

2011

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SYMPOSIUM

Diet Selectivity of Juvenile Blue Crabs (*Callinectes sapidus*) in Chesapeake Bay

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From the symposium “Population Dynamics of Crustaceans” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2011, at Salt Lake City, Utah.

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Synopsis Shallow coves in Chesapeake Bay have abundant food and serve as nursery grounds for juvenile blue crabs. In this study, we examined the relationships between the diet of very small (4–40 mm CW) juvenile blue crabs and the benthic infauna in shallow, unvegetated nursery coves. We compared infauna in benthic samples with gut contents of juvenile blue crabs from six shallow coves in each of two sub-estuaries (Rappahannock and York Rivers) in Chesapeake Bay, Virginia, USA. Benthic communities differed depending on river and location, with abundant clams in upriver regions and abundant polychaetes in downriver regions. Juvenile crabs, like adults, appeared to be opportunistic feeders, with gut contents including clams, amphipods, polychaetes, small crustaceans, plant matter, and detritus. There was a positive relationship between polychaetes in the benthic samples and in crab guts, suggesting that juvenile crabs are opportunistic feeders on polychaetes in the benthos. Moreover, Ivlev’s electivity index and foraging ratio showed that clams and polychaetes were selectively eaten at all locations. Alternatively, crabs selectively rejected amphipods. Crab densities corresponded positively with polychaete densities, which suggests that there may be bottom–up control of crab distributions and that food resources are important in nursery habitats.

Introduction

The blue crab, *Callinectes sapidus* Rathbun (Arthropoda: Crustacea: Portunidae), is dispersed widely along the Atlantic and Gulf coasts of North America and is abundant throughout Chesapeake Bay (Norse 1977; Williams 1984; Hines et al. 1987; Lipcius and Van Engel 1990). The blue crab is well linked in Chesapeake Bay’s food web (Lipcius et al. 2007), and it plays an important role both ecologically and economically (Miller et al. 2005). Juvenile blue crabs are preyed upon by higher-order carnivores, and adults are benthic omnivores (Baird and Ulanowicz 1989). In recent decades, the blue crab population in Chesapeake Bay has been declining, except for a recent upswing after the closing of the dredge fishery in 2008 (Miller et al. 2010). Furthermore, the spawning stock has concurrently decreased by 84%, suggesting that the population is overexploited (Lipcius and Stockhausen 2002).

Typically, seagrass and other structured habitats are nurseries for juvenile crabs; in the traditional paradigm, juvenile crabs move first to seagrass habitats and secondarily to unvegetated habitats as they become larger (>30 mm) and outgrow the protection afforded by seagrass beds (Lipcius et al. 2007). With the abundance of seagrass declining in Chesapeake Bay (Orth et al. 2006), unvegetated shallow-water habitats are becoming more important as primary nurseries. As shallow-water unvegetated areas serve as excellent nurseries, it is important to determine the availability of prey in such habitats and examine how juvenile blue crabs respond to their prey base. Our first objective was to concurrently estimate the density of infaunal benthic organisms and juvenile crabs in two sub-estuaries of Chesapeake Bay: the York and Rappahannock Rivers.

For larger juvenile and adult blue crabs, clams comprise up to 50% of the diet, while blue crabs,

polychaetes, amphipods, and other benthic prey make up the balance (Laughlin 1982; Hines et al. 1990; Mansour and Lipcius 1991; Mansour 1992). Although they are opportunistic feeders, blue crabs can use special foraging techniques for abundant prey such as periwinkles in the marsh (Hamilton 1976). Availability of food, a bottom-up factor (Posey et al. 1995), may be important in influencing the distribution and suitability of potential nurseries for young juveniles (Seitz et al. 2005), whereas, predation, a top-down factor, is unlikely to control the distribution of large juveniles [>75 mm carapace width (CW)] or adults, which obtain a size refuge from predation (Hines et al. 1990; Moody 2001).

Bivalves can encompass up to 90% of the benthic biomass (Hagy 2002; Seitz et al. 2008), whereas, polychaetes often dominate the benthos in terms of density (Diaz and Schaffner 1990). Major species of bivalves common in the benthos of the lower Chesapeake Bay include the Baltic macoma (*Macoma balthica*), the hard clam (*Mercenaria mercenaria*), and the stout razor clam (*Tagelus plebeius*) (Boesch 1977; Holland 1985). Previous studies have shown the importance of clams in the diet of larger juvenile and adult blue crabs (Hines et al. 1990; Mansour 1992), but there is a lack of information on the diet of smaller juveniles. Thus, we examined concurrent densities of prey and crabs, small juveniles' gut contents, as well as selectivity indices, in multiple locations to assess selectivity in crabs' feeding.

In previous small-scale (single-system) studies, the biomass of benthic prey was correlated with crab biomass (i.e., bottom-up control) (Seitz et al. 2008). In a meta-analysis of previous blue crabs' gut contents for individuals >30 mm CW (Laughlin 1982; Hines et al. 1990; Mansour 1992), there was an ontogenetic shift in diet (Lipcius et al. 2007). Thus, the diet of the smallest juvenile crabs (<40 mm CW) may well be different from that of larger crabs.

Our second objective was to determine the diet of small juvenile crabs (4–40 mm CW) and thereby to determine whether juvenile crabs have discernable prey selectivity. This was accomplished through field collection of crabs and prey during mid-summer 2006. Benthic samples were taken 7–12 days after crabs were collected.

Methods

Our study areas were in various shallow coves of the Rappahannock River, a 110-km-long sub-estuary with salinity of 3–14 at our sampling sites, and the York River, a 40-km-long sub-estuary with a salinity

of 12–20 at our sampling sites (Fig. 1). In June 2006, we randomly selected six coves in the Rappahannock River—Piscataway Creek, Cat Point Creek, Harry George Creek, Mulberry Creek, Mill Creek, and Myer Creek—and six coves in the York River—Perrin Creek, Wormley Creek, Indian Field, King Creek, Cedarbush, and Propotank Bay—for concurrent sampling of benthos and crabs. Within each cove, we had six replicate sampling locations for benthic suction cores and 12 replicate locations for crab scrapes. From the 12 coves, 2 in each river were chosen based on river position for a detailed examination of crabs' gut contents; one site was at the highest point upriver (Rappahannock: Cat Point Creek; York: Propotank Bay) and one at a point downriver (Rappahannock: Harry George Creek; York: Indian Field Creek) for a total of four locations.

Benthic infauna were sampled using a suction core, which samples a large surface area and penetrates ~ 40 cm into the sediment. This deep penetration is essential for accurate estimation of densities of large bivalves that dwell 30–40 cm in the sediment and are sparsely distributed (Hines and Comtois 1985). The suction apparatus had an attached 1-mm mesh bag (Eggleston et al. 1992) and sampled within a cylinder of 0.11 m² surface area. The contents of the bags were subsequently frozen until sorted. In the laboratory, the samples were sorted twice, and organisms were identified to the lowest possible taxonomic level (usually species) and enumerated. Ash-free dry weights (AFDWs) were obtained for bivalves, polychaetes, and crustaceans.

Crabs in all coves were quantified using a modified crab scrape (1-m width) towed for 20 m at 12 replicate locations in each cove. The back of the scrape was comprised of a fine-mesh net (6 mm) that caught and reliably retained crabs >5 mm CW. All crabs were labeled and immediately placed on ice to arrest digestion. The iced crabs were taken to the laboratory, frozen, and later processed for gut-content analysis (see below).

Densities of each benthic taxon were compared among coves using an Analysis of Variance (ANOVA) using cove as a fixed factor with 6–12 replicates per cove. Some of the analyses were interpreted at $\alpha=0.1$, when differences among means were biologically relevant and there was high variation in field sampling. Relationships between crabs and benthos for all coves in 2006 were compared, using regression analysis of mean number of crabs from each cove and mean clam biomass (g AFDW).

Carapace widths of the crabs collected for this study were measured and notes made on any lost

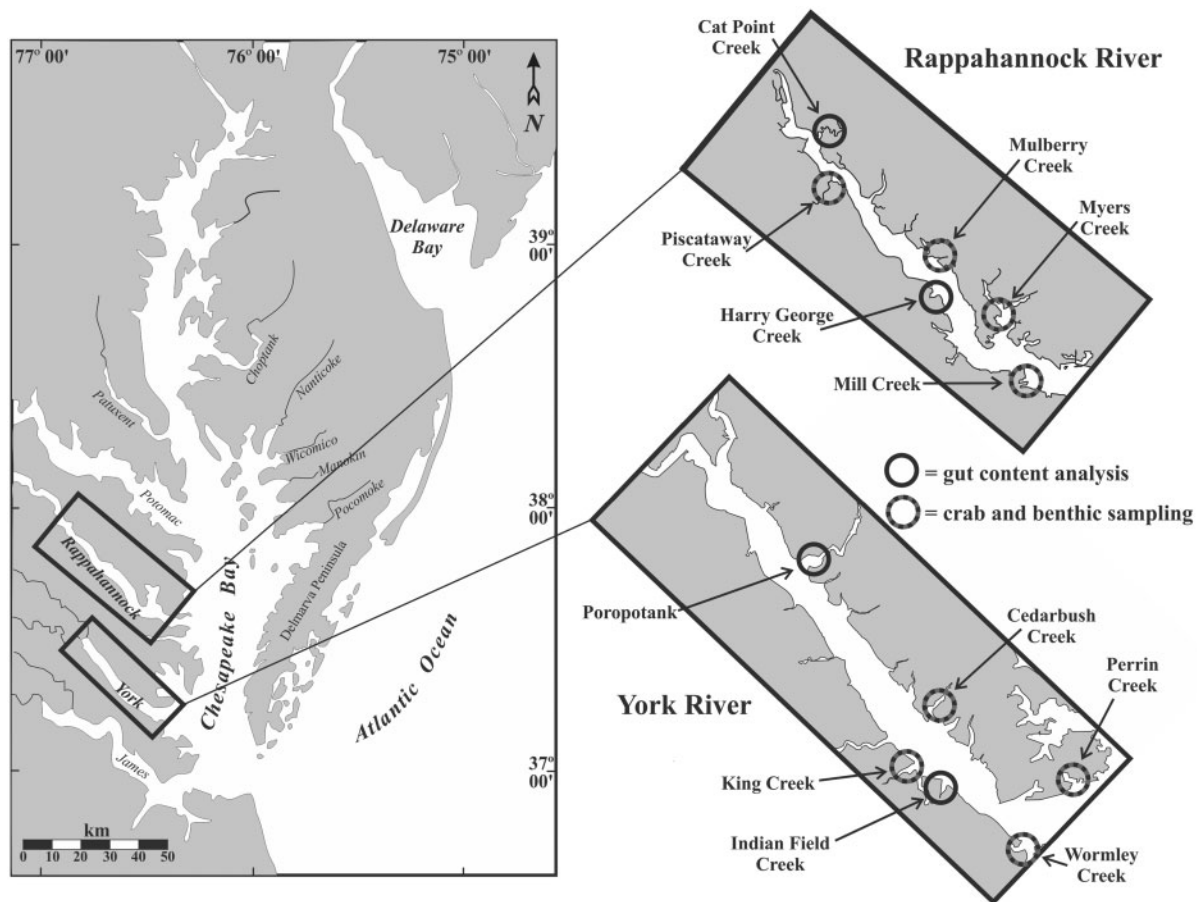


Fig. 1 Study sites at six replicate coves in two sub-estuaries: the Rappahannock and York Rivers, Chesapeake Bay. Black solid circles indicate sites where crabs and other benthos were sampled and from which analyses of gut contents of crabs were performed. Stippled circles indicate sites where crabs and other benthos were sampled, but gut contents not analyzed.

or damaged appendages. Percent fullness of guts was estimated as displacement volume by placing the guts in a graduated cylinder with liquid. Foreguts were dissected out and kept in 70% EtOH until analysis. For analysis, foreguts were teased open with forceps and rinsed with 70% EtOH into a gridded glass Petri dish. Gut contents were allowed to settle in the dish for at least 1 h. After settling, the gut contents were viewed under a dissecting microscope at $\times 40$, and contents were classified into taxa: amphipods, barnacles, clams, copepods, crabs, gastropods, isopods, ostracods, polychaetes, shrimp, plant matter, and detritus (combined into one category), and miscellaneous. Estimations were made of the percent gut contents of each taxon. Abundance percentages of various taxa in juvenile crabs' guts (based on counts) and in the benthos were compared to determine whether prey preferences were indicated. Electivity indices were used to further assess the use of food types in relation to their availability in the environment. Foods that constituted a larger

proportion of the diet than of that available in the environment were considered preferred, whereas, those foods with a lower proportion in the diet than available in the environment were deemed to have been avoided (Lechowicz 1982). Ivlev's Electivity (E), and Ivlev's foraging ratio (FR) were used to determine crabs' selectivity for various types of prey.

For any particular prey item, r_i is a measure of the relative abundance of prey item i in the gut (as a proportion or percentage based on counts), and p_i is the relative abundance of the same prey item in the environment. The equation for Ivlev's electivity is $E_i = (r_i - p_i) / (r_i + p_i)$. The range in values for E varies from -1.0 to 1.0 with negative numbers indicating avoidance of an item, zero indicating random selection, and positive numbers indicating a preference for a given item. For the FR , the equation is $FR = (r_i / p_i)$, with relative abundance of the prey item i in the gut (r_i) versus the abundance in the environment (p_i); the range in values is unlimited, but

those from 0 to 1 indicate negative selection, and those above 1.0 indicate preference for a given item. If r and p are equal for all food types, then the items are selected at random, or in proportion to their occurrences in the environment.

Results

Benthic infaunal analyses

Benthic infaunal communities differed among the 12 sampling coves. Several species of bivalves, polychaetes, amphipods, and other taxa were collected (Table 1). Overall, infaunal densities varied by site from 85 to 1500 individuals/m² (Fig. 2a). In the Rappahannock, the highest densities were at the mid-river sites, with lower densities farthest upriver and downriver, whereas, in the York River, infauna was moderately dense throughout the river. Amphipods tended to be rare in the most downriver sites and ranged in densities from 200 to 1100/m², where abundant. Alternatively, polychaetes tended to occur at higher percentages in downriver sites (Fig. 2b).

For sites where gut contents were analyzed, both York River sites (Poropotank and Indian Field) had relatively high percentages of clams in the benthos compared to sites on the Rappahannock River (Cat Point and Harry George), but the York River had comparatively lower percentages of amphipods at most sites, particularly in Perrin and Wormley Creeks (Fig. 2b). The downriver sites in both the rivers, Harry George and Indian Field Creeks, tended to have higher densities of polychaetes than did upriver sites; this difference was significant at the $\alpha = 0.1$ level (ANOVA; $P = 0.069$). The York River sites tended to have higher densities of polychaetes than did the Rappahannock sites, and this difference was significant at the $\alpha = 0.1$ level ($P = 0.098$). The upriver Rappahannock site, Cat Point Creek, had a lower mean salinity than did the other sites, at 3.4 (Table 1), and the benthic infauna was also unique; there was an average of 70 insects/m² (mainly midge larvae) and very few polychaetes, in contrast to no

insects and a moderate number of polychaetes at the other three sites where gut contents were taken (Fig. 2b and Table 1). In the Rappahannock, the upriver site (Cat Point Creek) had significantly more freshwater insect larvae than did the upriver York site (ANOVA, $P < 0.005$).

Gut-content analyses

Gut contents of juvenile crabs included remains of clams, amphipods, polychaetes, small crustaceans, and vegetation (plant matter plus detritus) (Fig. 3). At Cat Point Creek on the Rappahannock, with salinity of 3.4, clams made up as much as 30% of the gut contents, followed by crustaceans, including copepods and ostracods. At Harry George Creek on the Rappahannock, with a salinity of 13.1, clams again made up the greatest percentage, at almost 10% of the gut contents, along with polychaetes. Crabs in both Rappahannock sites had insects in their guts. At Poropotank Bay on the York River, with a salinity of 12.2, plant matter and detritus comprised ~20% of the crabs' diet. This was not surprising for this site, because the benthic samples included a large volume of detritus along with clams and polychaetes. At Indian Field Creek on the York, with a salinity of 18.9, polychaetes and clams made up the majority of the crabs' diet.

The taxa making up the largest percentages in the guts were generally those making up the majority of taxa in the infauna. With increases in salinity (i.e., in Harry George and Indian Field Creeks), the percentages of polychaetes in the diet increased. In contrast, amphipods were not in large percentage of gut contents. Where crabs were found in the guts, mud crabs, not conspecific blue crabs, were the species consumed. Only one crab had any evidence of potential cannibalism, a blue crab shell in its gut.

In general, gut contents included the same items that were found in the benthos in each particular cove (although small crustaceans, plant matter, and detritus were not quantified in the benthos). For example, at the site with the lowest salinity, Cat Point Creek, insect larvae were found in the benthos and in

Table 1 Salinity, density of various benthic organisms, and locations of sites at which samples were collected in Chesapeake Bay.

River	Cove	Position of cove in river	Mean salinity	Mean number per square meter of:				
				Clams	Amphipods	Isopods	Insects	Polychaetes
York	Poropotank Bay	Upper	12.2	362	252	12	0	62
Rappahannock	Cat Point Creek	Upper	3.4	102	655	9	70	5
York	Indian Field Creek	Lower	18.9	245	39	0	0	126
Rappahannock	Harry George	Lower	13.1	114	505	12	0	67

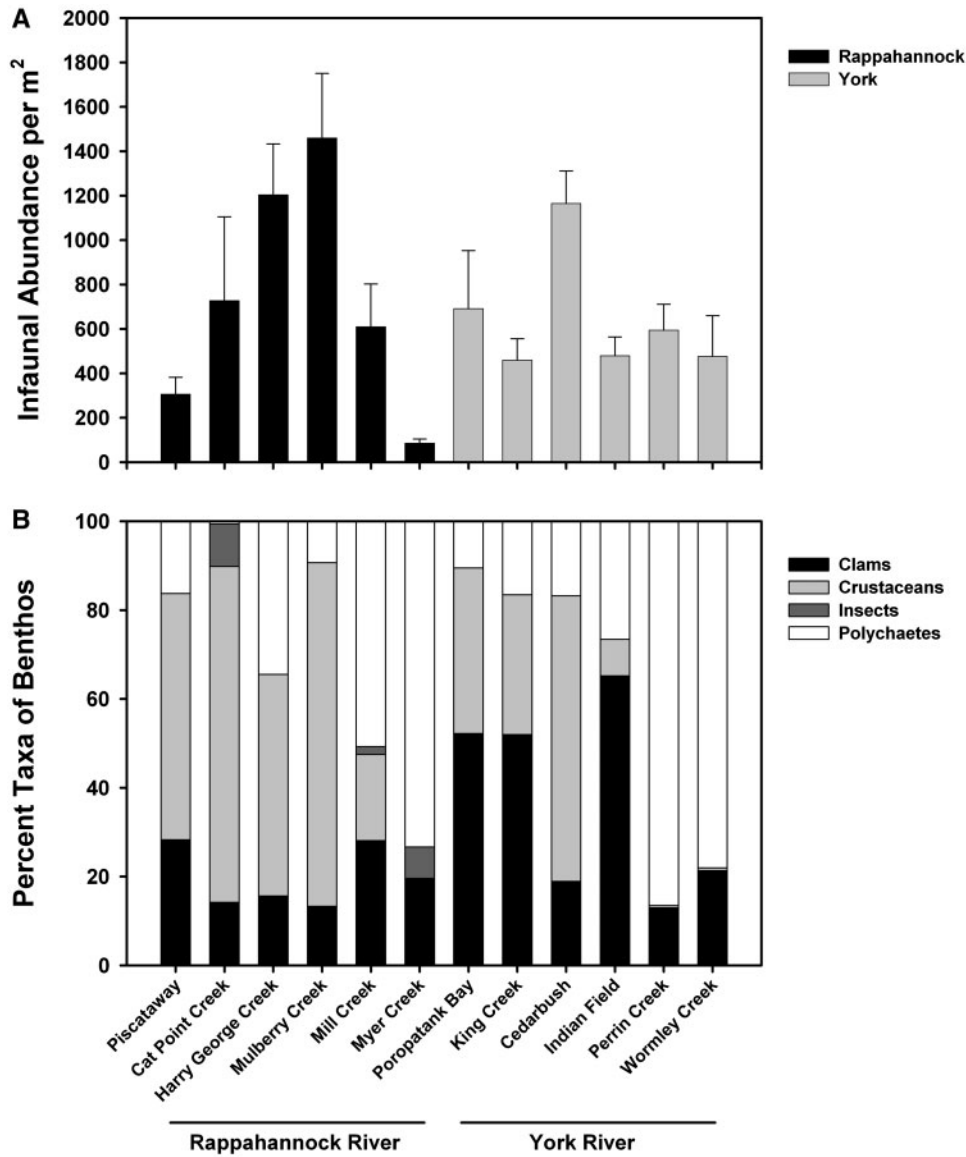


Fig. 2 (A) Mean density (± 1 SE) of benthic infauna in six coves each in the Rappahannock and York Rivers. Sites are arranged on the x-axis according to salinity from lowest values (farthest left) to highest values (farthest right); black bars = Rappahannock River, gray bars = York River. (B) Percent representation of major infaunal taxa including clams, crustaceans, insects, and polychaetes, for each cove sampled.

the foreguts of crabs. There was a significant positive relationship between numbers of polychaetes in the benthos and the percentage of polychaetes in crabs' foreguts (Regression, $P=0.002$, $R^2=99.3\%$; Fig. 4); correlations between gut contents and benthos of other taxa were not significant.

Dietary preferences

If blue crab juveniles feed opportunistically or randomly, there should be no preference for particular dietary items, but rather the same percentages of benthic taxa should occur in the environment as in gut contents. However, there was a preference for

clams in the Rappahannock, with the percentage of clams in the guts exceeding the percentage found in the environment (Fig. 5). In these two sites, polychaetes were rare, and the percentage of clams in the environment was much greater than that of polychaetes (Fig. 5). In contrast, in the York, where abundances of clams were high, there was a higher percentage of clams in the environment versus in the crabs' guts. In Cat Point Creek, polychaetes were rare in the environment, crabs fed on clams instead, and the percentage of clams in the guts rose to $>30\%$ in some cases. At all sites, amphipods in the environment made up a much larger percentage of the fauna

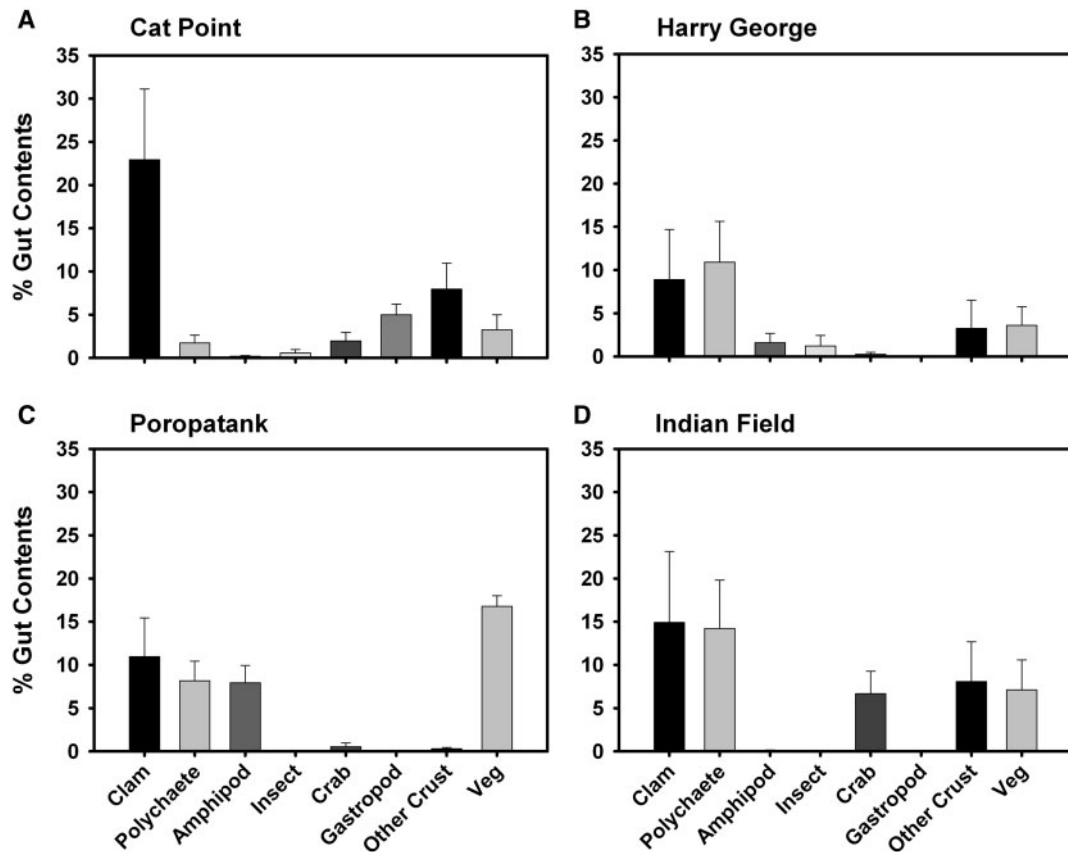


Fig. 3 Gut contents of crabs (\pm SE) from each of the four coves sampled. The major taxa found in the guts were: clams, polychaetes, amphipods, insects, crabs, gastropods, other crustaceans (including shrimp, ostracods, and copepods), and vegetation (plant matter plus detritus) (percent miscellaneous not shown). Patterns in the four sampling sites are listed separately: (A) Cat Point, (B) Harry George, (C) Poropotank, and (D) Indian Field.

in the environment than they did in crabs' foreguts, suggesting that amphipods are not a favored food (Fig. 5).

The two indices of dietary preferences were in agreement with each other (Table 2). Both were used, because each uses a different algorithm to calculate electivity, each has strengths and weaknesses (Lechowicz 1982), and two indices will allow more potential for comparisons with other studies, where only one or the other index is used. There was a preference for clams at Rappahannock, but not at York sites, a preference for polychaetes at all sites, and lack of preference for amphipods at all sites.

Crabs and clams

Clams made up the majority of the biomass (85–94%); thus, we compared crab densities with clam biomass to examine whether crabs were responding to the biomass (grams carbon) of a major food source available in the benthos. Some of our lowest crab densities occurred at sites where there was low clam biomass (e.g., Cat Point and Wormley Creeks) (Fig. 6). In contrast, there were

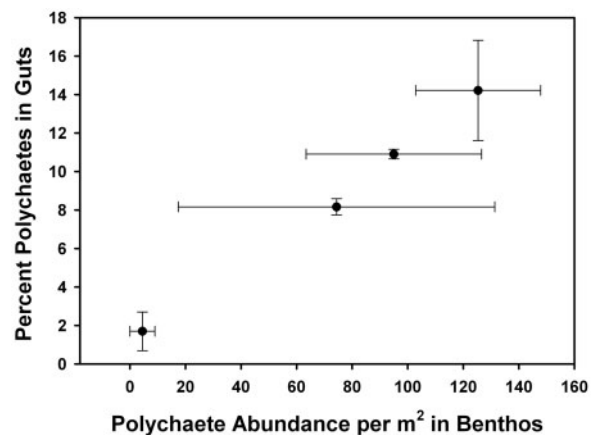


Fig. 4 Percent of polychaetes in the foreguts of crabs (\pm SE) versus mean number of polychaetes per square meter (\pm SE) in the benthos for the four sites for which analyses of crabs' gut contents were conducted.

sometimes low densities of crabs where clam biomass was high (e.g., Harry George and King Creeks). In general, there tended to be more crabs at downriver sites than at upriver sites in both rivers.

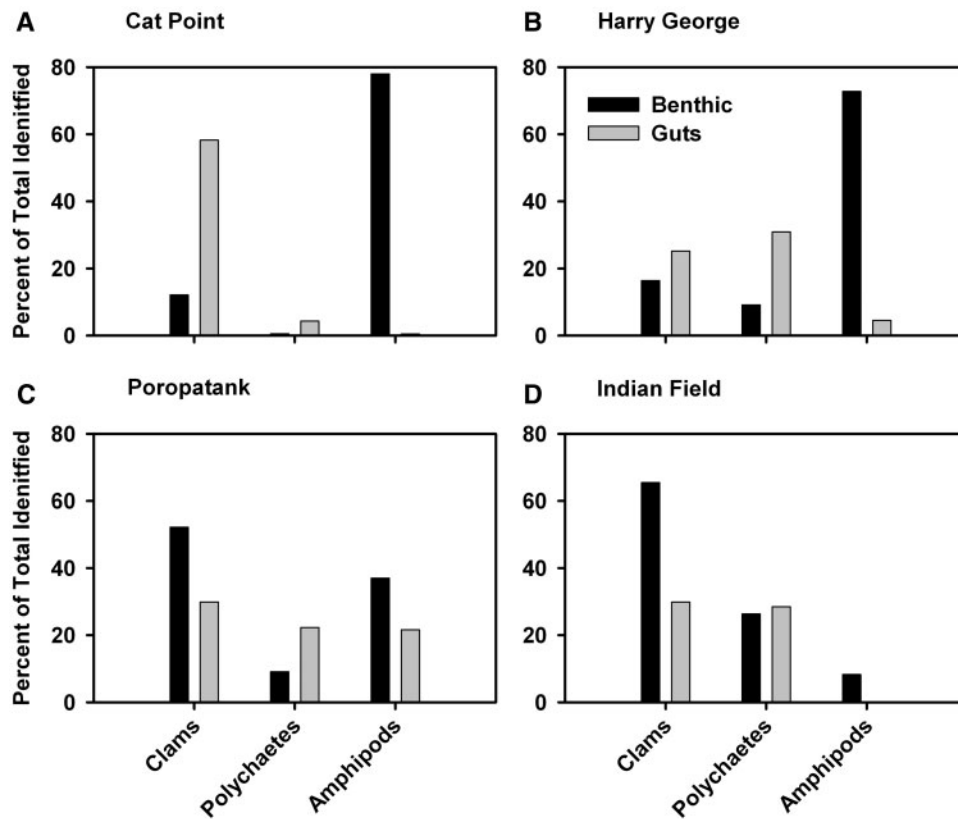


Fig. 5 Percent representation of taxa in the total gut contents identified from crabs versus percent representation of taxa identified in the benthos, with prey preference for a particular taxon indicated when the percentage in the guts exceeds the percentage in the benthos; black bars = benthos, gray bars = gut contents. Patterns in the four sampling sites are listed separately: (A) Cat Point, (B) Harry George, (C) Poropotank, and (D) Indian Field.

Consequently, there was no correlation between clam biomass and crab density (regression $R^2=5.9\%$; $P=0.44$). Adding total infauna improved the relationship (regression $R^2=21.7\%$, $P=0.12$).

Discussion

There were abundant benthic resources for crabs at all sites studied in the Rappahannock and York Rivers, and benthic infauna varied among sites. Much of the variation was likely due to changes in salinity (e.g., freshwater insect larvae at the site with lowest salinity). Although infaunal densities at all sites were high, the number of clams in the York River was much greater than that in the Rappahannock. The York River has been defined as a productive system compared to other tributaries of the Chesapeake Bay (Seitz and Lipcius 2001); thus, it is not surprising that we saw high densities of high-biomass clams in the system. When amphipods were present, their densities were high; typical densities were $800/m^2$ (Lewis and Stoner 1983).

The gut contents of the crabs revealed that small juvenile blue crabs (<40 mm CW) are opportunistic feeders, like their larger conspecifics (Laughlin 1982;

Table 2 Ivlev's electivity (E) and FR indices for prey preference for the three main food items at the four sites where gut-content analyses were conducted.

Location	Clams	Amphipods	Polychaetes
Rappahannock River			
Cat Point Creek			
E	0.65 (+)	-0.98 (-)	0.78 (+)
FR	4.81 (+)	0.01 (-)	8.04 (+)
Harry George Creek			
E	0.21 (+)	-0.88 (-)	0.54 (+)
FR	1.52 (+)	0.06 (-)	3.37 (+)
York River			
Poropotank River			
E	-0.27 (-)	-0.26 (-)	0.41 (+)
FR	0.57 (-)	0.58 (-)	2.44 (+)
Indian Field Creek			
E	-0.37 (-)	-0.96 (-)	0.04 (+)
FR	0.45 (-)	0.02 (-)	1.08 (+)

Equations for the indices are given in the 'Methods' section of the text. For E , positive values indicate selection for an item (+) and negative values, selection against (-). For FR , values ≥ 1.0 indicate selection for an item (+), whereas values $0-1$ indicate selection against an item (-).

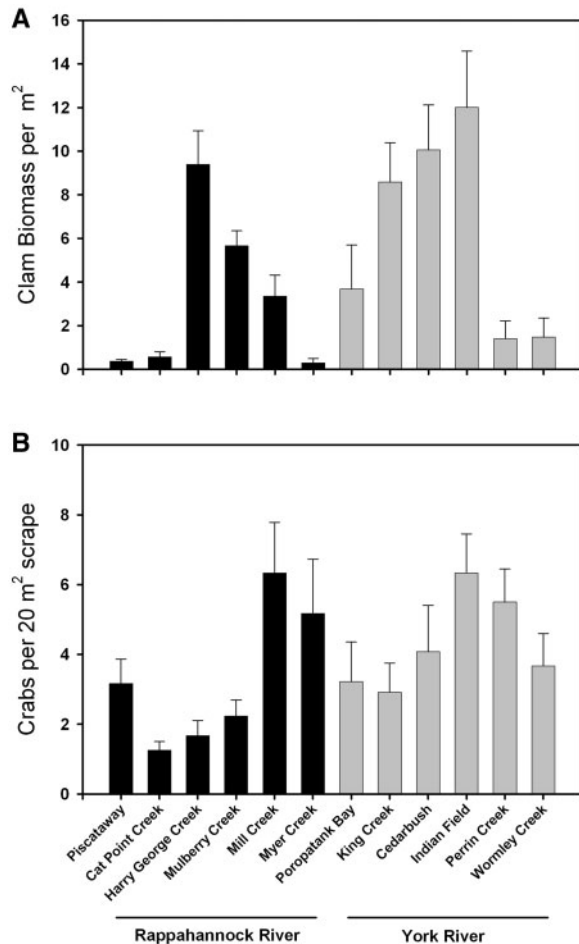


Fig. 6 (A) Mean clam biomass (g AFDW) per square meter + SE, and (B) crab density per 20 m² scrape sample + SE. Sites are arranged on the x-axis by salinity with lowest values (farthest left) to highest values (farthest right). Black bars = Rappahannock River; gray bars = York River.

Hines et al. 1990; Mansour and Lipcius 1991; Mansour 1992). This can be seen clearly in the wide diversity of taxa found in their guts. The large percentage of clams, polychaetes, and other crustaceans is in accord with previous studies on adult blue crabs in the system (Hines et al. 1990; Mansour 1992), although relative percentages of the various items differed for the smaller juvenile crabs. We were able to detect a dietary preference for polychaetes and sometimes for clams, but avoidance of amphipods.

The percentage of clams in crabs' guts typically remained ~30%, except in instances when there were very few polychaetes to serve as alternative prey, for example, in Cat Point Creek, where the percentage of clams in guts increased. In habitats where densities of clams are highest, the growth of blue crabs is elevated (Seitz et al. 2003, 2005); thus,

this food source is key to the growth of juvenile crabs. We know that adult blue crabs can consume 7 clams/day (Hines et al. 1990) and they will stop foraging for clams when clam densities drop to 12–50 clams/m² (Clark et al. 1999a, 1999b; Seitz et al. 2001); however, crabs may also have a maximum percentage of clams that they prefer to obtain, consuming other taxa that may provide additional sources of nutrients (Phil et al. 1992). Clam densities remained above a low-density threshold of 12–50/m² (Eggleston et al. 1992; Seitz et al. 2001) in all except one of our experimental coves, suggesting that these shallow-water coves have abundant food for juvenile crabs.

The main difference in the gut contents of the small juvenile crabs examined here, relative to larger juveniles and adults reported previously in the literature (Mansour 1990; Hines et al. 1987), is that generally there was a larger percentage of polychaetes, and little evidence for cannibalism of conspecifics. Although, one juvenile crab had an apparent blue crab shell in its gut; however, this may not have been cannibalism, as crabs sometimes consume their own shells after molting (R. Lipcius, personal communication). Although cannibalism is common in blue crabs, and it can account for a large percentage of juvenile blue crab mortality (see Heck and Coen 1995; Heck and Spitzer 2001; Heck et al. 2001), the potential for cannibalism is reduced when crab densities in unvegetated habitats are low (0.1–1/m²) (Posey et al. 2005; Lipcius et al. 2005, 2007), as in our Rappahannock and York River sites (Fig. 6). Some of the taxa found in crabs' guts were not found in our benthic samples. This is likely due to the sieve size used in the field (1 mm), which was too large to retain the meiofauna that the smallest juvenile crabs were eating (e.g., ostracods).

The selectivity indices revealed that some prey items are preferred and others not. The tight correlation between polychaetes in the benthos and polychaetes in crabs' guts, along with the selectivity indices, suggest that small juvenile crabs have a feeding preference and that polychaetes are a major food resource in these unvegetated nursery habitats. On the other hand, there was a much higher abundance of amphipods found in the benthos than in the guts; thus, crabs either tend to avoid eating them or are unable to do so. The benthic samples were taken 1–2 weeks after the crab samples were taken, and amphipods are mobile, short-lived, and ephemeral. It is common in the Chesapeake Bay system for amphipods to have short periods of relatively high abundance, especially in the early summer (Seitz et al. 2008). It is possible that, when the crab samples

were taken, the amphipods were in low abundance, and that they subsequently had a population spike that resulted in the large number of individuals found 2 weeks later in the benthic samples. Another possibility is that amphipods are more mobile than many other infauna and, thus, are potentially more difficult for crabs to capture and eat (Corona et al. 2000).

The increased crab densities in the more downriver coves of each river was likely a consequence of being closer to the mouth of Chesapeake Bay where crab post-larvae re-enter after spawning (Lipcius and Van Engel 1990). The weak evidence of bottom-up control of crabs by benthos may have been because our samples were taken in mid-summer, after initial benthic densities had been reduced through predation (Seitz and Lipcius 2001; Seitz et al. 2008).

We show that juvenile blue crabs do not consume prey in proportion to availability, but instead exhibit some prey selection, thereby potentially altering relative abundances of benthic species. It is clear that crabs are consuming infauna found in the benthos in their local area. We saw relationships between the benthos and the diet of small juvenile blue crabs, when we compared the gut contents to the density of the benthic infauna. Although these small crabs have a varied diet, selectivity was evident.

The relative value of a habitat can be defined by high survival of prey and ready availability of food (Coen et al. 1981; Minello and Zimmerman 1991; Kenyon et al. 1997), but the physical complexity of the habitat typically had been the focus of previous studies (Coen et al. 1981; Heck and Thoman 1984; Holmlund et al. 1990; Everett and Ruiz 1993). Food availability is key in contributing to the value of unvegetated nursery habitats. The relative value of estuarine habitats can be determined through investigations of the resources present in various locations and from study of predator-prey interactions. Thus, understanding the prey preferences of juvenile crabs is important for preserving the unvegetated nursery habitats that hold highly productive infaunal communities.

Acknowledgments

Thanks for collaborations with the University of Maryland Biotechnology Institute, Center of Marine Biotechnology (Y. Zohar, A. Place, O. Zmora, and staff), Smithsonian Environmental Research Center (A. H. Hines, E. Johnson, and staff), and North Carolina State University (D. Eggleston) as well as contributions from many VIMS students and staff,

and Virginia Governor's School High School interns. This is contribution number 3168 from the Virginia Institute of Marine Science.

Funding

Senator Barbara Mikulski and NOAA, Chesapeake Bay Office; the National Science Foundation (grant for M.J.W.); SICB and the Crustacean Society.

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