

Abstract—Blue (*Callinectes sapidus*) (Portunidae), lady (*Ovalipes ocellatus*) (Portunidae), and Atlantic rock (*Cancer irroratus*) (Cancridae) crabs inhabit estuaries on the northeast United States coast for parts or all of their life cycles. Their distributions overlap or cross during certain seasons. During a 1991–94 monthly otter trawl survey in the Hudson-Raritan Estuary between New York and New Jersey, blue and lady crabs were collected in warmer months and Atlantic rock crabs in colder months. Sex ratios, male:female, of mature crabs were 1:2.0 for blue crabs, 1:3.1 for lady crabs, and 21.4:1 for Atlantic rock crabs.

Crabs, 1286 in total, were subsampled for dietary analysis, and the dominant prey taxa for all crabs, by volume of foregut contents, were mollusks and crustaceans. The proportion of amphipods and shrimp in diets decreased as crab size increased. Trophic niche breadth was widest for blue crabs, narrower for lady crabs, and narrowest for Atlantic rock crabs. Trophic overlap was lowest between lady crabs and Atlantic rock crabs, mainly because of frequent consumption of the dwarf surfclam (*Mulinia lateralis*) by the former and the blue mussel (*Mytilus edulis*) by the latter. The result of cluster analysis showed that size class and location of capture of predators in the estuary were more influential on diet than the species or sex of the predators.

The Hudson-Raritan Estuary as a crossroads for distribution of blue (*Callinectes sapidus*), lady (*Ovalipes ocellatus*), and Atlantic rock (*Cancer irroratus*) crabs

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The blue crab (*Callinectes sapidus*) (Portunidae), the lady crab (*Ovalipes ocellatus*) (Portunidae), and the Atlantic rock crab (*Cancer irroratus*) (Cancridae) are the largest and most common brachyuran crabs inhabiting both estuaries and inner continental shelves of the northeast coast of North America. The centers of abundance of these three species overlap in estuarine and coastal waters from New York to Virginia, although their ranges along the northwest Atlantic coast are broad. The blue crab is nearly always an estuarine resident, except during its larval stages, and ranges from the waters off Nova Scotia to Argentina (Williams, 1984). The northernmost estuaries where the species is abundant enough for commercial harvest are in New Jersey and New York (Briggs, 1998; Stehlik et al., 1998). The lady crab is distributed from the waters off Prince Edward Island to those off Georgia but it is most numerous from Georges Bank to Cape Hatteras (Williams, 1984). The Atlantic rock crab (referred to as “rock crab” in this article) is distributed in waters from off Labrador to Florida but is most common in estuaries from Nova Scotia to Virginia (Williams, 1984; Stehlik et al., 1991). Seasonal migrations are common for all three species. Although Jonah crabs (*Cancer borealis*) are present on the continen-

tal shelf, they are not included in the present study because they are rare within the Hudson-Raritan Estuary where our study was conducted.

Physiological tolerances and habitat preferences of these crabs have been extensively studied. In eastern United States estuaries the blue crab occurs in shallow to deep, sandy to muddy estuaries and tributaries along marsh edges, and in seagrass (Van Engel, 1958; Milliken and Williams, 1984; Hines et al., 1987; Wilson et al., 1990; van Montfrans et al., 1991; Rountree and Able, 1992). In the colder portions of its range, it becomes less active at about 15°C (Leffler, 1972), and buries itself, without eating, when the temperature is <5°C (Auster and DeGoursey, 1994). It survives at 34°C (Leffler, 1972) and at salinities from 0 to 50 ppt (Guerin and Stickle, 1992). The lady crab is most common on sand substrates (Williams, 1984). It is present on the inner continental shelf from off Cape Cod to off the Carolinas throughout the year (Stehlik et al., 1991). Its temperature tolerance is unknown, but it does not survive in <21 ppt (Birchard et al., 1982). The rock crab’s optimum temperature range for activity is 14–22°C (Jeffries, 1966); thus the species avoids high summer temperatures. It is found on many substrates, such as sand, mud, bare rock, cobble, and algal beds.

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The diet of the blue crab is generally mollusks, crabs, and fish, depending on crab size (Virnstein, 1977; Laughlin, 1982; Ryer, 1987; Hines et al., 1990). The diet of the lady crab is mainly bivalves such as *Mya arenaria* and *Spisula solidissima*, and some crustaceans (McDermott, 1983; Ropes, 1989; Stehlik, 1993). The rock crab consumes mollusks, small crustaceans, crabs, urchins, and fish (Scarratt and Lowe, 1972; Drummond-Davis et al., 1982; Hudon and Lamarche, 1989; Ojeda and Dearborn, 1991; Stehlik, 1993). In some of the aforementioned studies these crabs have been considered opportunistic and as such may be competitors for the same prey taxa. However, differences in maximum body size, chela structure, and the presence or absence of swimming appendages among blue, lady, and rock crabs indicate that they may have differences in diet (Warner and Jones, 1976; Williams, 1984).

Within the Hudson-Raritan Estuary, blue, lady, and rock crabs are all abundant, providing an opportunity to study partitioning of habitat and food resources by these species. The objectives of our study were to determine the temporal and spatial overlap of blue, lady, and rock crabs in this estuary and to differentiate the composition of their diets by the species, sex, and size of predators, and by location of collection.

This study has potential practical applications. Resource managers could use the results to consider when and where crabs depend upon certain locations to complete their life cycles, if dredging, filling, or sanctuaries were proposed. Dietary analysis of these crabs could indicate if they are a cause of mortality for young stages of commercially important species. For instance, the northern quahog (*Mercenaria mercenaria*) and the soft-shell clam (*M. arenaria*) recently have supported and presently support commercial and recreational harvests in the Hudson-Raritan Estuary (MacKenzie, 1990; 1997) and when young these clams are consumed by crabs. The blue crab supports lucrative fisheries in the estuary (Stehlik et al., 1998) and predation by various species of crabs upon blue crab juveniles may affect recruitment.

Materials and methods

Study area

The Hudson-Raritan Estuary, bordered by New Jersey on the south and Staten Island and Brooklyn, New York, on the north (Fig.1), has a surface area of about 280 km². The Hudson, Raritan, and Navesink-Shrewsbury rivers flow into the estuary from the north, west, and south, respectively. The study area is bounded on the west by the 74°15' longitude line; on the east by a line between the northeast corner of Sandy Hook, NJ, and the tip of Rockaway Point, NY; and on all sides by the 3 m contour. The area was divided into nine strata according to physiographic features (Wilk et al.¹). Sandy-bottom strata included Sandy Hook Bay (stratum 1), Raritan Bay south of Raritan Channel (stratum 2), and Lower Bay north of Raritan Channel (stratum 3). Eastern

strata of more irregular depths were Romer Shoals (stratum 4), East Bank between Ambrose Channel and Rockaway, NY (stratum 5), and Gravesend Bay at the mouth of the Hudson River (stratum 6). Three strata were channels: Ambrose (stratum 7), Chapel Hill (stratum 8), and Raritan (stratum 9). Raritan Channel is maintained at a depth of 13.7 m, and the average depth of adjacent nonchannel stations is 7.1 m. Gravesend Bay is more than 13 m deep in its center.

The bottom of the Hudson-Raritan Estuary consists mostly of soft sediments (Jones et al., 1979; Coch, 1986; Wilber²). The substrates in semi-sheltered southern strata 1 and 2 are predominantly fine sand, silt, and clay; those of stratum 3 are mainly medium sand, with a mixture of sand, silt, and clay near channels; those of ocean-exposed strata 4, 5, 6, and 7 are gravel, sand, silt, broken shell, and have beds of blue mussels (*Mytilus edulis*). The bottom of Ambrose Channel is silt and clay near its head and fine sand toward the ocean. The sediments of the other two channels, and their immediate borders, are sand, silt, and clay. Based on physiographic form, temperature ranges, and sediments, strata 1, 2, 3, 8, and 9 were considered inner or riverward strata, whereas 4, 5, 6, and 7 were considered outer or oceanic-influenced strata.

Collections and analyses

Crabs were collected during monthly otter trawl surveys of the Hudson-Raritan Estuary from June 1991 to December 1994 (Wilk et al.¹). Sampling was done from the 18-m research vessel *Gloria Michelle* by towing a 9.1-m otter trawl with a chain sewn to the bottom opening, and a 76-mm mesh net with a 51-mm codend liner. Wooden trawl doors were deployed to spread open the net. The net was towed once per station for 10 min at 5.6 km/h to cover a distance of approximately 1 km. All tows were made between 8 am and 2 pm. During 1991, fixed stations were towed (number of stations in 1991: 10 in June, 8 in July; 11 in August; 18 in September; 22 in October; 23 in November; 34 in December). Beginning in 1992, a stratified random sampling design was used, in which the nine strata were divided into 190 blocks of approximately 0.5 minutes latitude by 0.5 minutes longitude. Each month, 40 blocks were randomly sampled without replication, and the number of blocks in each stratum was proportional to the area of the stratum. Because of conflicting schedules, the vessel was not available in May or September 1992 or 1994. Temperature and salinity of water 1 m above the bottom were measured after each tow. During 1991

¹ Wilk, S. J., E. M. MacHaffie, D. G. McMillan, A. L. Pacheco, R. A. Pikanowski, and L. L. Stehlik. 1996. Fish, megainvertebrates, and associated hydrographic observations collected in the Hudson-Raritan Estuary, January 1992–December 1993, 95 p. Northeast Fish. Sci. Cent. Ref. Doc. 96-14, NMFS, Woods Hole, MA.

² Wilber, P. 2000. Unpubl. data. Coastal Services Center, National Ocean Survey, NOAA, 2234 Hobson Avenue, Charleston, SC, 29405.

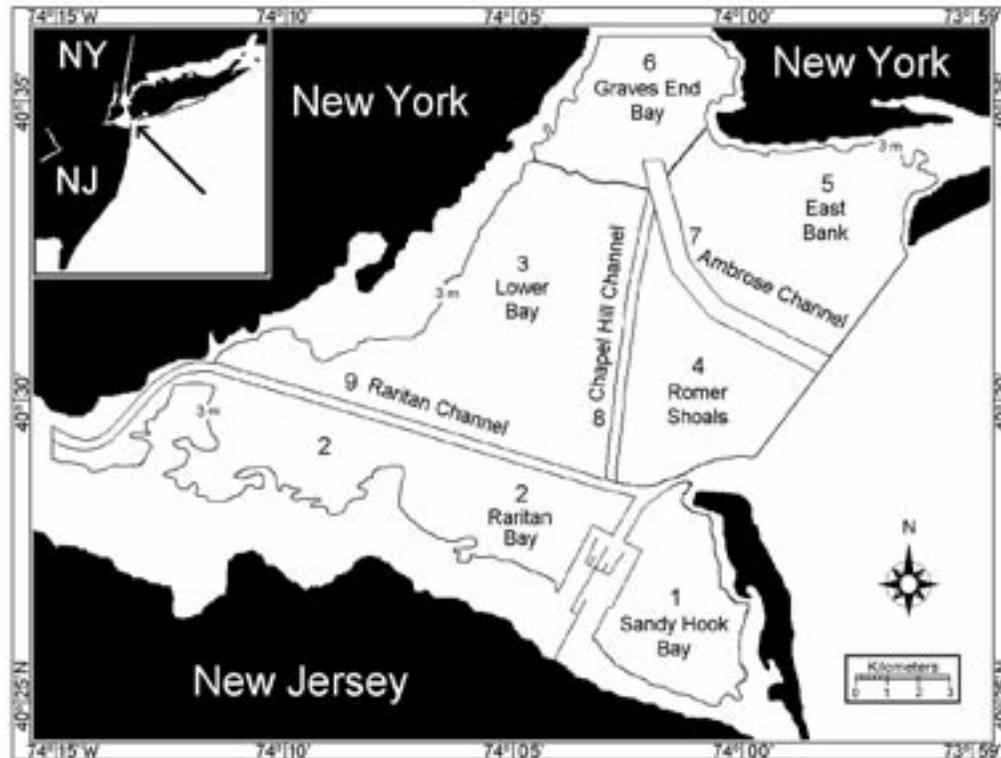


Figure 1

Hudson-Raritan Estuary, from New York to New Jersey, with 3-m contour, drawn boundaries, and the nine strata of the Hudson-Raritan Estuary trawl survey. The inset shows the location of the estuary on the United States coast off New York and New Jersey.

and 1992 temperature and salinity were determined by using a Niskin bottle, a thermometer, and an induction salinometer. Beginning in January 1993 a Hydrolab® Surveyor III multiprobe was used.

Fish and large invertebrates were counted, weighed, and measured (± 1.0 cm), and sexes of the crabs were recorded. Catch per unit of effort or number per tow was used to estimate relative abundance. Crabs were measured by carapace width (CW) between the tips of the anterolateral teeth. Specimens were saved for dietary analysis from June 1991 through June 1992. These specimens were measured (± 1.0 mm) and molt stages were classified as intermolt (hard-shelled), premolt (new skin separates easily from inside the carapace), soft-shelled, or postmolt (early and late papershell).

For some analyses, we separated crabs into two size classes based on maturity because preferred habitats, tolerances, or reproductive needs may be different for different life stages. Most researchers use a carapace width at which $\geq 50\%$ or $\geq 80\%$ of the individuals are mature (produce viable eggs or sperm) as a separation boundary. Maturity in males is determined by dissection or by allometric changes in growth of appendages (Hartnoll, 1978; Block and Rebach, 1998; de Lestang et al., 2003). Most female blue crabs in our study area and in Virginia had completed their pubertal molt and thus could reproduce by 12 cm CW (Van Engel, 1958;

Fisher, 1999; Stehlik, unpubl. data). In Virginia, 80% of male blue crabs are mature by 11.9 cm (Van Engel, 1990). In lady crabs from the New York coast, nearly all males are mature at ≥ 6 cm, and females at about 5 cm (Briggs and Grahn³). In the middle-Atlantic portion of their range, male rock crabs mature at 5 cm (Haefner, 1976) and some females < 5 cm bear eggs (Reilly and Sails, 1978). We chose the following CW boundaries for $\geq 80\%$ maturity: blue crabs, ≥ 12 cm both sexes; lady crabs, ≥ 5 cm both sexes; and rock crabs, males ≥ 5 cm and females ≥ 4 cm.

Data on blue, lady, and rock crabs from NEFSC (Northeast Fisheries Science Center, NOAA) fall bottom trawl surveys on the northeast United States continental shelf, 1992–94, were used to expand the geographical viewpoint of our study. The presence of each species in each tow was plotted to show distributions in a representative year, 1992. The plots were made with Surfer® (version 6, Golden Software Inc., Golden, CO). Methods on the trawl surveys are described elsewhere (Azarovitz, 1981).

³ Briggs, P. T., and C. M. Grahn. 1996. Aspects of the fishery biology of the lady crab (*Ovalipes ocellatus*) in New York waters, 8 p. An in-house paper, New York State Department of Environmental Conservation, 205 North Belle Mead Road, Suite 1, East Setauket, NY, 11733.

Foregut contents were analyzed as in Stehlik (1993). The foregut of each crab was removed and preserved in 70% ethanol. After opening the foregut, we estimated fullness of the gut (from 0% to 100%) visually, and prey items were identified to the lowest possible taxon. The proportion of the total volume of the foregut contents contributed by each prey taxon was estimated visually—a less labor-intensive modification of the methods of Williams (1981), Hyslop (1980), and Steimle et al. (1994). The volume of each prey taxon was multiplied by the percentage of gut fullness. Combining all foreguts, the volumes of prey taxa were listed in descending order. The top 12 prey categories on the list (with the exception of “unidentified” and nonexclusive categories such as Mollusca) were selected for use in most of the subsequent analyses. Foreguts that did not contain prey in any of the 12 categories were dropped from numerical analyses.

The dietary data were grouped in turn by predator species, sex, size class, and collection stratum, and the mean percentage volumes of each of the 12 mutually exclusive prey categories were calculated. For graphic representation of ontogenetic differences in diet, blue and rock crabs were grouped for convenience into 20-mm CW classes, and lady crabs were grouped in 10-mm CW classes because of their smaller size range. For numerical analyses, two maturity classes were used. We used Mann-Whitney tests to compare diets between sexes within predator species and between maturity stages within predator species. The test statistic was a chi square approximation.

Group average cluster analysis was used to graph the separation of diets by species, sexes, maturity stages, and strata by using the 12 prey categories as dependent variables. A Bray-Curtis similarity matrix was generated for each of the groupings, cluster analysis was performed by using Systat® (version 10, SPSS Inc., Chicago, IL), and dendrograms were generated by using the Bray-Curtis values as distance measures (Romesburg, 1984; Marshall and Elliott, 1997). A percent similarity level was chosen *a posteriori* that generated a reasonable number of classes.

Analysis of similarity (ANOSIM) was used to test for statistical significance of dietary differences among predator species and for sexes within species. Analysis of dissimilarity (SIMPER) was used to determine which prey taxa contributed most to the differences between species pairs (Clarke and Warwick, 1994).

Spatial, temporal, and trophic niche breadth and overlap indices were calculated from the number per tow (1992–94) and diets (June 1991–June 1992) of each crab species and sex. Temporal niche and overlap were calculated by month for combined years. Female rock crabs were dropped from consideration of trophic niche overlap due to low sample size.

Niche breadth (Colwell and Futuyama, 1971; Marshall and Elliot, 1997) is a measure of exploitation within a particular resource (for example, substrates or prey taxa within an estuary by a species). Niche breadth values are relative and can be compared only within one study. The highest value corresponds to the

broadest niche, or to habitat or a diet generalist rather than to a specialist. Niche breadth (B) was calculated by the formula of Colwell and Futuyama (1971), and modified for measuring trophic niche breadth according to Hines et al. (1990):

$$B = 1 / \sum (p_{kj})^2 \text{ from } j = 1 \text{ to } n,$$

where $p_{kj} = N_{kj} / Y_k$ (p_{kj} is the proportion of crabs of species k associated with resource state j);

j = resource states (months, strata, diet categories);

n = number of resource states;

N_{kj} = catch per tow of species k at resource state j ; and

Y_k = catch per tow of species k over all resource states.

When trophic niche breadth was calculated,

N_{kj} = total volume of diet category j consumed by predator k ;

Y_k = total volume of all diet categories consumed by predator k .

Niche overlap is a measure of the joint use of a resource by two species (Colwell and Futuyama, 1971). Niche overlap (C_{hi}) between species h and i was calculated by the following formula (Colwell and Futuyama, 1971; Hines et al., 1990):

$$C_{hi} = 1 - 0.5 \left(\sum |p_{hj} - p_{ij}| \right) \text{ from } j = 1 \text{ to } n,$$

where p_{hj} and p_{ij} are calculated in the same manner as p_{kj} above.

This index ranges from 0 (no overlap) to 1 (complete overlap) and is independent of sample size and differential resource availability (Eggleston et al., 1998).

Results

Temperature and salinity

Bottom water temperature in the study area followed a temperate seasonal cycle. The range during 1992–94 was from 0° to 26.6°C. Using the monthly mean temperature below or above 10°C, and migration cycles of the crabs, we grouped the months into two seasons: winter (November through April) and summer (May through October). The mean temperature in the winter months 1992–94 was 5.5°C, and that for summer was 18.9°C. Temperature nearest the estuary mouth was usually a few degrees lower in summer months and higher in the winter months each year, compared with the average throughout the estuary.

Bottom salinity in the study area ranged from 15.0 to 33.5 ppt. The majority of stations had salinities between

Table 1

Species, sex, number collected (*n*), and sex ratio (SR, male:female) of all crabs collected during the Hudson-Raritan Estuary trawl survey, June 1991–December 1994. Maturity boundaries are explained in the text. For the subsample examined for stomach contents (June 1991–June 1992), number (*n*), number of non-empty stomachs, and the mean and range of carapace width (CW, mm) are presented.

Crab species, sex	<i>n</i> collected	SR (m:f) immature	SR (m:f) mature	<i>n</i> stomachs opened	<i>n</i> not empty	Subsample CW	
						Mean	(Range)
Blue, male	2803	1:1.13	1:1.97	167	120	112	(35–185)
Blue, female	4816			272	208	129	(21–169)
Lady, male	14,903	1:1.30	1:2.12	173	124	60	(34–88)
Lady, female	29,681			255	228	55	(30–89)
Atlantic rock, male	15,503	4.65:1	21.43:1	400	281	92	(28–130)
Atlantic rock, female	822			19	14	51	(29–80)
Total	68,528			1286	975		

25 and 30 ppt. Salinity decreased with distance from the bay mouth and in any one month, the difference in salinity between stations at the estuary mouth and those at the westernmost part of the study area was approximately 5–10 ppt.

Catch by species, size, and sex

From June 1991 through December 1994, more than 68,000 blue, lady, and rock crabs were caught in 1200 otter trawl tows (Table 1). Other mega-invertebrates in the tows included the northern moonsnail (*Euspira heros*), the horseshoe crab (*Limulus polyphemus*), the American lobster (*Homarus americanus*), the portly spider crab (*Libinia emarginata*), the flatclaw hermit crab (*Pagurus pollicaris*), mud crabs (Xanthidae), and the sea star (*Asterias* sp.)

Catch per tow of crabs by size class increased as they became large enough to be retained by the mesh of the net (Fig. 2). Abundances of female blue and lady crabs in the study area were greater than those of the males. In rock crabs, males predominated (Table 1). Immature blue and lady crabs had sex ratios fairly close to 1:1 (male:female). Sex ratio in mature blue crabs, however, was 1:1.97, and in mature lady crabs, 1:2.12. In all sizes of rock crabs, sex ratio strongly favored males, particularly in mature crabs, in which the ratio was 21.43:1.

Temporal and spatial variation in catch

The maximum relative abundance of blue and lady crabs occurred during the warm months each year, whereas rock crabs were abundant only in the cold months (Fig. 3). Blue crabs were scarce in the otter trawls from January through May or June. We believe that many of them do remain in the study area, but are relatively inactive and are not accessible to otter trawls, as discussed below. Lady crabs migrated into the estuary in April and May and left in October and November.

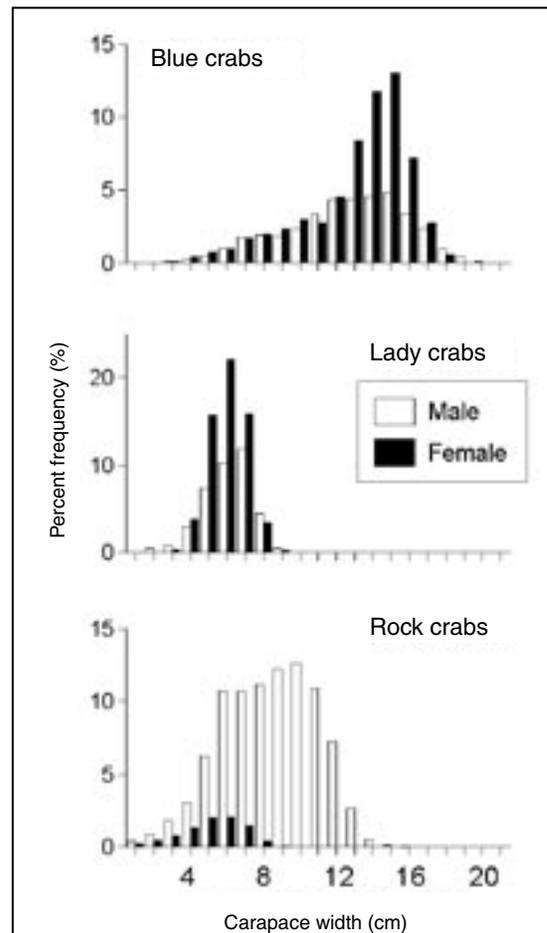


Figure 2

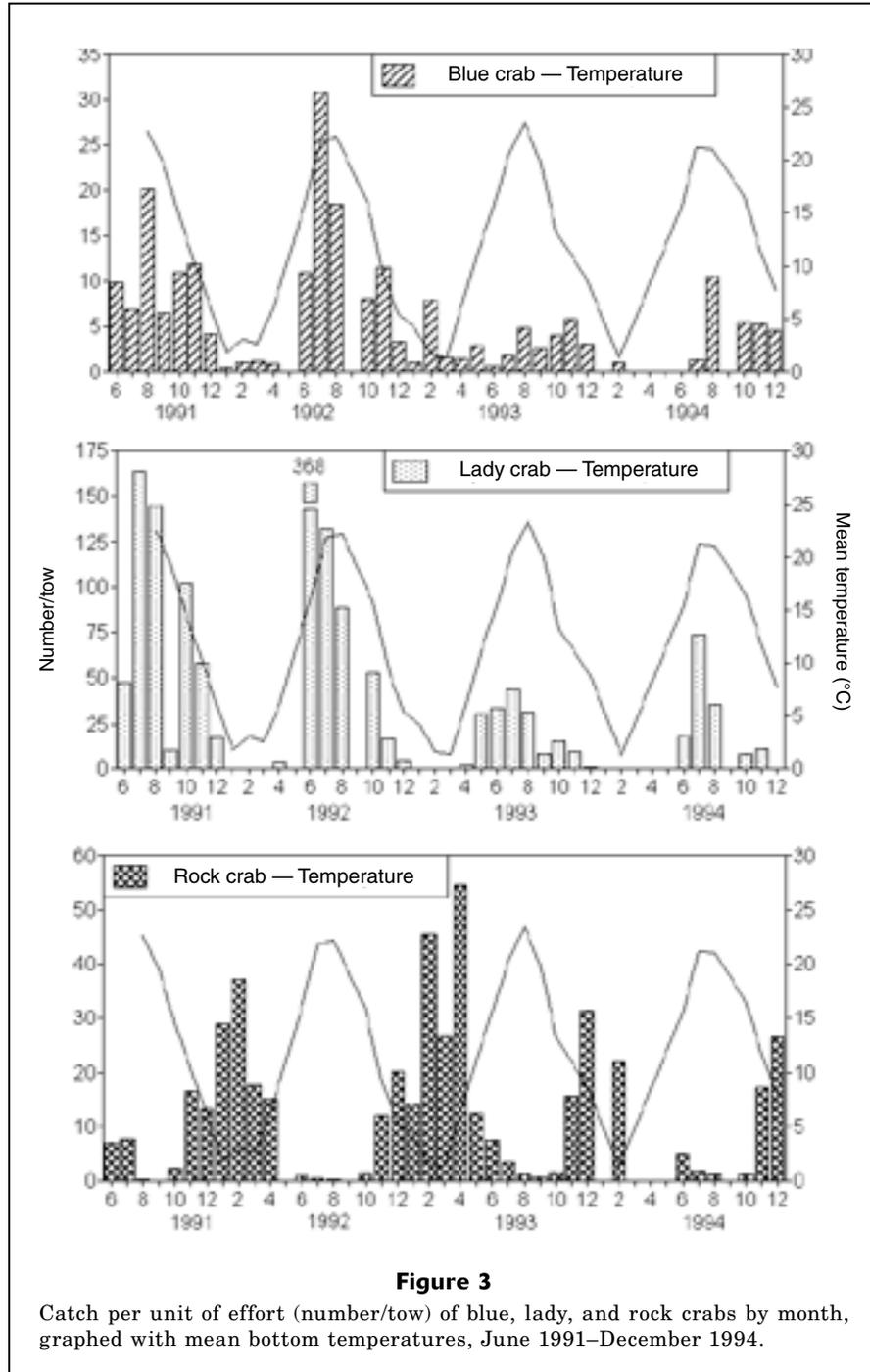
Carapace width (cm) frequencies for male and female blue, lady, and rock crabs collected during the Hudson-Raritan Estuary trawl survey, June 1991–December 1994, by percent frequency of the total catch of each species.

Rock crabs migrated into the estuary in November and gradually left during April, May, and June.

Hundreds of soft and postmolt male rock crabs were caught each winter in the study area (Fig. 4). The highest numbers of molting rock crabs were collected each December and January, and almost all of these crabs had completed molting by February. Very few molting or postmolt blue or lady crabs were caught.

The relative abundances of the three species varied by stratum (Fig. 5, A–C; Fig. 6). Blue crabs of both

sexes were caught mainly in strata near river mouths (strata 1, 2, and 6), in the Chapel Hill and Raritan channels (strata 8 and 9) in summer, but mainly in stratum 6 and in the channels in winter. Lady crabs were widely distributed and were caught throughout the study area, including the outer strata close to the ocean. Male rock crabs were most frequently collected in and near the channels and in strata 1 and 6, whereas female rock crabs were sparsely scattered throughout the study area.

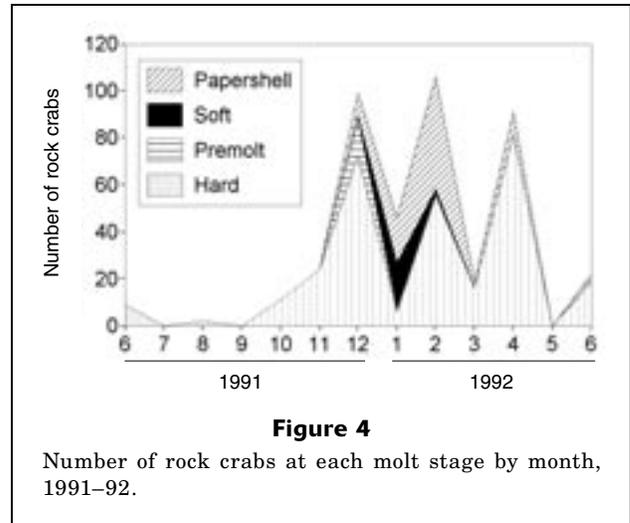


Foregut fullness

The total number of blue, lady, and rock crab foreguts examined was 1286. Foregut fullness varied by month in blue and rock crabs. The average fullness of blue crabs was 1% by volume from January through April, and 34% for the rest of the year. Ovigerous blue crabs ($n=27$) averaged 40% full. Lady crabs' average fullness was 41% during the months when they were present. The average fullness of rock crabs was 30% in all months when they were present; a minimum occurred in January when fullness was 7%. Of 419 rock crabs examined, intermolt crabs ($n=293$) were 33% full, premolt crabs ($n=9$) were empty, soft crabs ($n=22$) were empty, and postmolt crabs ($n=95$) were 20% full. Some rock crabs in the late postmolt stage were full even though their chelae were not completely calcified.

Diet composition

The number of crabs containing food was 975, and they consumed 44 identifiable taxa (Table 2). Most of the mollusks preyed upon were <15 mm in shell length. The crabs consumed were mud crabs (Xanthidae) and juvenile stages of other Anomura and Brachyura. When foreguts were only partially full, well-digested remains of prey frequently could be identified by pieces of shell or opercula, mandibles (for shrimp), or chela tips and carapace fragments (for crabs) (Elner et al., 1985). Recognizable prey taxa were grouped into 12 mutually exclusive categories (Table 3), which contributed 80.1% of the volume of all prey. The prey category "CRABS" represented pooled fragments of all crabs except Pagu-

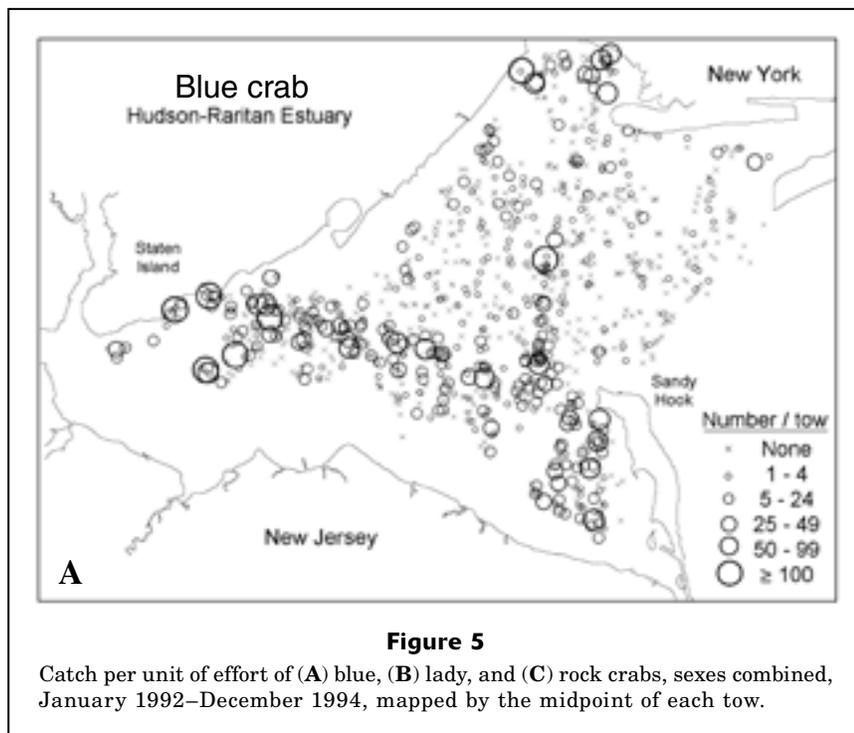


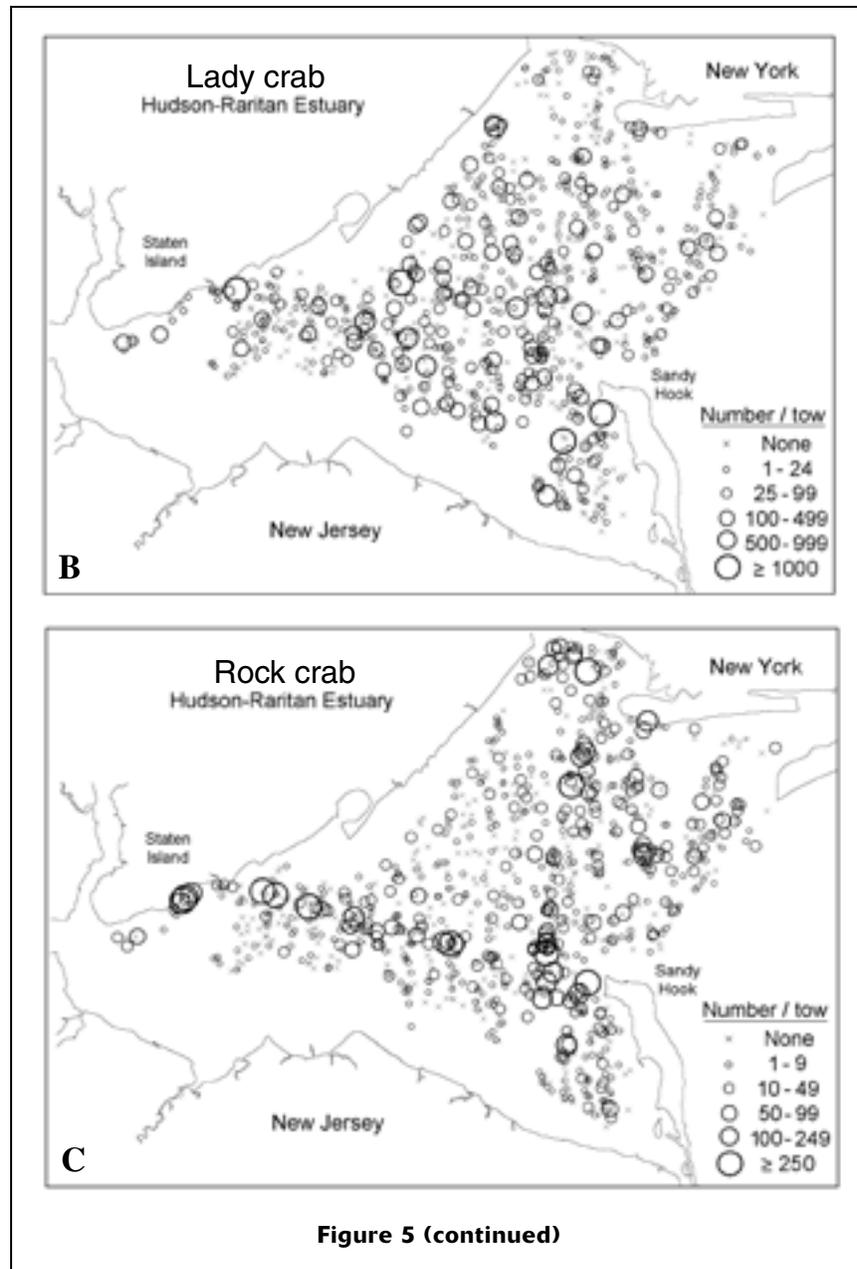
ridae and Xanthidae. Crabs containing prey in one or more of the 12 categories numbered 713.

Differences in diet by predator species, sex, and size

Although the three predator species shared most prey taxa, there were differences in the proportions of the taxa consumed (Fig. 7). Mann-Whitney tests comparing diets of sexes within each species showed only two significant differences out of 36 comparisons. After cluster analysis upon the 12 prey types by species, sex, and size class (immature and mature), the resulting dendrogram showed that diets were most similar between size classes within a species (Fig. 8). Female rock crabs were not included because of their small sample size. When the diets of the three species were compared by analysis of similarity (ANOSIM) they were found to be different ($P=0.067$), but the data were extremely variable and not normally distributed. No significant differences were found between sexes within species and we therefore pooled sexes within species.

Pairwise comparisons of the species were performed by analysis of dissimilarity (SIMPER). Four taxa contributed significantly to the difference in diets of the first pair: the bivalves *M. edulis* and *M. lateralis* were more important in the diets of lady crabs, and Xanthidae and CRABS, were more important in the diets of blue crabs. The diets of blue crabs and rock crabs were significantly different in four taxa: CRABS and *M. lateralis* were more important for blue crabs, and *M. edulis* and Xanthidae for rock crabs.





The diets of lady crabs and rock crabs were significantly different in two taxa: *M. lateralis* for lady crabs and *M. edulis* for rock crabs.

Within the crab size ranges sampled adequately by our gear, we found some ontogenetic differences in diets (Fig. 9). Notably, amphipods and shrimp were consumed by smaller sizes of all three predators. Certain mollusks, such as *N. trivittatus* and the Atlantic jack-knife clam (*Ensis directus*), increased in occurrence in foreguts with increasing crab size. Smaller lady crabs primarily fed upon *M. lateralis*, but larger ones broadened their diets to include other mollusks such as slip-persnails (*Crepidula* spp.) and *M. edulis*. Blue and rock crabs exhibited two peaks in consumption of *M. edulis*:

the foreguts of small crabs contained recently settled mussels, whereas those of large crabs contained shell fragments and meat of larger mussels. Xanthidae and Paguridae, small in body size, were eaten mostly by intermediate-size predators.

Mann-Whitney tests showed that amphipods were the only prey significantly different ($P < 0.01$) between maturity classes for all three crab species.

Spatial variability in diets

Cluster analysis of the diets by species and stratum defined six groups at 50% similarity (Fig. 10). Group A consisted of lady and rock crabs caught at oceanward

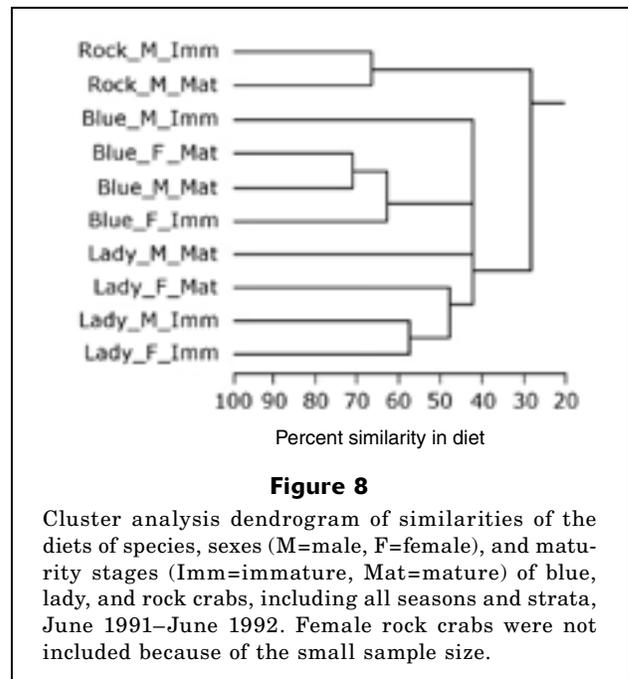
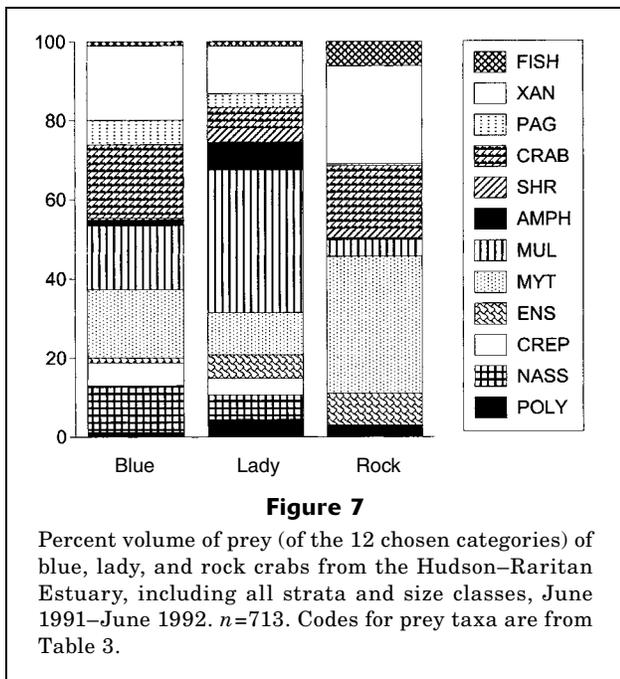
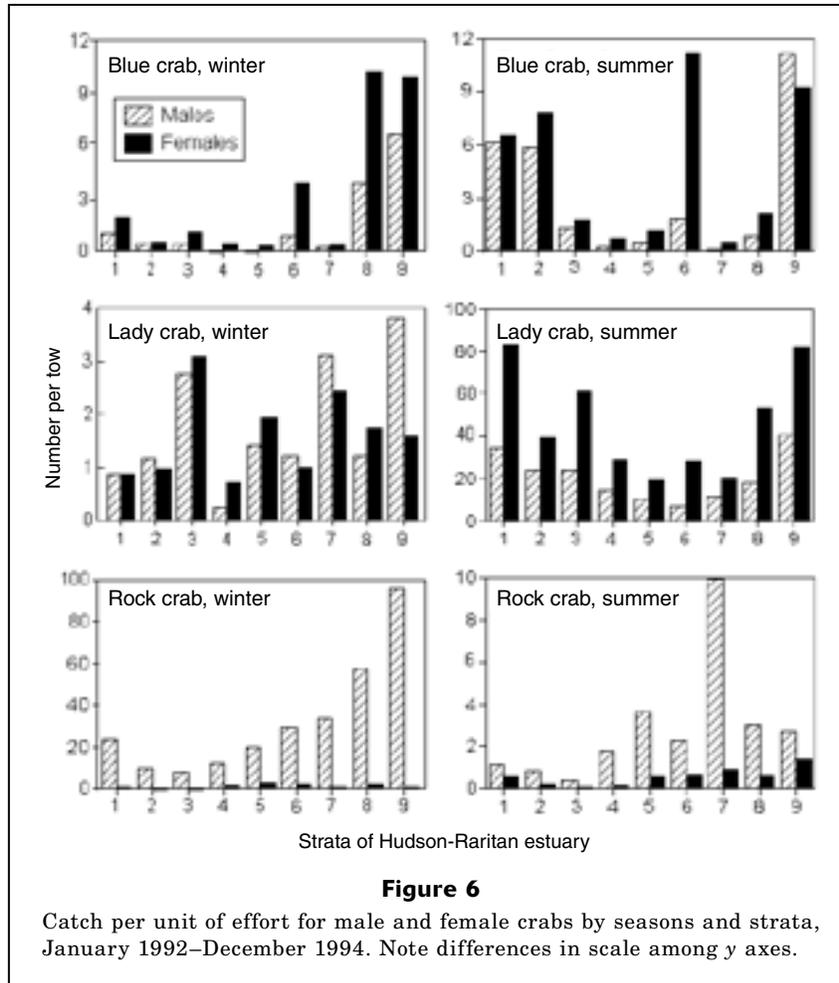


Table 2

Percent frequency of occurrence (%FRE) and percent volume (%VOL) of prey of blue, lady, and rock crabs collected during the trawl survey, June 1991–June 1992. Dashes mean that the dietary item was not found in any stomachs of that crab species. "Unid." means unidentified; "other" means uncommon identified taxa not listed below.

	Blue crab		Lady crab		Rock crab	
	%FRE	%VOL	%FRE	%VOL	%FRE	%VOL
Number of nonempty foreguts	328		352		295	
Plant material	1.5	<0.1	2.8	0.3	4.4	0.1
Hydrozoa	0.6	<0.1	1.4	<0.1	1.4	0.1
Mollusca, unid.	6.7	0.9	3.4	0.9	12.3	14.2
Bivalvia, unid., other	12.2	1.4	11.1	1.6	7.8	4.6
<i>Anadara transversa</i>	—	—	0.3	0.1	—	—
<i>Ensis directus</i>	2.4	0.8	9.9	4.8	8.2	6.2
<i>Lyonsia hyalina</i>	—	—	0.3	<0.1	—	—
<i>Mercenaria mercenaria</i>	0.3	<0.1	0.3	<0.1	—	—
<i>Mulinia lateralis</i>	9.3	13.6	43.5	33.1	6.8	1.4
<i>Mya arenaria</i>	—	—	0.3	0.4	—	—
<i>Mytilus edulis</i>	19.6	14.3	13.9	9.8	28.7	27.3
<i>Nucula proxima</i>	3.4	0.4	5.1	0.6	0.7	0.1
<i>Petricola pholadiformis</i>	1.2	0.1	2.3	0.8	—	—
<i>Pitar morrhuanus</i>	—	—	0.3	<0.1	—	—
<i>Spisula solidissima</i>	—	—	1.7	0.5	—	—
<i>Tellina agilis</i>	4.6	1.5	9.4	2.1	1.4	0.2
Gastropoda, unid., other	6.4	0.7	4.0	0.2	1.0	0.1
<i>Crepidula fornicata, convexa</i>	8.6	2.5	5.4	2.8	0.3	<0.1
<i>Crepidula plana</i>	0.6	<0.1	0.3	<0.1	—	—
<i>Nassarius obsoletus</i>	1.5	1.2	0.3	0.2	0.3	<0.1
<i>Nassarius trivittatus</i>	20.8	6.8	15.6	4.6	0.3	<0.1
Naticidae	—	—	0.6	<0.1	—	—
<i>Rictaxis punctostriatus</i>	—	—	0.9	0.1	0.3	<0.1
Cephalopoda	0.3	0.8	0.6	0.3	—	—
Polychaeta, unid., other	2.4	0.2	4.3	0.3	2.7	0.9
Glyceridae	—	—	0.9	0.3	—	—
<i>Hydroides dianthus</i>	—	—	0.3	<0.1	—	—
Nephtyidae	—	—	0.9	0.3	—	—
Nereidae	1.5	0.3	1.7	0.1	0.7	0.3
<i>Pherusa affinis</i>	—	—	—	—	0.3	0.1
<i>Pectinaria gouldii</i>	2.4	0.8	15.9	2.4	0.7	<0.1
Polynoidae	—	—	0.3	<0.1	1.4	0.1
Insecta	0.3	<0.1	—	—	—	—
Crustacea, unid., other	4.9	0.6	3.4	0.3	5.8	1.4
Amphipoda, unid., other	2.8	0.6	7.7	1.4	1.4	0.2
<i>Ampelisca</i> sp.	1.5	0.6	6.8	1.3	0.7	0.4
<i>Corophium</i> sp.	0.6	0.2	1.7	0.7	—	—
<i>Gammarus</i> sp.	—	—	3.1	3.3	—	—
Mysidacea	—	—	0.3	<0.1	—	—
Caridean shrimp, unid., other	0.6	<0.1	2.0	0.1	0.7	<0.1
<i>Crangon septemspinosa</i>	2.8	0.6	6.0	2.3	3.1	2.0
Crabs unid., other ¹	17.7	7.4	8.8	2.7	11.3	4.2
<i>Callinectes sapidus</i>	0.3	<0.1	0.6	0.1	1.4	1.8
<i>Cancer irroratus</i>	1.5	1.0	2.3	0.5	2.0	1.4
<i>Libinia</i> sp.	0.9	0.6	0.9	0.6	1.0	0.5

continued

Table 2 (continued)

	Blue crab		Lady crab		Rock crab	
	%FRE	%VOL	%FRE	%VOL	%FRE	%VOL
Crabs unid., other ¹ (cont.)	0.6	<0.1	2.0	0.1	0.7	<0.1
<i>Ovalipes ocellatus</i>	3.4	3.6	0.6	0.2	1.0	1.0
<i>Pagurus longicarpus</i>	2.1	1.5	1.7	0.6	—	—
<i>Pagurus</i> sp.	8.0	4.3	5.4	2.3	1.7	0.1
Xanthidae	21.1	20.8	15.9	10.6	21.2	18.4
Fish remains and scales	2.1	0.9	3.4	0.7	6.4	3.7
Inorganic debris, sand, mud	0.9	<0.1	0.9	0.2	0.7	0.1
Shell hash	2.4	1.5	—	—	—	—
Human-made objects	4.0	<0.1	4.8	<0.1	1.7	<0.1
Unid. organic matter	—	9.2	—	5.3	—	9.0
<i>Mytilus byssus</i>	1.8	<0.1	2.0	<0.1	3.1	0.2

Table 3

Twelve mutually exclusive prey categories that contributed 80% of the prey volume of all crabs examined. Codes are used in Figures 7 and 9. “Other” means uncommon identified taxa.

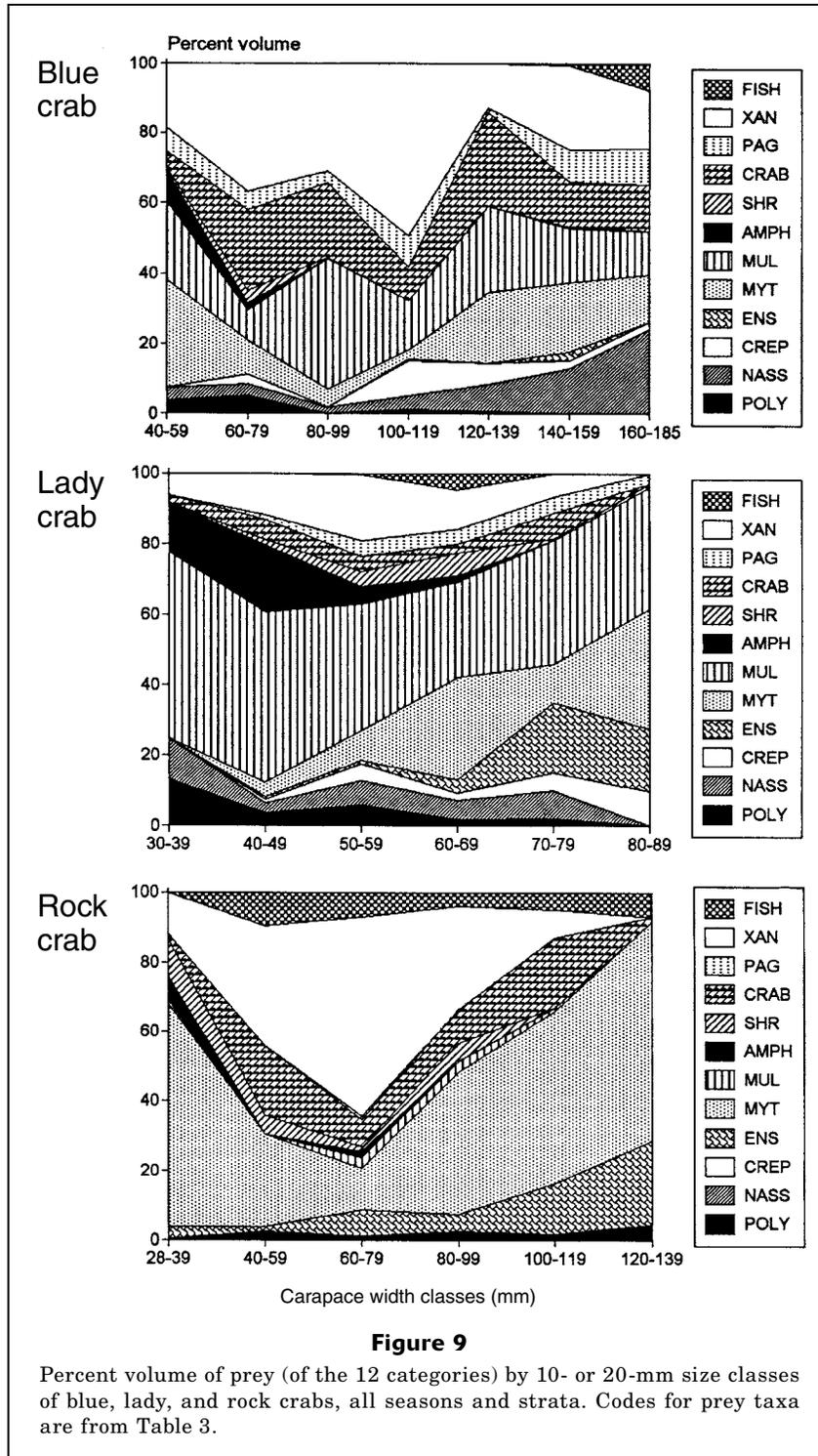
CODE	Category	Identifiable species
NASS	mud snails	<i>Nassarius trivittatus</i> , <i>N. obsoletus</i>
CREP	slipper shells	<i>Crepidula fornicata</i> , <i>C. convexa</i> , <i>C. plana</i>
ENS	razor clam	<i>Ensis directus</i>
MYT	blue mussel	<i>Mytilus edulis</i>
MUL	dwarf surfclam	<i>Mulinia lateralis</i>
POLY	Polychaeta	all
AMPH	Amphipoda	all
SHR	shrimp	<i>Crangon septemspinosa</i> , unid., other
CRAB	crabs	<i>Libinia</i> sp., <i>Cancer irroratus</i> , <i>Ovalipes ocellatus</i> , <i>Callinectes sapidus</i> , crab unid., and others excluding Paguridae or Xanthidae
PAG	hermit crabs	<i>Pagurus acadianus</i> , <i>P. longicarpus</i> , unid., other
XAN	mud crabs	Xanthidae: <i>Dyspanopeus sayi</i> , unid., other
FISH	fish, fish scales	all

outer strata (4, 5, and 7) that consumed large quantities of *M. edulis*. Clumps of recently settled and larger mussels were frequently collected in trawl nets in these strata. Group B contained crabs from Gravesend Bay, (stratum 6) that ate primarily *M. edulis* and *M. lateralis*. Group C contained crabs caught in the siltier southern strata and nearby channel (strata 1, 2, and 9) that consumed mainly *M. lateralis*, *M. edulis*, and CRABS. Group D consisted of rock crabs collected at inner strata (2, 3, and 8) that fed primarily upon *E. directus* and Xanthidae. *Ensis directus* was most common in diets in the northern sandier strata (strata 3, 5, 6, and 7). Groups E and F consisted of lady and rock crabs that consumed

mainly *M. lateralis*. Four species-stratum combinations did not cluster with any groups.

Temporal, spatial, and trophic niche breadth and overlap

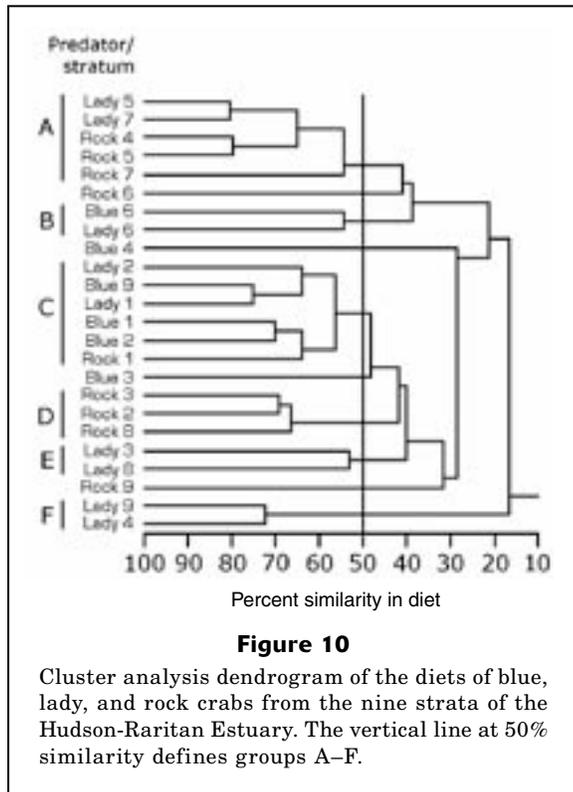
Niche breadth and overlap were calculated for both sexes of the three crab species (Table 4). Lady crabs of both sexes had the narrowest temporal niches (3.896 and 4.592), reflecting their presence in the estuary strictly in warm months. The temporal niche breadth of female blue crabs (8.187) was greatest, reflecting their year-long presence in the study area, even in the cold months when many males remain in rivers. The temporal overlaps of



male and female lady crabs with male rock crabs were the lowest in the matrix (0.149 and 0.186).

The spatial niche breadths of lady crabs were largest (7.320 and 7.324) (a result of their nonaggregative distribution throughout the study area), whereas the other two species tended to aggregate in certain

locations, particularly in or near channels. Female rock crabs also had a broad spatial niche, although they were caught much less frequently than the other groups. Spatial overlap was highest within species, particularly between male and female lady crabs (0.908).



Trophic niche breadth was greatest in male and female blue crabs (5.234 and 6.563) and male lady crabs (6.166) (Table 4). It was narrowest for female rock crabs, but sample size was low. Overlap was highest within species: blue crab males and females (0.819), and lady crab males and females (0.861). Overlap was lowest between lady and rock crabs, sexes combined (0.427).

Discussion

Temporal and spatial overlap within the estuary

The scatter plots (Fig. 5) and spatial niche overlap indices indicate substantial likelihood of co-occurrence and encounter among blue, lady, and rock crabs in the Hudson-Raritan Estuary. However, the species were not all active in the study area at the same time. Seasonal migration and winter torpor are two mechanisms that, at times, prevent interspecies encounters. Rock crabs had low temporal overlaps with blue and lady crabs because when rock crabs migrate in from the coastal ocean, lady crabs migrate out and blue crabs become less active and sometimes bury themselves. Although otter trawling does not adequately sample buried blue crabs, commercial crab dredgers catch large numbers of overwintering blue crabs from December through March in and near the Raritan and Chapel Hill channels (Stehlik et al., 1998).

Temporal overlap between blue crabs and lady crabs was fairly high because of their co-occurrence in the

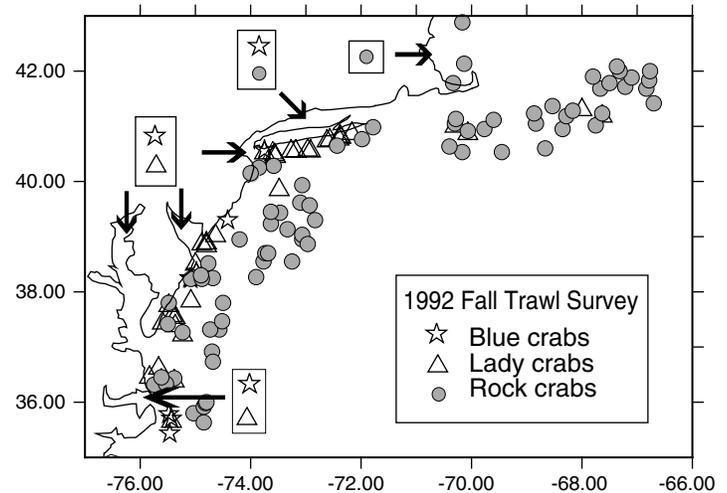


Figure 11
Presence of blue, lady, and rock crabs at stations from the fall 1992 bottom trawl survey, (Northeast Fisheries Science Center, Woods Hole, MA). Each point represents presence at a station. Occurrence inside the estuaries (boxed symbols) was derived from the literature cited in this article.

warm months. It was expected that intra-estuarine spatial separation might minimize contact between these species because they are reported to prefer different substrates. The blue crab is known to occupy a variety of substrate types, including sand, mud, and submerged vegetation (Milliken and Williams, 1984; Wilson et al. 1990), whereas the lady crab is primarily collected on sand (Williams and Wigley, 1977). The lady crab buries itself in sand more readily than in mud (Barshaw and Able, 1990) and it is able to forage more efficiently in sand than in sand-gravel or sand-shell substrates (Sponaugle and Lawton, 1990). However, as shown in Figures 5 and 6, lady crabs were not confined to sandy strata but were most abundant on the fine-grained sediment strata 1, 2, and 9.

The pattern of seasonal estuarine use by blue and lady crabs is not unique to the Hudson-Raritan Estuary. Other estuaries in which the two Portunidae are abundant in summer months but uncommon in winter are Barnegat Bay, NJ (Milstein et al., 1977; pers. observ.), Delaware Bay (Winget et al., 1974), and Chesapeake Bay (Haefner and Van Engel, 1975).

Rock crabs undergo seasonal migrations from coastal waters into and out of estuaries, but the timing differs by latitude. In Canada, the Gulf of Maine, and northern Massachusetts, rock crabs are much more abundant in immediate coastal waters, estuaries, and in the intertidal zone in warmer months (Krouse, 1972; Scarratt and Lowe, 1972). Rock crabs are more numerous in Narragansett Bay, Rhode Island, in warmer months (Jeffries, 1966; Clancy⁴). Juveniles are present inside

⁴ Clancy, M. 2002. Personal commun. Boston University, College of General Studies, Division of Natural Science, Boston, MA, 02115.

Table 4

Niche breadth and overlap for temporal, spatial, and trophic dimensions among blue, lady, and rock crabs. For temporal and spatial niches, all crabs (of all sizes) collected in 1992–94 are included. For trophic analyses, only the crabs containing one or more of the 12 prey categories were included. Female rock crabs were not included in trophic overlap because of the small sample size.

	Number of crabs	Mean CW, mm	Niche breadth		Overlap matrices				
Temporal niche									
<i>(n</i> =12 months, 1992–94)									
					BCF	LCM	LCF	RCM	RCF
Blue crab male (BCM)	2191	125	6.104	BCM	0.854	0.604	0.618	0.297	0.463
Blue crab female (BCF)	3483	129	8.187	BCF		0.649	0.576	0.376	0.564
Lady crab male (LCM)	11883	62	4.592	LCM			0.894	0.186	0.417
Lady crab female (LCF)	25312	61	3.896	LCF				0.149	0.339
Rock crab male (RCM)	14530	85	6.764	RCM					0.479
Rock crab female (RCF)	778	51	5.782						
Spatial niche									
<i>(n</i> =9 strata, 1992–94)									
					BCF	LCM	LCF	RCM	RCF
Blue crab male	2191	125	3.927	BCM	0.757	0.720	0.703	0.675	0.474
Blue crab female	3483	129	5.343	BCF		0.679	0.685	0.746	0.641
Lady crab male	11883	62	7.324	LCM			0.908	0.677	0.616
Lady crab female	25312	61	7.320	LCF				0.678	0.638
Rock crab male	14530	85	5.447	RCM					0.763
Rock crab female	778	51	7.191						
Trophic niche									
<i>(n</i> =12 prey categories, 1991–92)									
					BCF	LCM	LCF	RCM	
Blue crab male	84	111.0	5.234	BCM	0.819	0.570	0.580	0.576	
Blue crab female	139	127.9	6.563	BCF		0.629	0.651	0.609	
Lady crab male	98	59.4	6.166	LCM			0.861	0.437	
Lady crab female	200	54.9	4.655	LCF				0.417	
Rock crab male	181	88.8	4.139						
Rock crab female	11	53.7	2.620						
Trophic niche, sexes combined									
<i>(n</i> =12 prey categories, 1991–92)									
					LC	RC			
Blue crab (BC)	223	121.6	6.250	BC	0.628	0.623			
Lady crab (LC)	298	56.4	5.140	LC		0.427			
Rock crab (RC)	192	86.8	4.008						

that bay all year (Reilly and Saila, 1978). In contrast, in Delaware Bay and Chesapeake Bay they occur in coastal waters and estuaries mainly in colder months (Winget et al., 1974; Haefner and Van Engel, 1975; Haefner, 1976). Our data showed that rock crabs in the Hudson-Raritan Estuary conform to the pattern of migration typical of the latter southern bays.

A crossroads or overlap in distribution of the three crab species is more evident when a broader area on the continental shelf from Cape Cod to Cape Hatteras is considered. Crab presence was plotted by using data from the fall 1992 continental shelf trawl survey (Fig. 11). Fall surveys are done in September and October when waters are still warm. In the coastal waters off Raritan, Delaware, and Chesapeake Bays, blue and lady crabs were collected, whereas rock crabs were collected mainly on the central shelf. Estuarine presence in warm months, compiled from citations in the present study, is marked by symbols.

Sex ratios

In the Hudson-Raritan Estuary, sex ratios of blue, lady, and rock crabs were different from 1:1. In mature blue crabs, the sex ratio favored females because the study area is in the deeper oceanward portion of the estuarine system, where females release their eggs and overwinter. Many males spend their entire lives in water of relatively low salinity (Van Engel, 1958), such as is found in the nearby Hudson, Raritan, and Navesink-Shrewsbury rivers. In the Navesink River, the sex ratio of male to female blue crabs ≥ 12 cm over a two-year period was 2.6:1 (Meise and Stehlik, 2003).

In the Hudson-Raritan Estuary, female lady crabs ≥ 5 cm outnumbered males 2:1. Many of these females were ovigerous and therefore estuarine use may be related to reproduction. We were unable to locate published reports of lady crabs or other *Ovalipes* spp. mating locations, single-sex migrations, or locations of lar-

val release, any of which might be a reason for the use of the estuaries by female lady crabs.

The rock crabs that enter the estuary were predominantly males, and many females may never enter the estuary. Males use the estuary to molt, and possibly to avoid predators offshore. In comparison, on the north-west Atlantic continental shelf, the sex ratio in winter dredge collections was 1:2.2 males:females (Stehlik et al., 1991).

Feeding periodicity

Food consumption in crabs is affected by daily and seasonal cycles, temperature changes, reproductive rhythms, and molt (Warner, 1977; Stevens et al., 1982; Ryer, 1987; Mantelatto, 2001). In our study area, blue crabs ate little when inactive during the winter months, as reported above. Choy (1986) reported less feeding during egg-brooding in Portunidae, but in our study we found that fullness was about 40% in both egg-bearing and non-egg-bearing females in summer. A lack of feeding before and during molt, until calcification has sufficiently progressed, is typical of crabs (Warner, 1977). Empty stomachs in premolt and soft rock crabs in our study supported this observation.

Diet composition

We found that in the Hudson-Raritan Estuary, the most important prey items of blue crabs by volume were Xanthidae, then the mollusks *M. edulis* and *M. lateralis*, whereas only 2% of the prey volume was from cannibalism. In contrast, small blue crabs are of major importance in the diets of large blue crabs in Florida (Laughlin, 1982) and Maryland (Hines et al., 1990), and cannibalism is the source of more than 75% of the mortality of juveniles near estuarine shores (Hines and Ruiz, 1995). The major targets of cannibalism, early instars or molting juveniles, may be more abundant in rivers adjacent to our study area (Meise and Stehlik, 2003).

The diets of rock crabs in estuarine and coastal Canada and Maine usually contained a larger number of prey categories than did the diets in the present study (Scarratt and Lowe, 1972; Drummond-Davis et al., 1982; Hudon and Lamarche, 1989; Ojeda and Dearborn, 1991). These northern studies were done on rock, boulders, cobble, sand, and algal beds, where the diversity of habitats within a study area may offer a larger assortment of potential prey than the soft-bottom habitat of our estuary.

In the Hudson-Raritan Estuary, juveniles of commercially or recreationally harvested species were rarely consumed by the three species of crabs. Among mollusks, *M. arenaria* and *M. mercenaria* were scarce in crab stomachs, perhaps because other taxa such as *M. lateralis*, *N. trivittatus*, and Xanthidae provided abundant prey. The other commercially important species eaten by crabs was the blue crab juvenile, but infrequently as mentioned above.

Differences in diet among species, sexes, and size classes of predators

Our data did not support our hypotheses, based on existing studies, that blue, lady, and rock crabs would have different diets as a consequence of their species-specific body and chela structures. Blue and lady crabs (unlike rock crabs) swim, allowing them a greater foraging area than rock crabs. Chela structure affects the type and size of prey that can be crushed (Vermeij, 1978; Seed and Hughes, 1995; Behrens Yamada and Boulding, 1998). In Portunidae, the long chelae (in relation to their CW) have short muscle fibers better suited to quick grabbing than to prolonged crushing (Warner and Jones, 1976; Seed and Hughes, 1997). The chelae of Cancridae are monomorphic (same characteristics left and right sides), have relatively short, stout teeth, and close relatively slowly because of their muscle fibers (Warner and Jones, 1976). Chela crushing force (Newtons), measured with a force transducer, is positively correlated with chela height and thickness (Govind and Blundon, 1985; Block and Rebach, 1998). Although the chela structures of blue and rock crabs are quite different, the chelae of mature rock crabs (9–13.5 cm CW) generate crushing forces comparable to those of cutter and crusher chelae of mature male blue crabs (12–16 cm) (Govind and Blundon, 1985).

Chela crushing force in mature blue and rock crabs is likely to be more than sufficient for successful foraging upon all but the largest prey (Block and Rebach, 1998) and may not be a major determinant of diet. In fact, crabs often prey upon small or young bivalves rather than on large sizes, perhaps because the latter require more handling time and may damage chelae (Juanes, 1992; Seed and Hughes, 1995). Because Portunidae swim and have more versatile chelae, they may be expected to have broader trophic niches than Cancridae. In our study, blue crabs had the broadest trophic niche, lady crabs had an intermediate trophic niche, and rock crabs had the narrowest trophic niche.

We found no significant differences in diet by sex within species. Sexual dimorphism within a crab species accelerates after puberty (Hartnoll, 1978), but our study included many immature crabs. Some experimenters using force transducers found no significant difference in crushing force between the sexes of blue crabs of a broad size range (Blundon and Kennedy, 1982; Seed and Hughes, 1997), but in blue crabs >135 mm, males produced significantly more force than females (Eggleston, 1990). Sexual dimorphism is found in chela length, but not chela height, in lady crabs (significantly different slopes of CL/CW by regression; Stehlik, unpubl. data).

Carapace width and the proportion of chela height to carapace width are positively correlated with crushing force, which makes it possible for larger crabs to consume larger, harder-shelled mollusks or crustaceans (Hartnoll, 1978; Block and Rebach, 1998). The largest lady crabs do not grow to the carapace widths or chela lengths of mature blue crabs; therefore the force

of their chelae cannot match those of blue crabs. As they grow, Cancridae and Portunidae undergo shifts in diet, and may be divided into ontogenetically distinct trophic units (Laughlin, 1982; Stevens et al., 1982; Stoner and Buchanan, 1990; Rosas et al., 1994). In our study, larger crabs dropped amphipods and shrimp from their diets, but otherwise only minor changes occurred in prey identity and relative volumes of prey taxa among size classes (Fig. 9). An interesting ontogenetic shift was in the size of prey eaten: small crabs ate small individuals of prey taxa, such as *M. edulis*, and Xanthidae, and large crabs ate large individuals of the same taxa. Thus in our study the influence of physical structure upon diet was greater as body size increased within a species than among species.

Spatial variability and overlap in diets

The three predators were scattered throughout the cluster diagram of diet among strata of the estuary (Fig. 10), yet crabs from inner and outer groups of strata usually clustered separately. We concluded that location influenced diet more than did predator identity. The inner, outer, and channel strata differ in depth, sediment type, currents, and mean temperature, and therefore in benthic and epibenthic prey assemblages. Our results support the concept that these species are mainly opportunistic in diet, as was suggested for blue crabs (Laughlin, 1982), and rock crabs (Hudon and Lamarche, 1989). The Hudson-Raritan and other nearby coastal and estuarine areas from Long Island Sound to Chesapeake Bay are crossroads where blue, lady, and rock crabs share space and resources.

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