study of relationships between ecological roles and morphological adaptations of species and individuals).

**2.** Here, we examine relationships between diet and gut morphology for 15 species of brachyuran crabs, a group of pervasive and highly successful consumers for which trophic predictions would be highly valuable.

**3.** We show that patterns in crab stomach volume closely match some predictions of metabolic theory and demonstrate that individual diet differences and associated morphological variation reflect, at least in some instances, individual choice or diet specialization.

**4.** We then present examples of how stomach volume can be used to predict both the per cent herbivory of brachyuran crabs and the relative consumption rates of individual crabs.

**Key-words:** brachyuran, ecological prediction, ecomorphology, functional morphology, metabolic ecology, niche variation hypothesis, omnivory

## Introduction

A primary goal of ecology is to understand natural systems sufficiently to explain or even predict their dynamics. Attaining this goal is often complicated by high levels of interspecific and intraspecific variation in nearly every biological or ecological metric. This variation, far from acting simply as ‘noise’, is central to basic ecological and evolutionary processes. For example, variation across species facilitates niche partitioning and thus ecological diversity (Hutchinson 1959). Within populations, intraspecific variation provides the raw material for natural selection (Darwin 1859). However, despite the central importance of variation in ecological and evolutionary processes, it is often ignored and deference is given instead to testing dissimilarity among mean values (i.e. ‘the tyranny of the golden mean’, Bennett 1987). Yet, understanding this variation may be key to predicting the dynamics of many systems.

Variation often occurs both in form and in function, and discovering the evolutionary link between morphological and ecological variation is the realm of ecomorphology. While ecomorphology has historically been primarily a descriptive field, there is considerable potential to exploit the

link between form and function as a tool not only to explain but to predict ecological patterns and dynamics. For example, ecomorphology has been used to accurately predict paleohabitat use by bovid mammals from skeletal remains (DeGusta & Vrba 2005a,b) and resource partitioning in insectivorous bats (Saunders & Barclay 1992). However, detecting correlations between ecological variables and morphological characteristics can lead to spurious predictions (e.g., Shoup & Hill 1997), and ecomorphological predictions have historically been fraught with methodological and conceptual pitfalls (Motta & Kotrschal 1992). Ultimately, the predictive capabilities of ecomorphology hinge on the strength of mechanistic links between morphology and the behavioural or physiological requirements and constraints that underlie ecological function (Wainwright 1996; Ferry-Graham, Bolnick & Wainwright 2002).

Nowhere is variation more prevalent than in dietary habits, and broad variation in diet (function) is associated with similarly broad variation in gut morphology (form). Understanding the role of gut morphology in nutrition has played an important role in metabolic ecology (Karasov & Martínez del Rio 2007). For example, an early prediction of metabolic theory derived from assumptions of optimal digestion is that animal gut sizes should be inversely correlated with diet quality (Sibly 1981) because organisms that eat

\*Correspondence author. E-mail: bgriffen@biol.sc.edu

low-quality food must eat large volumes to attain sufficient nutrition. This prediction has been supported in a broad range of systems including mammals, fish, reptiles, insects and annelids (reviewed in Eubanks 2005; Newman 2007). It has also been supported in comparisons both across and within species. For example, interspecific comparisons in fish with different diets demonstrate that more herbivorous species have longer digestive tracts, relative to body size, than carnivorous species (Suyehiro 1942; Kappor, Smith & Verighina 1975; Montgomery 1977; Hoffer 1988). Additionally, intraspecific comparisons demonstrate that size-specific gut length in fish increases with age to compensate for ontogenetic diet shifts towards increasing herbivory (Lassuy 1984; Benavides, Cancino & Ojeda 1994). The general ubiquity and fidelity of the correlation between diet and gut size suggests that gut ecomorphology may be useful in understanding and predicting trophic ecology of consumers.

Brachyuran crabs are a prominent group of consumers that often exert strong top-down control in food webs and that also display a large amount of trophic variation. There are approximately 10 500 described species of Brachyuran crabs found in marine, estuarine, freshwater, semiterrestrial and terrestrial environments (Brusca & Brusca 2003). Crabs are voracious consumers and notoriously omnivorous (Marshall & Orr 1960), and each species has its own trophic strategy. Given the vast number of crab species, their diverse trophic strategies and their ecological importance across a variety of habitats, developing methods to predict the trophic impacts of these consumers (what they eat, how much they eat, etc.) could have several benefits. For example, the ability to predict the trophic impacts of crabs could help clarify the numerous trophic webs where crabs play a dominant role. Additionally, this ability to predict could assist in ecological forecasting, given the high propensity of crabs to move into new habitats as invasive species (Galil & Clark *In Press*), and given shifting food webs, for example through over-harvesting of large predatory fish which can release crabs from trophic control and elevate their importance in near-shore food webs (e.g., Steneck & Carlton 2001; Holdredge, Bertness & Altieri 2009).

Gut morphology of Brachyuran crabs is relatively conserved across species. Consumed food is passed first to the large cardiac stomach where it is stored for later processing. Food is then passed in small amounts to the gastric mill which macerates the food before passing it to the smaller pyloric stomach. This arrangement allows food to be taken in quickly in bulk and then processed later (Brusca & Brusca 2003). This is ideally suited to the general crab strategy of active foraging bouts during specific times of the day (night-time high tides or day-time low tides, depending on the species) with only limited foraging activity during other parts of the day. One implication of this combined foraging strategy and gut morphology is that food consumption by crabs is ultimately limited by the volume of the cardiac stomach. In this paper, we examine both inter- and intraspecific variation in cardiac stomach volume for 15 crab species using both observational and field experimental evidence to examine the

feasibility of using stomach volume to derive the following four types of predictions.

#### PREDICTING MEAN PER CENT HERBIVORY OF A SPECIES

Herbivorous crabs are generally nitrogen limited (Kennish 1997; Linton & Greenaway 2000). Animal tissue is commonly more nitrogen rich than plant material (Mattson 1980). Thus, based on the widely supported hypothesized relationship between gut size and diet quality (Sibly 1981), we expect cardiac stomach volume to increase with per cent herbivory in crabs. Comparison of results of previous studies suggests that this general trend likely holds true for crabs (Wolcott & O'Connor 1992). Here, we examine whether quantitative estimates of relative stomach size may be used to predict the contribution of plants to diets of crab species.

#### PREDICTING RELATIVE MAXIMAL CONSUMPTION RATES OF DIFFERENT SPECIES

Total maximum consumption at any given time is limited by gut capacity. Thus, if different species have relatively distinct gut sizes, then comparing size-specific volume of the cardiac stomach should facilitate predictions of approximate relative maximum consumption rates of different species or of different-sized conspecifics.

#### PREDICTING DIET BREADTH OF A SPECIES

Several factors may influence intraspecific diet breadth, including seasonal effects (e.g., Sardina & Cazorla 2005), ontogenetic diet shifts (e.g., Garcia-Berthou & Moreno-Amich 2000), genetic variation (e.g., Futuyma & Peterson 1985), sexual or other phenotypic variation (e.g., McDermott 1998) and interspecific interactions (e.g., Griffen, Guy & Buck 2008). Another prediction of ecological theory is that species with wider niches should have more individual variation than species with narrower niches (the 'niche variation hypothesis' of Van Valen 1965). If this holds true for gut size, then we should expect that intraspecific variation in stomach volume should increase with, and may be used to predict, diet diversity.

#### PREDICTING THE DEGREE OF INDIVIDUAL DIET SPECIALIZATION WITHIN A POPULATION

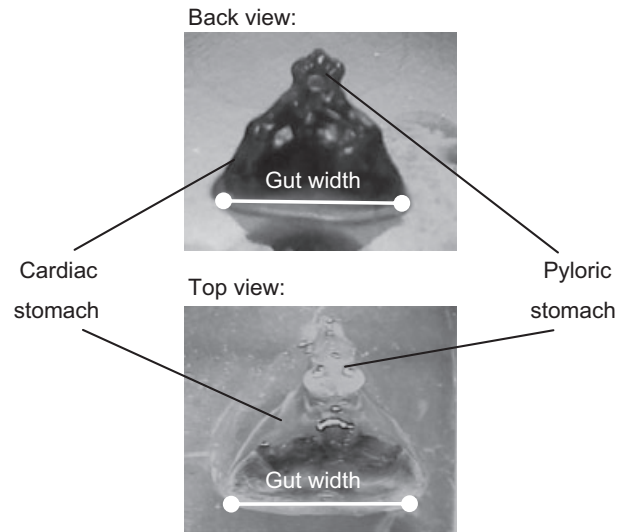
While species are often broadly categorized as 'herbivorous' or 'carnivorous', a high degree of intraspecific diet variation and individual diet specialization has been observed across a broad range of taxa (Bolnick *et al.* 2003). Previous studies have used individual morphology to infer individual dietary specialization (e.g., Robinson *et al.* 1993; Fermon & Cibert 1998), and it has been suggested that this approach may be generally applicable (Bolnick *et al.* 2003). Thus, intraspecific variation in gut size may reflect individual diet specialization. If so, then intraspecific patterns should follow interspecific patterns – larger guts for more herbivorous individuals.

## Materials and methods

### STUDY SYSTEM

We chose 15 species of brachyuran crabs found at various locations along the east coast of the United States (Table 1). These species were selected because of their ecological and/or economic importance. For example, several of the study species are species of management concern because they are problematic invaders (*Dyspanopeus sayi* in the Adriatic, *Hemigrapsus sanguineus* in the Northwest Atlantic and in Europe and *Carcinus maenas* in numerous areas worldwide), or because they have recently increased in abundance owing to reduced consumer pressure and are now having severe negative impacts (*Sesarma reticulatum* in New England salt marshes), or because they support active fisheries (*Callinectes sapidus*). Other species are dominant consumers in their respective habitats (*Armases cinereum*, *Cancer irroratus*, *Eurypanopeus depressus*, *Eurytium limosum*, *Panopeus* spp., *Rhithropanopeus harrisi*, *Uca* spp.). Further, these species were chosen because they represent a broad range of dietary omnivorous strategies, from almost purely carnivorous to almost purely herbivorous (Table 1).

Brachyuran crabs have three characteristics that make them an ideal system for this study. First, while each of the species listed in Table 1 will consume both plant and animal prey, there is considerable inter- and intraspecific diet variation. Second, as noted above, general gut morphology is very similar across species. Third, the crab cardiac stomach has a very distinctive shape that facilitates the calculation of gut volume. The gut bears a striking resemblance to a triangular pyramid (Fig. 1). Thus, the volume of the cardiac stomach can be calculated using gut width and the equation



**Fig. 1.** Back and top view of *Hemigrapsus sanguineus* stomachs demonstrating that the cardiac stomach is accurately approximated by a triangular pyramid. Cardiac stomachs from all crab species reported here have similar gross morphology.

$$\text{Volume} = a \frac{\sqrt{2}}{12} \times \text{width}^3 \quad \text{eqn 1}$$

We verified that this equation provided accurate volume estimates by comparing values predicted using eqn 1 to values measured by

**Table 1.** Crab species used in this study

Species	Diet	Diet refs	Sample size	Genbank accession number
<i>Armases cinereum</i> (Grapsid), SC	Fresh and decaying plant material, animal prey	Seiple & Salmon (1982)	70; 36	AJ784010
<i>Callinectes sapidus</i> (Portunid), SC	Annelids, bivalves, fish, crustaceans, gastropods, plants	Laughlin (1982), Alexander (1986)	66; 3491	AJ298190
<i>Cancer irroratus</i> (Cancrid), ME	Mussels, barnacles, ectoprocts, polychaetes, algae	—	82; 20	AJ130812
<i>Carcinus maenas</i> (Portunid), NH	Crustaceans, mussels, other animals, red algae, green algae, brown algae, gastropods	Elner (1981), Ropes (1989)	126; 1059	AY583901
<i>Dyspanopeus sayi</i> (Xanthid), NH	Bivalves, algae, barnacles, polychaetes	Ropes (1989)	63; 70	AJ274694
<i>Eurypanopeus depressus</i> (Xanthid), SC	Algae, detritus, bivalves, annelids, sponges, amphipods	Lohrer <i>et al.</i> (2000)	47; 50	AJ274688
<i>Eurytium limosum</i> (Xanthid), SC	Crustacean, <i>Spartina</i> , bivalve, annelid, detritus	(Kneib & Weeks 1990)	54; 217	AJ274696
<i>Hemigrapsus sanguineus</i> (Grapsid), NH	Algae, barnacles, mussels, crustaceans	McDermott (1998)	124; 78	EU367395
<i>Panopeus herbstii</i> (Xanthid), SC	Bivalve, barnacles, algae, detritus, crustaceans, <i>Spartina</i>	—	123; 19	AJ130815
<i>Panopeus obesus</i> (Xanthid), SC	<i>Spartina</i> , barnacle, crustacean, detritus	—	35; 14	AJ274680
<i>Rhithropanopeus harrisi</i> (Xanthid), NH	(Primarily dead animal tissues) bivalves, annelids, crustaceans, algae	—	76; 16	AJ274697
<i>Sesarma reticulatum</i> (Grapsid), MA	<i>Spartina</i> and other vegetation, crustaceans	Seiple & Salmon (1982)	81; 47	AJ225867
<i>Uca minax</i> (Ocypodid), SC	Microalgae, detritus	—	67; 15	Z79670
<i>Uca pugilator</i> (Ocypodid), SC	Microalgae, bacteria, detritus, meiofauna	—	105; 28	Z79659
<i>Uca pugnax</i> (Ocypodid), SC	Microalgae, bacteria, nematods	—	69; 11	Z79675

Column 1 provides scientific names and phylogenetic families, and the abbreviation of the state where the species was collected. Column 2 lists food items commonly included in the diets of each crab, given in order of their relative contribution to the diet. Column 3 gives references that were used in conjunction with diet data collected here to calculate the weighted mean per cent herbivory. A lack of references indicates that no data were available on per cent herbivory in the literature and that all diet data are from the present study. Column 4 gives the number of crabs used in this study for gut size analysis (first number) and the cumulative number used for diet analysis from this study and previous studies (second number). Column 5 gives the Genbank accession number for each species for 16S rRNA data.

submerging full stomachs into water-filled graduated cylinders. For this comparison, we used a subset of crabs (selected haphazardly based on stomach fullness,  $n = 141$ ) that encompassed >95% of the range of gut volumes encountered in our study. We used linear regression for this comparison and found a tight linear relationship between predicted and measured values ( $P < 0.001$ ,  $R^2 = 0.987$ ). However, the slope for this relationship was  $0.92 \pm 0.009$ , indicating that predictions provided by eqn 1 overestimated gut volumes by 8%. We therefore used  $a = 0.92$  in this equation to account for this overestimate. (We performed subsequent analyses using gut volume because this is the ecologically relevant value. However, we also repeated all analyses using gut width, which was directly measured rather than calculated, and our results were qualitatively identical. We therefore only report results using gut volume.)

#### SAMPLING AND DISSECTIONS

Crabs were sampled intertidally by hand during low tides throughout June and July of 2009 (see Table 1 for sampling sites and sample sizes). For each species, we sampled both male and female individuals over a broad range of sizes. Crabs were placed on ice immediately upon collection and were transferred to a freezer within 2 h of collection for later dissection. Crabs were dissected by first noting the sex and measuring the carapace width (CW) to the nearest 0.1 mm. We then removed the carapace, extracted the stomach with forceps and measured the width of the cardiac stomach (posterior ventral edge) to the nearest 0.1 mm using a dissecting microscope (Fig. 1).

#### DIET DETERMINATION

We obtained the diet of each species as follows. In June 2010, we again sampled crabs from each of the locations given in Table 1 (see Table 1 for sample sizes). Using a dissection microscope, we identified gut contents for individuals. Gut contents were separated by food type into grid cells on a Petri dish. We determined proportional contribution of each food type from the number of grid cells (or portions of grid cells) that each occupied. This provided an estimate of the per cent of each food type in the diet. From this, we then calculated the per cent herbivory.

Crabs of each species were sampled for gut content analysis at a single site and at a single time. However, consumer diets, including those of crabs, often vary across space and time. Therefore, when dietary information was available in the literature for any of our study species at other times or locations, we combined that data with our own to determine the mean per cent herbivory from all available studies, weighted by sample size in each study (Table 1 gives studies used in conjunction with our own data and the overall number of crabs examined in all studies to determine per cent herbivory for each species).

#### INTERSPECIFIC GUT SIZE COMPARISONS

We compared gut size between species as follows. We first calculated gut volume for each crab using eqn 1. We then used reduced major axis (RMA) regression of log gut volume against log CW. From this regression, we determined the residual gut size for each crab, which was used for comparison across species. A positive residual indicated a larger-than-expected stomach for a given size crab, while a negative residual indicated a stomach that was smaller than anticipated. To ensure that differences in gut size across crab species were a result of herbivory rather than evolutionary relationships between species, we conducted

analyses using phylogenetically independent contrasts. We determined the phylogenetic relationship between species based on overlapping regions of 16S rRNA obtained for each species from Genbank (see Table 1 for Genbank accession numbers). Phylogeny and branch lengths were calculated using neighbour joining based on the number of base pair differences between species using MEGA 4.0.2. (Tamura *et al.* 2007). We used the resulting phylogenetic tree and branch lengths to calculate phylogenetically independent contrasts for mean residual gut volume and mean per cent herbivory in the diet following methods given in Felsenstein (1985). Finally, we used linear regression to compare phylogenetically independent contrasts for residual gut volume with those for herbivory. A positive relationship here would support the hypothesis that herbivory results in larger gut size in crabs.

#### INTRASPECIFIC GUT SIZE COMPARISONS

The above-mentioned analyses ignore intraspecific variation in gut size. We examined this variation by comparing the link between individual diet and gut size in two ways: by testing the niche variation hypothesis that intraspecific variation in gut size should increase with niche width of the population and by a field experiment that explored the link between individual gut size and diet choice for a single species.

##### *Test of niche variation hypothesis*

The niche variation hypothesis applied to gut size predicts that consumers with greater dietary niche width will have greater intraspecific variation in gut size. We tested this hypothesis using the variation in the residuals from the RMA regression between cardiac stomach volume and crab CW discussed in the previous section. We determined dietary total niche width (TNW) for each species from our gut dissections using the TNW as defined by Roughgarden (1972). Specifically, we calculated the TNW based on methods described in Bolnick *et al.* (2002) and using the freeware program INDSPEC4.0, also described in Bolnick *et al.* (2002). This method, based on the Shannon–Weaver diversity index, simultaneously accounts for the number of food items included in the diet and the relative contributions of each. We again used phylogenetically independent contrasts using the same tree and branch lengths as described earlier. We used linear regression to examine the change in the contrasts of the residual stomach volume with the contrasts in the dietary TNW. A positive relationship would support the niche variation hypothesis that variation in gut size should increase with dietary niche width. Because a species' dietary niche width is not necessarily related with greater individual specialization (i.e. you could have a species where all individuals have the same broad diet), we repeated this analysis using the between individual component of TNW (i.e. BIC, Bolnick *et al.* 2002). Because of the strong correlation between TNW and BIC ( $R^2 = 0.96$  in our data set), results of this analysis using BIC were almost identical to results using TNW. We therefore only report results using TNW.

##### *Field experiment*

We conducted an experiment to determine whether intraspecific variation in stomach volume reflects individual diet choices (i.e. individual diet specialization). It has been suggested that individual morphological variation can be used to infer diet specialization (Bolnick *et al.* 2003), an approach that assumes that all food resources are identically available to each member of the population

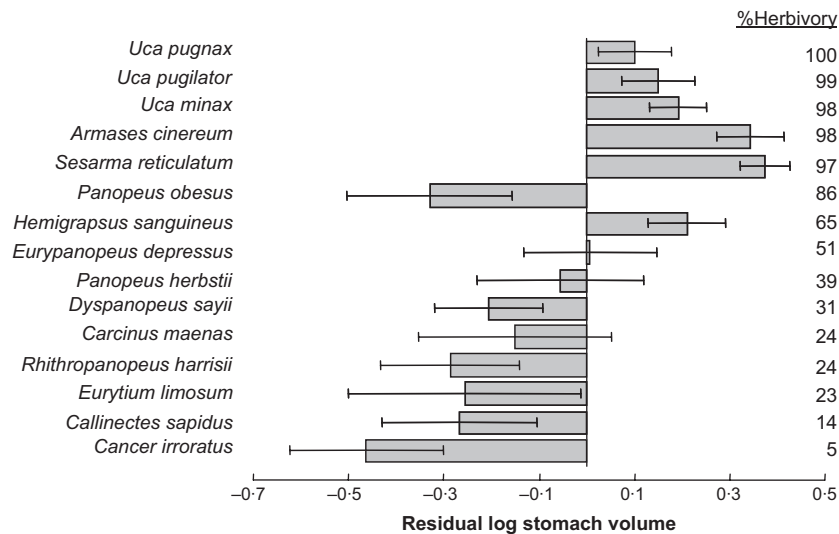


Fig. 2. Increasing residual gut volume (mean  $\pm$  SD) for crabs with increasing contribution of algae to the diet. Residuals are deviations from predicted gut volume based on reduced major axis regression of log gut volume on log carapace width. Per cent herbivory are weighted averages from gut dissections that we conducted, combined with data available in the literature (see Table 1), weighted by sample size from each source.

and that individual diet differences are not the result of differences in resource availability stemming from heterogeneous conditions (e.g. prey patchiness, individual interactions or morphological state). In reality, each of these factors naturally varies for each individual consumer, and observed diet differences may reflect transient heterogeneous conditions rather than actual food preferences or specialization. We held each of these potentially confounding variables constant to determine whether a relationship still exists between diet choice and individual stomach volume. We did this using data from a field experiment conducted with *Hemigrapsus sanguineus* at Odiorne Point, NH (see Griffen, Guy & Buck 2008 for a description of this site). We chose *H. sanguineus* because of its relatively even use of plant and animal foods (see Results) and because of our previous experience conducting field experiments to assess the diet of this species (Griffen & Delaney 2007; Griffen, Guy & Buck 2008; Griffen & Byers 2009). A positive relationship between stomach volume and herbivory would confirm that gut size can be used to infer diet specialization of individual consumers.

Crabs were placed into one of six field enclosures ( $0.5 \times 0.6 \times 0.3$  m) in groups of 10 crabs per enclosure. This density is within the range of densities observed for this crab in its invaded range along the US east coast (Griffen & Delaney 2007). This species is sexually dimorphic, and larger claws on male crabs allow them to consume a wider range of animal prey than females (McDermott 1998). Therefore, only adult male crabs within a small size range were used (CW  $26.6 \pm 3.0$  mm, mean  $\pm$  SD). In addition, we standardized the prey base qualitatively and quantitatively in each enclosure. Prey included all the commonly available food choices in the surrounding area: mussels, barnacles, snails, brown algae and red algae. Each of these potential food sources was added in abundance so that food would not be limiting. Thus, differences in food availability and consumer morphology were eliminated in this experiment, and differences in food consumption by each crab were a result of individual preference or specialization only. Crabs were allowed to forage for 24 h. The experiment was terminated at dawn on a receding tide so that crab guts would be as full as possible. Despite this, not all crabs foraged. Only crabs whose guts were estimated to be  $\geq$  half full were used in the analysis ( $n = 47$ ). Upon dissection, we determined residual stom-

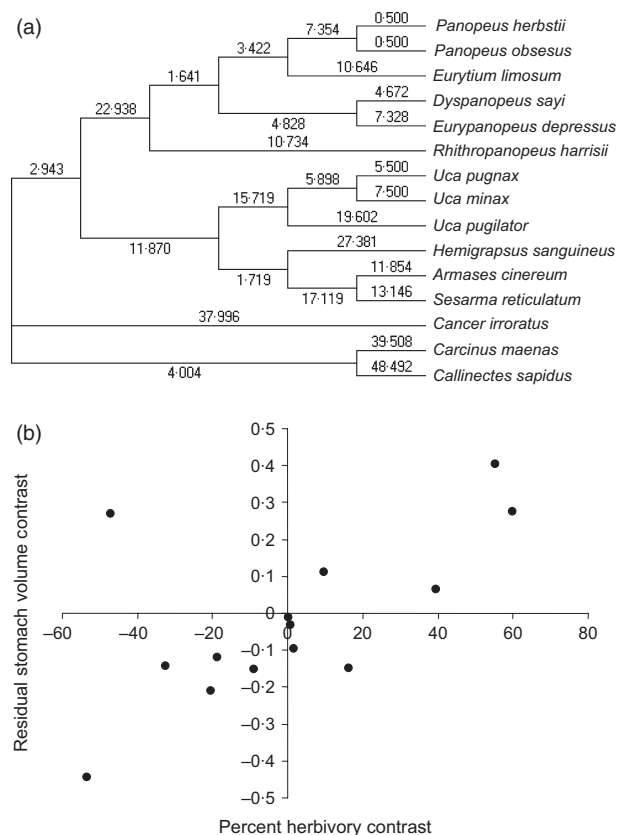


Fig. 3. (a) Phylogenetic relationship between crabs used in this study based on 16S rRNA. (b) Phylogenetically independent contrast demonstrating positive relationship between gut size and per cent herbivory.

ach volume and per cent herbivory in the diet as described earlier. We then used linear regression to test the hypothesis that crabs that had a greater per cent herbivory in their diet also had larger residual stomach volumes.

## Results

### INTERSPECIFIC GUT SIZE COMPARISON

We found that stomach volume generally increased with per cent herbivory in diet across crab species (Fig. 2). However, analysis using 16S rRNA indicated that several of the crab species examined are closely related (Fig. 3a), thus requiring phylogenetically independent contrasts. Even after accounting for phylogenetic relationships, we found that stomach volume increased with per cent herbivory in diet across crab species (regression on PIC,  $F_{1,12} = 7.79$ ,  $P = 0.016$ ,  $R^2 = 0.34$ , Fig. 3b). The outlier in Fig. 3b is the contrast between *Panopeus herbstii* and *Panopeus obesus*. We had reason to suspect that our diet estimate for *P. obesus* was not reflective of the diet of the population as a whole (see Discussion). Omitting this outlier and repeating the analysis greatly improves the amount of variation in stomach volume explained by diet ( $F_{1,11} = 48.96$ ,  $P < 0.0001$ ,  $R^2 = 0.80$ ).

### INTRASPECIFIC GUT SIZE COMPARISON

#### Test of niche variation hypothesis

Our data did not support predictions of the niche variation hypothesis that variation in residual stomach volume should increase with dietary TNW. Instead, we found no correlation between these two metrics (regression on PIC,  $F_{1,12} = 1.36$ ,  $P = 0.27$ ,  $R^2 = 0.03$ , Fig. 4).

#### Field experiment

Finally, there was a positive relationship between per cent herbivory by individual *H. sanguineus* foraging under standardized experimental conditions and the residual of stomach volume (linear regression,  $F_{1,45} = 15.84$ ,  $P < 0.001$ ,  $R^2 = 0.26$ , Fig. 5).

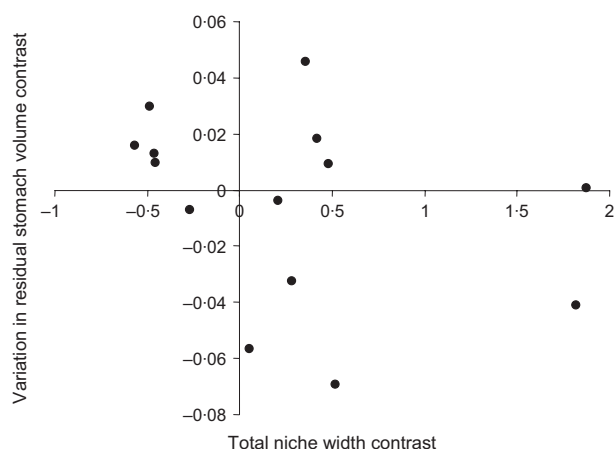


Fig. 4. Phylogenetically independent contrast of variation in gut size versus the total dietary niche width of the population, based solely on our diet assessments, testing the niche variation hypothesis that variation in gut size should increase with diet breadth.

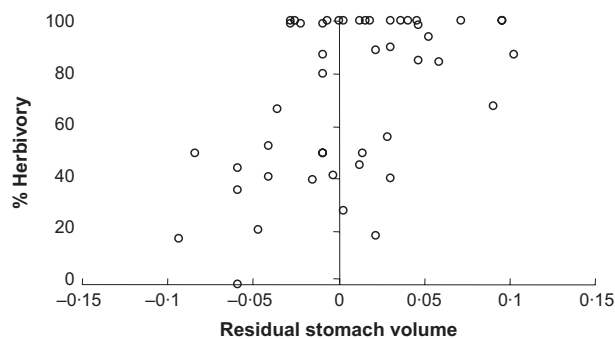


Fig. 5. Positive correlation between residual gut size, after accounting for crab size, and per cent herbivory that reflects individual diet choice for *Hemigrapsus sanguineus* foraging in field cages under standardized conditions.

## Discussion

Consistent with theoretical predictions (Sibly 1981), and with studies on other taxa, we found that stomach volume was inversely correlated with food quality, with larger stomach sizes occurring in more herbivorous species (Figs 2 and 3). In fact, we found that crabs that were almost exclusively herbivorous had guts that were nearly 10 times larger than similarly sized crabs that were almost exclusively carnivorous. For example, an individual *Armases cinereum* (98% herbivory as a species) with a CW of 20.1 mm has a gut volume that is 9.3 times larger than an individual *Cancer irroratus* (5% herbivory as a species) with a CW of 20.3 mm. Herbivorous crabs are nitrogen limited in general, and sufficient nitrogen acquisition is required for normal growth and reproduction (Wolcott & O'Connor 1992; Kennish 1996, 1997). This difference in gut size may be an adaptation for acquiring sufficient nitrogen, as plants are generally much lower than animals in nitrogen content (plants are commonly 0.5–2% N by dry weight, while animals are commonly 7–14% N, Mattson 1980). Gut size may further be influenced for some of the species examined here by the amount of refractory material consumed, such as sediment consumption by the three fiddler crab species *Uca pugnax*, *U. pugilator*, and *U. minax*.

This general trend at the species level was replicated at the individual level for the single species examined here (*H. sanguineus*, Fig. 5). Individual morphological variation has been correlated with diet specialization in other consumer species as well (e.g., Robinson *et al.* 1993; Fermon & Cibert 1998). The correlation observed here is a direct result of individual preference, as all individuals were at the same ontogenetic stage, were the same gender and were held under similar conditions. These results lend credence to the previous suggestion that morphology can be used to infer consistent trends in individual resource use (Bolnick *et al.* 2003) and suggests that these long-term diet trends may reflect persistent individual choice rather than simply spatial differences in availability and/or forced dietary differences owing to ecological interactions (e.g., Griffen, Guy & Buck 2008). Additional work is required to determine the length of time that individual

dietary specialization must persist before morphological changes in gut size are elicited (Wainwright 1996; Ferry-Graham, Bolnick & Wainwright 2002), although evidence suggests that for *H. sanguineus*, changes in individual gut size are sufficiently fast to reflect seasonal diet shifts (Griffen BD, Altan I, Bess B, unpublished data).

Contrary to predictions of the niche variation hypothesis, we did not find an increase in stomach volume variation with increasing dietary TNW (Fig. 4). Previous studies using morphological data have commonly failed to find support for this hypothesis, and Bolnick *et al.* (2007) suggested that perhaps variation in behaviour would be more appropriate. Regardless, the lack of relationship between diet breadth and variation in stomach volume precludes using stomach volume variation as a predictor of diet breadth.

Overall, our results suggest that gut size should be useful for some predictions, but not for others. First, given the strong correlation between per cent herbivory in the diet and gut volume, gut volume may profitably be used to predict dietary plant use in crabs. Second, the distinct gut volumes of each species suggest that relative gut volumes may be used to assess relative consumption rates across species (with some fairly stringent assumptions). However, our results also suggest variation in gut size will likely provide little useful information on the diet breadth of a given species. In the following sections, we provide examples demonstrating how gut size can profitably be used to predict both individual species diet (per cent herbivory) and relative consumption rates of different species.

#### GUT MORPHOLOGY AS A PREDICTOR OF SPECIES DIET

The strong correlations observed between diet and gut volume presented here suggest that gut morphology may profitably be used to predict the per cent herbivory of individual species. We provide two such predictions that grew out of the present study, one prediction that has subsequently been confirmed and one that remains to be examined.

Previous studies that document the diet of *Dyspanopeus sayi* report that this species is essentially carnivorous, consuming primarily bivalves (Mackenzie 1977; Strieb, Bricelj & Bauer 1995; Mistri 2004) and juvenile lobster (Barshaw & Lavalli 1988). Our intention was therefore to include this species in our study as an example of a strict carnivore. However, gut size comparison revealed that this species had a size-specific gut volume that was larger than that of *Cancer irroratus*, a strict carnivore (Fig. 2), but similar in size to *Carcinus maenas*, *Eurytium limosum* and *Rhithropanopeus harrisi*, all species that include algae as a substantial component of their diets (Fig. 2). From the relative stomach volumes of these species, we predicted that, despite previous reports of carnivory only, algae should contribute approximately 25%–33% to the diet of *D. sayi*. This prediction was subsequently confirmed from our own diet analyses of *D. sayi* reported here (31% herbivory, Fig. 2).

The gut volume of the mud crab *P. obesus* suggests that its diet also may be different than indicated by available evi-

dence. The diet of *P. obesus* has not previously been reported. The only diet estimate therefore comes from our dissections reported here, which reflect a relatively small sample size for this species ( $n = 14$ , Table 1). Additionally, all of the *P. obesus* collected for diet analysis came from North Inlet, SC, from the edge of a marsh tidal creek where this species constructs burrows at the base of the marsh plant *Spartina alterniflora*. Our diet analyses indicated that *S. alterniflora* comprised 86% of the diet of this species, yet its relatively small stomach volume suggests a diet that is much less herbivorous (Fig. 2). We have since learned from our own observations and from discussion with other researchers working at this site that *P. obesus* also inhabits intertidal oyster reefs alongside its congener *P. herbstii* and *Eurypanopeus depressus*. We therefore predict that *P. obesus* in oyster reef habitats consumes less plant material and more animal prey and that the overall gut size of the species reflects this broader diet. This prediction, however, remains to be tested.

In addition to the above two specific examples, inspection of Fig. 2 presents another apparent contradiction between gut volume and diet in the three *Uca* spp. Our gut content analyses suggested that these fiddler crabs are all entirely herbivorous, consuming benthic microalgae, while their guts are smaller than would be expected for herbivorous crabs (compare *Uca* spp. with *Sesarma reticulatum* and with *Armases cinerium*). However, our gut content analyses did not account for consumption of bacteria, which is known to be important for these fiddler crabs. In fact, *U. pugilator* and *U. pugnax* are similar in their ability to remove bacteria from sediment grains, consuming as much as 60% of available bacteria, while *U. minax* is much less efficient and removes only 22% (Robertson & Newell 1982). Thus, if bacteria make a substantial contribution to the diet, we may expect that *U. minax* would have a larger gut than either of the other two *Uca* species (as we found here, Fig. 2), but that all three should have smaller guts than if they consumed only algae as observed in

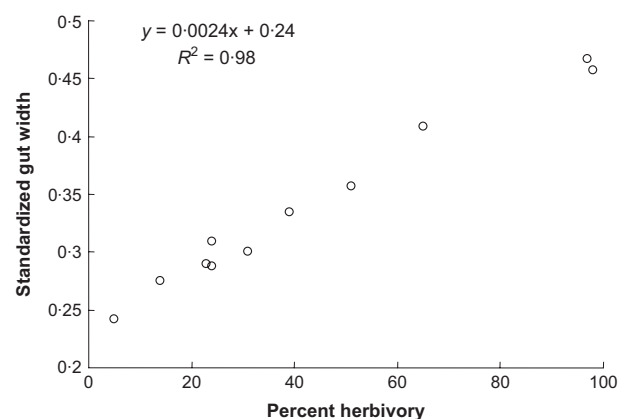


Fig. 6. Relationship between per cent herbivory in the diet and the standardized gut width (cardiac stomach width/carapace width) for all species examined here except *Panopeus obesus* and *Uca* spp. (see text for explanation). We propose that this relationship may be used to provide preliminary predictions of the per cent herbivory in the diet of other crab species not examined here.

our gut content analyses (also consistent with our findings, Fig. 2). As mentioned previously, the diet of *Uca* spp. is further complicated by the consumption of indigestible sediments.

Figure 6 provides a simplified relationship that can be used to predict the per cent herbivory in other species. Figure 6 includes 11 of the 15 species examined in this study – it does not include *P. obesus* or any of the three *Uca* spp., removed because of uncertainty about their diets as described in the preceding two paragraphs. The *y*-axis of Fig. 6 (standardized gut width) is simply the width of the cardiac stomach divided by the CW of the crab. Analyses presented here were conducted more rigorously using residuals from allometric relationships and phylogenetically independent contrasts (see Methods). However, the strong correlation between this standardized value and the per cent herbivory in the diet ( $R^2 = 0.98$ ) suggests that this simplified relationship may be used as a benchmark to approximate the per cent herbivory of other species not included in this study using simply the ratio of gut width/CW (two metrics that can be easily and quickly measured, even in the field).

#### GUT MORPHOLOGY AS A PREDICTOR OF RELATIVE CONSUMPTION RATES AMONG SPECIES

Numerous factors may influence consumption rates, such as food availability, competition, predation risk and gut passage time. Individual consumption rates are therefore not expected to reflect gut capacity alone. However, many intertidal crab species (including all those examined here) forage most actively during specific times of the day, such as night-time high tides (e.g., Lindberg 1980; Willason 1981; Batie 1983) or day-time low tides (*Uca* sp., salt marsh grapsid crabs). During these limited foraging times, crabs actively consume as much food as possible, leaving the digestion process for later (Brusca & Brusca 2003). When this type of periodic foraging strategy is employed, consumption rates may often be influenced by total gut volume. Three studies that we

are aware of have compared consumption rates between subsets of species examined here, and each of these studies provides perfect qualitative agreement and at least approximate quantitative agreement with predicted relative consumption rates of different species based on gut volume alone. These are discussed separately.

DeGraaf & Tyrrell (2004) measured consumption rates of *Carcinus maenas* and *Hemigrapsus sanguineus* foraging on the mussel *Mytilus edulis*. *H. sanguineus* and *C. maenas* in their experiment were 22 and 26 mm CW, respectively. Using the allometric relationships between CW and gut width for each species (see Table 2), we obtain a gut width of 7.71 and 8.97 mm for the two species. Using eqn 1 to convert these gut widths to volume yields volumes of 49.7 mm<sup>3</sup> for *C. maenas* and 78.4 mm<sup>3</sup> for *H. sanguineus*. Thus, in the experiment by DeGraaf & Tyrrell (2004), *C. maenas* had a gut capacity approximately 0.63 times that of *H. sanguineus*, and if both crabs eat maximally, their relative consumption rates should reflect this ratio. This is close to the reported finding that *C. maenas* consumption was approximately 0.77 times that of *H. sanguineus* (Table 2).

Similarly, Breen & Metaxas (2008) compared consumption rates of *C. maenas*, *Cancer irroratus* and *Dyspanopeus sayi* foraging on *M. edulis*. Using analogous calculations to those in the previous paragraph to convert from the CW of experimental crabs to gut width (using empirical allometric relationships for each species given in Table 2) and from gut width to gut volume (using eqn 1), we determine that based on gut volume alone, *D. sayi* should have the highest consumption rate, that *C. irroratus* should have the lowest rate, consuming approximately 58% of what *D. sayi* consumes, and that *C. maenas* should have an intermediate consumption rate, consuming approximately 92% of what *D. sayi* consumes. Consistent with this, Breen & Metaxas (2008) found that *D. sayi* had the highest consumption rate and that *C. irroratus* consumed approximately 56% of that consumed by *D. sayi*. Contrary to predictions, they found that *C. maenas* consumed only 10% of that consumed by *D. sayi*

**Table 2.** Comparison between predicted and observed relative consumption rate from published studies based on gut size only

References	Species	CW (mm)	Gut width vs. CW relationship ( $R^2$ )	Predicted relative consumption	Observed relative consumption
DeGraaf & Tyrrell (2004)	<i>Hemigrapsus sanguineus</i>	22.0	$0.34 \times CW^{1.06}$ (0.98)	1	1
	<i>Carcinus maenas</i>	26.0	$0.18 \times CW^{1.16}$ (0.96)	0.63	0.77
Breen & Metaxas (2008)	<i>Dyspanopeus sayi</i>	14.8	$0.40.72 \times CW^{0.89}$ (0.87)	1	1
	<i>C. maenas</i>	15.8		0.92	0.1; 1 <sup>a</sup>
	<i>Cancer irroratus</i>	16.0	$0.20 \times CW^{1.05}$ (0.93)	0.58	0.56
Seed (1980)	<i>Callinectes sapidus</i>	65.0	$0.23 \times CW^{1.04}$ (0.93)	1	1
	<i>Panopeus herbstii</i>	36.5	$0.72 \times CW^{0.76}$ (0.71)	0.31	0.34
	<i>P. herbstii</i>	24.5		0.13	0.16
	<i>P. herbstii</i>	10.0		0.02	0.05

Columns 1 and 2 provide the reference for the original study and the scientific names of study species, respectively. Column 3 provides the mean carapace width (CW) of the experimental crabs. Column 4 provides the empirically derived (from data collected here) relationship used to convert CW to gut width for each species. This value was subsequently converted to stomach volume using eqn 1 (see text). Columns 5 and 6 provide the predicted and observed relative consumption rates for each study based on gut volume.

<sup>a</sup>Value from field experiment; value from laboratory experiment.

in field experiments. However, when the same experiments were repeated in the laboratory (potentially removing some confounding factors), *C. maenas* increased its consumption to the point that it was indistinguishable from that of consumption by *D. sayi*, reflecting more closely the predictions based on gut volume alone.

Finally, Seed (1980) compared consumption rates of *Callinectes sapidus* and three different sizes of *Panopeus herbstii* on the ribbed mussel *Geukensia demissa*. Again, using analogous calculations to those above and allometric relationships in Table 2, we predict that *C. sapidus* should have the highest consumption rate, followed by large, medium and then small *P. herbstii* (Table 2). Observed consumption rates were in precise agreement with this relative order and were in close agreement with relative quantitative consumption rates (Table 2). These comparisons suggest that gut size may provide rough predictions of relative consumption rates of different crab species. This may profitably be used to provide *a priori* expectations for experiments that examine crab consumption and could also be used to derive rough estimates of consumption rates for use in trophic models.

In addition to morphological variation discussed here, crab digestion and nutrition are also influenced by environmental factors that interact with gut physiology. For example, digestion depends on enzyme activity (Johnston & Freeman 2005), and the activity of specific enzymes in omnivorous crabs varies with pH and temperature (Pavasovic *et al.* 2004). Thus, gut morphology and physiology likely interact to determine the efficiency of and constraints on crab digestive ecology.

In conclusion, we have shown that variation in stomach size is strongly correlated to species-specific and individual diet differences, with larger stomachs associated with greater herbivory in Brachyuran crabs. These findings strongly support metabolic theory and, because of the strength of the relationships and the clear mechanistic underpinning, suggest that this information may prove useful for predicting species general diets (per cent herbivory) and relative consumption rates.

## Acknowledgements

This research was supported by the University of South Carolina. Thanks to B.J. Toscano and R. Decker for providing comments on an earlier draft of the manuscript.

## References

Alexander, S.K. (1986) Diet of the Blue-Crab, *Callinectes sapidus* Rathbun, from nearshore habitats of Galveston Island, Texas. *Texas Journal of Science*, **38**, 85–89.

Barshaw, D.E. & Lavalli, K.L. (1988) Predation upon postlarval lobsters *Homarus americanus* by cunners *Tautoglabrus adspersus* and mud crabs *Neopanope sayi* on 3 different substrates – eelgrass, mud and rocks. *Marine Ecology-Progress Series*, **48**, 119–123.

Batie, R.E. (1983) Rhythmic locomotor activity in the intertidal shore crab *Hemigrapsus oregonensis* (Brachyura, Grapsidae) from the Oregon coast. *Northwest Science*, **57**, 49–56.

Benavides, A.G., Cancino, J.M. & Ojeda, F.P. (1994) Ontogenetic changes in gut dimensions and macroalgal digestibility in the marine herbivorous fish, *Aplodactylus punctatus*. *Functional Ecology*, **8**, 46–51.

Bennett, A.F. (1987) Interindividual variability: an underutilized resource. *New Directions in Ecological Physiology* (eds M.E. Feder, A.F. Bennett, W.W. Berggren & R.B. Huey), pp. 147–169. Cambridge University Press, New York.

Bolnick, D.I., Yang, L.H., Fordyce, J.A., Davis, J.M. & Svanback, R. (2002) Measuring individual-level resource specialization. *Ecology*, **83**, 2936–2941.

Bolnick, D.I., Svanback, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D. & Forister, M.L. (2003) The ecology of individuals: incidence and implications of individual specialization. *American Naturalist*, **161**, 1–28.

Bolnick, D.I., Svanback, R., Araujo, M.S. & Persson, L. (2007) Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. *Proceedings of the National Academy of Sciences of the USA*, **104**, 10075–10079.

Breen, E. & Metaxas, A. (2008) A comparison of predation rates by non-indigenous and indigenous crabs (juvenile *Carcinus maenas*, juvenile *Cancer irroratus*, and adult *Dyspanopeus sayi*) in laboratory and field experiments. *Estuaries and Coasts*, **31**, 728–737.

Brusca, R.C. & Brusca, G.J. (2003) *Invertebrates*, 2nd edn. Sinauer Associates, Inc., Sunderland, MA.

Darwin, C.R. (1859) *On the Origin of Species by Means of Natural Selection*. Murray, London.

DeGraaf, J.D. & Tyrrell, M.C. (2004) Comparison of the feeding rates of two introduced crab species, *Carcinus maenas* and *Hemigrapsus sanguineus*, on the blue mussel, *Mytilus edulis*. *Northeastern Naturalist*, **11**, 163–166.

DeGusta, D. & Vrba, E. (2005a) Methods for inferring paleohabitats from discrete traits of the bovid postcranial skeleton. *Journal of Archaeological Science*, **32**, 1115–1123.

DeGusta, D. & Vrba, E. (2005b) Methods for inferring paleohabitats from the functional morphology of bovid phalanges. *Journal of Archaeological Science*, **32**, 1099–1113.

Elner, R.W. (1981) Diet of green crab *Carcinus maenas* (L.) from Port Herbert, southwestern Nova Scotia. *Journal of Shellfish Research*, **1**, 89–94.

Eubanks, M.D. (2005) Predaceous herbivores and herbivorous predators: the biology of omnivores and the ecology of omnivore–prey interactions. *Ecology of Predator–Prey Interactions* (eds P. Barbosa & I. Castellanos), pp. 3–16. Oxford University Press, New York.

Felsenstein, J. (1985) Phylogenies and the comparative method. *American Naturalist*, **125**, 1–15.

Fermon, Y. & Cibert, C. (1998) Ecomorphological individual variation in a population of *Haplochromis nyererei* from the Tanzanian part of Lake Victoria. *Journal of Fish Biology*, **53**, 66–83.

Ferry-Graham, L.A., Bolnick, D.I. & Wainwright, P.C. (2002) Using functional morphology to examine the ecology and evolution of specialization. *Integrative and Comparative Biology*, **42**, 265–277.

Futuyma, D.J. & Peterson, S.C. (1985) Genetic variation in the use of resources by insects. *Annual Review of Entomology*, **30**, 217–238.

Galil, B.S. & Clark, P.F. (eds) (2011) *In the Wrong Place: Alien Marine Crustaceans – Distribution, Biology, and Impacts*. Springer, New York.

Garcia-Berthou, E. & Moreno-Amich, R. (2000) Food of introduced pumpkinseed sunfish: ontogenetic diet shift and seasonal variation. *Journal of Fish Biology*, **57**, 29–40.

Griffen, B. & Byers, J.E. (2009) Community impacts of two invasive crabs: the roles of density, prey recruitment, and indirect effects. *Biological Invasions*, **11**, 927–940.

Griffen, B.D. & Delaney, D.G. (2007) Species invasion shifts the importance of predator dependence. *Ecology*, **88**, 3012–3021.

Griffen, B.D., Guy, T. & Buck, J.C. (2008) Inhibition between invasives: a newly introduced predator moderates the impacts of a previously established invasive predator. *Journal of Animal Ecology*, **77**, 32–40.

Hoffer, R. (1988) Morphological adaptations of the digestive tract of tropical cyprinids and cichlids to diet. *Journal of Fish Biology*, **33**, 299–408.

Holdredge, C., Bertness, M.D. & Altieri, A.H. (2009) Role of crab herbivory in die-off of New England salt marshes. *Conservation Biology*, **23**, 672–679.

Hutchinson, G.E. (1959) Homage to Santa-Rosalía or why are there so many kinds of animals. *American Naturalist*, **93**, 145–159.

Johnston, D. & Freeman, J. (2005) Dietary preference and digestive enzyme activities as indicators of trophic resource utilization by six species of crab. *Biological Bulletin*, **208**, 36–46.

Kappor, B.C., Smith, H. & Verighina, I.A. (1975) The alimentary canal and digestion in teleosts. *Advances in Marine Biology*, **13**, 109–239.

Karasov, W.H. & Martínez del Río, C. (2007) *Physiological Ecology*. Princeton University Press, Princeton.

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

- Kennish, R. (1997) Seasonal patterns of food availability: influences on the reproductive output and body condition of the herbivorous crab *Grapsus albolineatus*. *Oecologia*, **109**, 209–218.
- Kneib, R.T. & Weeks, C.A. (1990) Intertidal distribution and feeding habits of the mud crab, *Eurytium limosum*. *Estuaries*, **13**, 462–468.
- Lassuy, D.R. (1984) Diet, intestinal morphology, and nitrogen assimilation efficiency in the damselfish, *Stegastes lividus*, in Guam. *Environmental Biology of Fishes*, **10**, 183–193.
- Laughlin, R.A. (1982) Feeding habits of the blue crab, *Callinectes sapidus* Rathbun, in the Apalachicola Estuary, Florida. *Bulletin of Marine Science*, **32**, 807–822.
- Lindberg, W.J. (1980) Behavior of the Oregon mud crab, *Hemigrapsus oregonensis* (Dana) (Brachyura, Grapsidae). *Crustaceana*, **39**, 263–281.
- Linton, S.M. & Greenaway, P. (2000) The nitrogen requirements and dietary nitrogen utilization for the gecarcinid land crab *Gecarcoidea natalis*. *Physiological and Biochemical Zoology*, **73**, 209–218.
- Lohrer, A.M., Whitlatch, R.B., Wada, K. & Fukui, Y. (2000) Home and away: comparisons of resource utilization by a marine species in native and invaded habitats. *Biological Invasions*, **2**, 41–57.
- Mackenzie, C.L. (1977) Predation on hard clam (*Mercenaria mercenaria*) populations. *Transactions of the American Fisheries Society*, **106**, 530–537.
- Marshall, S.M. & Orr, A.P. (1960) Feeding and nutrition. *The Physiology of Crustaceans* (ed. T.H. Waterman), pp. 227–258. Academic Press, New York.
- Mattson, W.J. (1980) Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics*, **11**, 119–161.
- McDermott, J. (1998) The western Pacific Brachyuran *Hemigrapsus sanguineus* (Grapsidae) in its new habitat along the Atlantic coasts of the United States: feeding, cheliped morphology and growth. *Proceedings of the Fourth International Congress*, **1**, 425–444.
- Mistri, M. (2004) Predatory behavior and preference of a successful invader, the mud crab *Dyspanopeus sayi* (Panopeidae), on its bivalve prey. *Journal of Experimental Marine Biology and Ecology*, **312**, 385–398.
- Montgomery, W.L. (1977) Diet and gut morphology in fishes, with special reference to monkeyface prickleback, *Cebidichthys violaceus* (Stichaeidae blennioides). *Copeia*, **1977**, 178–182.
- Motta, P.J. & Kotrschal, K.M. (1992) Correlative, experimental, and comparative evolutionary approaches in ecomorphology. *Netherlands Journal of Zoology*, **42**, 400–415.
- Newman, J. (2007) Herbivory. *Foraging: Behavior and Ecology* (eds D.W. Stephens, J.S. Brown & R.C. Ydenberg), pp. 175–220. University of Chicago Press, Chicago.
- Pavasovic, M., Richardson, N.A., Anderson, A.J., Mann, D. & Mather, P.B. (2004) Effect of pH, temperature and diet on digestive enzyme profiles in the mud crab, *Scylla serrata*. *Aquaculture*, **242**, 641–654.
- Robertson, J.R. & Newell, S.Y. (1982) A study of particle ingestion by three fiddler crab species foraging on sandy sediments. *Journal of Experimental Marine Biology and Ecology*, **65**, 11–17.
- Robinson, B.W., Wilson, D.S., Margosian, A.S. & Lotito, P.T. (1993) Ecological and morphological differentiation of pumpkinseed sunfish in lakes without bluegill sunfish. *Evolutionary Ecology*, **7**, 451–464.
- Ropes, J.W. (1989) The food-habits of 5 crab species at Pettaquamscutt River, Rhode-Island. *Fishery Bulletin*, **87**, 197–204.
- Roughgarden, J. (1972) Evolution of niche width. *American Naturalist*, **106**, 683–718.
- Sardina, P. & Cazorla, A.C.L. (2005) Feeding habits of the juvenile striped weakfish, *Cynoscion guatucupa* Cuvier 1830, in Bahia Blanca estuary (Argentina): seasonal and ontogenetic changes. *Hydrobiologia*, **532**, 23–38.
- Saunders, M.B. & Barclay, R.M.R. (1992) Ecomorphology of insectivorous bats – a test of predictions using 2 morphologically similar species. *Ecology*, **73**, 1335–1345.
- Seed, R. (1980) Predator–prey relationships between the mud crab *Panopeus herbstii*, the blue crab, *Callinectes sapidus* and the Atlantic ribbed mussel *Geukensia* (= *Modiolus*) *demissa*. *Estuarine and Coastal Marine Science*, **11**, 445–458.
- Seiple, W. & Salmon, M. (1982) Comparative social behavior of 2 Grapsid crabs, *Sesarma reticulatum* (Say) and *Sesarma cinereum* (Bosc). *Journal of Experimental Marine Biology and Ecology*, **62**, 1–24.
- Shoup, D.E. & Hill, L.G. (1997) Ecomorphological diet predictions: an assessment using inland silverside (*Menidia beryllina*) and longear sunfish (*Lepomis megalotis*) from Lake Texoma. *Hydrobiologia*, **350**, 87–98.
- Sibly, R. (1981) Strategies of digestion and defecation. *Physiological Ecology: An Evolutionary Approach to Resource Use* (eds C.R. Townsend & P. Calow), pp. 109–139. Sinauer Associates Inc., Sunderland, MA.
- Steneck, R.S. & Carlton, J.T. (2001) Human alterations of marine communities: students beware! *Marine Community Ecology* (eds M.D. Bertness, S.D. Gaines & M.E. Hay), pp. 445–468. Sinauer Associates, Inc., Sunderland, MA.
- Strieb, M.D., Bricelj, V.M. & Bauer, S.I. (1995) Population biology of the mud crab, *Dyspanopeus sayi*, an important predator of juvenile bay scallops in Long Island (USA) eelgrass beds. *Journal of Shellfish Research*, **14**, 347–357.
- Suyehiro, Y. (1942) A study on the digestive system and feeding habits of fish. *Japanese Journal of Zoology*, **10**, 1–303.
- Tamura, K., Dudley, J., Nei, M. & Kumar, S. (2007) MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) Software version 4.0. *Molecular Biology and Evolution*, **24**, 1596–1599.
- Van Valen, L. (1965) Morphological variation and width of ecological niches. *American Naturalist*, **99**, 377–390.
- Wainwright, P.C. (1996) Ecological explanation through functional morphology: the feeding biology of sunfishes. *Ecology*, **77**, 1336–1343.
- Willason, S.W. (1981) Factors influencing the distribution and coexistence of *Pachygrapsus crassipes* and *Hemigrapsus oregonensis* (Decapoda, Grapsidae) in a California Salt-Marsh. *Marine Biology*, **64**, 125–133.
- Wolcott, D.L. & O'Connor, N.J. (1992) Herbivory in crabs – adaptations and ecological considerations. *American Zoologist*, **32**, 370–381.

Received 19 November 2010; accepted 13 February 2011  
Handling Editor: Joseph Rasmussen