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Foraging ecology of the blue crab, Callinectes sapidus Rathbun, in lower Chesapeake Bay

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Foraging ecology of the blue crab, *Callinectes sapidus* Rathbun, in lower Chesapeake Bay

Mansour, Randa Ali, Ph.D.

The College of William and Mary, 1992

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FORAGING ECOLOGY OF THE BLUE CRAB, CALLINECTES SAPIDUS RATHBUN, IN LOWER CHESAPEAKE BAY

A DISSERTATION
PRESENTED TO
THE FACULTY OF THE SCHOOL OF MARINE SCIENCE
THE COLLEGE OF WILLIAM AND MARY IN VIRGINIA

In Partial Fulfillment
Of the Requirements for the Degree of
Doctor of Philosophy

by
Randa A. Mansour
1992

APPROVAL SHEET

This dissertation is submitted in partial fulfillment of
the requirements for the degree of
Doctor of Philosophy

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Dedicated to Brian and Connor Meehan, Marzell Deans and to the memory of Doris Deans.

TABLE OF CONTENTS

TABLE OF CONTENTS (continued)

TABLE OF CONTENTS (continued)

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LIST OF TABLES

LIST OF TABLES (continued)

LIST OF TABLES (continued)

LIST OF TABLES (continued)

Table Page

LIST OF FIGURES

LIST OF FIGURES (continued)

CHAPTER 1

FORAGING ECOLOGY OF THE BLUE CRAB, *CALLINECTES SAPIDUS* RATHBUN, IN THREE SUBESTUARIES OF LOWER CHESAPEAKE BAY, VIRGINIA, USA

ABSTRACT

This two-year investigation jointly examined the key features of predator-prey dynamics - predator abundance and distribution, predator feeding habits, including cannibalism, and prey abundance and distribution - in a model marine benthic system. Specifically, this study concurrently quantified blue crab feeding habits and preference, and examined the inter-relationships between diet, predator preference, and predator and prey abundance and distribution in three subestuaries of lower Chesapeake Bay - the James, York and Rappahannock Rivers, Virginia. Blue crab diets were separable on the basis of proportional consumption of three dominant dietary components: bivalves, crabs and polychaetes. Crab abundance, prey abundance and crab diet were correlated such that blue crabs aggregated in areas of highest preferred (i.e., bivalve) prey abundance, as determined through electivity analyses. Spatial (i.e., upriver/downriver) and size-related differences in diet selection occurred. At least two trophic groups were distinguished, based on their relative consumption of bivalves and crabs, including conspecifics (i.e., older juveniles and adults) or polychaetes and small crustaceans (i.e., younger juveniles and new recruits). Spatial differences were reflected by proportional bivalve consumption: crabs always preferred bivalves, but in areas of relatively lower bivalve abundance, opportunistically expanded their diets to include other prey taxa.

Cannibalism was common, but the frequency of occurrence varied with crab size, season, location, new juvenile recruit abundance, and the density of alternative preferred prey. Specifically, cannibalism frequency increased with crab size, was highest in areas of relatively lower bivalve densities and predominated during the period of new juvenile recruitment in the Fall.

The results of this and other investigations indicate that blue crab predation may be the most important biotic determinant of community structure in this marine soft-bottom system. Furthermore, since a seasonal decline in prey abundance and availability did not occur, cannibalism, rather than intraspecific competition for limited resources, may be the most likely compensatory mechanism of blue crab population regulation in Chesapeake Bay.

FORAGING ECOLOGY OF THE BLUE CRAB

INTRODUCTION

Predation regulates community structure and the organization of marine soft-bottom habitats (Peterson 1979, Virnstein 1977, 1979, Holland et al. 1980, Woodin 1981, Posey 1986, Hines et al. 1990). Investigations in rocky intertidal habitats indicate that predation can prevent competitive exclusion, thus determining species composition, diversity and abundance patterns (Peterson 1979, Paine 1966, 1980, Connell 1975, Dayton 1984, Menge 1978 a, b, 1983, Menge et al. 1986 a, b). This paradigm of community organization may not apply to marine soft-bottom communities where predator-prey interactions are dominated by guilds of generalized predators capable of switching among diverse prey, and few communities contain competitively dominant prey capable of monopolizing resources (Peterson 1979, Dayton 1984, Summerson & Peterson 1984). Although a single "keystone" predator (Paine 1966) has not been identified in soft-bottom habitats, investigations indicate that decapod crustaceans are a critical component of these guilds, often affecting the abundance, species composition and distributional patterns of benthic infauna (Virnstein 1977, 1979, Holland et al. 1980, Woodin 1981, Laughlin 1982, Hines et al. 1990), as well as providing internal feedbacks to their populations (Laughlin 1979, 1982, Kurihara et al. 1988, Smith 1990, Mansour & Lipcius 1991, Smith & Hines 1991). Similarly, Paine (1980, 1992) emphasized the importance of the functional role of species within guilds. For instance, an herbivore guild in the intertidal zone of Tatoosh Island, Washington had a weakly negative per capita influence on a competitively dominant prey (i.e., brown algae). Two herbivores (i.e., Katharina tunicata & Stronglyocentrotus purpuratus) had strongly negative, but nonadditive, effects. The effects of Stronglyocentrotus were further confounded by aggregation, whereby sea urchins can produce "barrens" devoid of brown algal canopies (Paine 1992). Therefore, identification of "strong interactions" and the habitat specificity (e.g., random or aggregated) of predators are critical in investigations of community organization (Paine 1980, 1992).

A quantitative focus on the major components of predation intensity is also required in investigations of marine predator-prey dynamics and community organization (Menge 1983). These components incorporate the effectiveness and abundance of predators, as well as the types and identities of predator species (Menge 1983). Similarly, Holling (1959) proposed that the impact of predation differs according to components that are basic (i.e., functional and aggregative responses) and subsidiary (i.e., prey characteristics, density and quality of alternate foods, characteristics of the predators), and emphasized the importance of a comprehensive approach -- determination of the total response of predators to prey -- to investigations of population dynamics. Thus, an investigation of predator-prey dynamics in marine systems requires attention to the basic features characterizing predator-prey interactions: the relationships between predator abundance and distribution, predator diet, and prey abundance and distribution.

In the aggregative response, predators regulate prey populations by congregating in areas of high prey density and leaving those prey patches where the rate of prey capture falls below a threshold (Readshaw 1973). The general aggregative response is sigmoid in form, can stabilize predator-prey systems, and is characterized by three parts: (1) where predators do not distinguish between different areas of low prey density that are unprofitable; (2) where predators do not distinguish between areas of high prey density which are all very profitable; and (3) intermediate density regions where predators respond strongly to the range of prey densities (Hassell & May 1974, Murdoch & Oaten 1975, Hassell 1978). Aggregative responses to uneven prey distributions can be quantified either in terms of predator numbers (i.e., abundance), or the time spent by a predator per unit area of different prey density (Hassell & May 1974). Therefore, the aggregative response is a function of predator behavior and measures relative predator and prey abundance and distributional patterns.

While predator aggregation can enhance the foraging efficiency of individual predators (Anger et al. 1977, Hassell & May 1973, 1974), mutual interference due to aggregation may adversely effect a predator's searching efficiency or feeding rate (Free et al. 1977, Hassell 1978). Furthermore, cannibalism, an extreme form of interference competition, has been documented in a wide variety of vertebrates and invertebrates. It is most frequent during periods of low availability of alternative prey or high predator density, and acts as a density-dependent regulator of population size (Fox 1975, Polis 1981, 1988).

The interactive effects of the functional, aggregative and interference responses and predator preference (e.g., diet analyses) have not been defined in investigations of predator-prey dynamics in marine communities. Therefore, this field investigation quantified predator diet and preference, interference (i.e., cannibalism), and the aggregative response of a key epibenthic predator, the blue crab, in a model soft-bottom system of Chesapeake Bay. Complementary laboratory investigations (Mansour & Lipcius 1991) estimated the combined effect of the functional, aggregative and interference (i.e., intraspecific competition) responses upon prey and predator survival and predator foraging rates for blue crabs and a common bivalve prey, Macoma balthica, in this system.

THE PREDATOR-PREY COMPLEX

The blue crab, Callinectes sapidus Rathbun, is a large (males up to 227 mm carapace width (CW)) epibenthic omnivore occurring in various habitats along the Northwest Atlantic Ocean, Gulf of Mexico and Caribbean Sea (Williams 1984). Blue crabs play a major role in energy transfer in estuaries, serving as both prey and consumers (Baird & Ulanowicz 1989). In Chesapeake Bay, blue crabs are abundant and actively foraging from late spring through autumn (Hines et al. 1987, 1990). The population is dominated by two year classes that occur concurrently in the tributaries of the Bay from April through December; during the colder months (i.e., January-March) blue crabs overwinter by shallow burial in benthic habitats (Schaffner & Diaz 1988, Hines et al. 1987, 1990, Lipcius and Van Engel 1990). Field and laboratory studies indicate that blue crab foraging efficiency and prey mortality rates vary significantly across gradients in prey availability, predator density, and habitat features (Blundon & Kennedy 1982 a, b, Arnold 1984, Lipcius & Hines 1986, West & Williams 1986, Hines et al. 1990, Mansour & Lipcius 1991, Eggleston et al. 1992).

Despite the blue crab's ecological and economic importance, there have been no comprehensive investigations of its natural feeding habits in Chesapeake Bay. Diet analyses are essential to understanding nutritional requirements, food webs, inter- and intraspecific interactions and resource partitioning, predator preference and predation effects (Hill 1976, Peterson & Bradley 1978, Williams 1981, Laughlin 1982). Ryer (1987) conducted a 24-hr study on feeding periodicity of blue crabs in a lower Chesapeake Bay tidal marsh creek and seagrass meadow. Crabs from the grassbed had fuller guts and exhibited a tendency towards nocturnal feeding, while feeding was related to tidal cycles in the marsh creek. Therefore, habitat was important in determining blue crab feeding patterns, and the quantity (i.e., measured as gut fullness) and types (i.e., plant or animal material) of foods consumed. Hines et al. (1990) investigated patterns of prey utilization through gut contents studies of large (mean size 124-133 mm CW (carapace width)) blue crabs in a small mesohaline subestuary of upper Chesapeake Bay. C. sapidus preyed extensively on clams, and to a lesser extent on fish, other blue crabs and amphipods (Hines et al. 1990). Laboratory and field investigations indicate that cannibalism is common (Laughlin 1979, Peery 1989, Hines et al. 1990, Mansour & Lipcius 1991). In the Apalachicola estuary, Florida, Laughlin (1979) observed an inverse relationship between blue crab recruitment levels and subsequent population abundance, and suggested that high densities of juveniles may stimulate cannibalism and exploitative competition. Blue crabs constituted 11 % of the total diet of large crabs (> 60 mm CW) in that estuary (Laughlin 1982). Hines et al. (1990) observed a significant increase in the incidence of cannibalism by blue crabs in Chesapeake Bay from 3.0 % in June to 10 and 12 % in mud and sand substrates, respectively, in September.

The benthic community of Chesapeake Bay is dominated by a diverse assemblage of species (Wass 1972, Holland 1985, Hines & Comtois 1985, Hines et al. 1987, Holland et al. 1987, Baird & Ulanowicz 1989, Diaz & Schaffner 1990). Salinity is the key abiotic factor determining benthic infaunal distribution and abundance (Boesch et al. 1976, Holland 1985, Holland et al. 1987, Diaz & Schaffner 1990). Other important abiotic factors include sediment type, oxygen availability, energy gradients and frequency of bottom disturbance (Diaz & Schaffner 1990). Predation appears to be the primary biotic factor determining species diversity and abundance patterns (Virnstein 1977, 1979, Holland et al. 1980, Hines et al. 1990), and in this system the dominant guild of epibenthic predators consists of blue crabs, and the fish, Leiostomus xanthurus, Micropogonias undulatus, and Trinectes maculatus (i.e., spot, croaker and hogchoker, respectively; Virnstein 1977, 1979, Hines et al. 1990).

The collective evidence suggests that blue crabs are opportunists, with spatial and seasonal variations in feeding habits reflecting the spatial and temporal availability of prey (Darnell 1959, Tagatz 1968, Odum & Heald 1972, Laughlin 1982, Alexander 1986, Ryer 1987, Baird & Ulanowicz 1989, Stoner & Buchanan 1990, Hines et al. 1990), and that cannibalism is common and may be important in blue crab population regulation (Laughlin 1979, Peery 1989, Hines et al. 1990, Lipcius & Van Engel 1990, Mansour & Lipcius 1991). Although several laboratory and field investigations have been conducted to determine the predatory impact of blue crabs on benthic infauna in Chesapeake Bay (Virnstein 1977, 1979, Holland et al. 1980, Blundon & Kennedy 1982a,b, Arnold 1984, Lipcius & Hines 1986, Hines et al. 1990, Mansour & Lipcius 1991, Eggleston et al. 1992), no study has assessed predation effects through diet analysis of different size classes over extensive spatial and temporal scales encompassing both a significant portion of their range of occurrence and the period of intensive feeding activity in lower Chesapeake Bay. The blue crab may be a "strong interactor" (sensu Paine 1980) within the guild of epibenthic predators in Chesapeake Bay. Although this hypothesis can only be tested through manipulative field experiments (as in Paine 1992), the evidence accumulated thus far (Virnstein 1977, 1979, Holland et al. 1980, Baird & Ulanowicz 1989, Hines et al. 1990, Eggleston et al. 1992), indicates that blue crabs play a critical role in the Chesapeake Bay system.

This quantitative investigation examines the key features of predator-prey dynamics (i.e., predator abundance and distribution, predator feeding habits including cannibalism, and prey abundance and distribution) in a marine benthic system to yield a unique comprehensive understanding of the patterns and underlying regulatory processes driving this predator-prey system at various scales of space and time. Therefore, this two-year study attempted to: (1) quantify the abundance and diet of blue crabs within three subestuaries of lower Chesapeake Bay - the James, York and Rappahannock Rivers, (2) assess annual, seasonal and river-specific sources of variation in blue crab abundance and diet, (3) determine the types and densities of potentially available benthic prey, (4) estimate and relate fluctuations in prey abundance to blue crab diet and abundance, (5) determine whether resource partitioning occurs between various size-classes of the blue crab, and (6) quantify the occurrence and extent of cannibalism in the blue crab in Chesapeake Bay.

MATERIALS AND METHODS

Study Sites

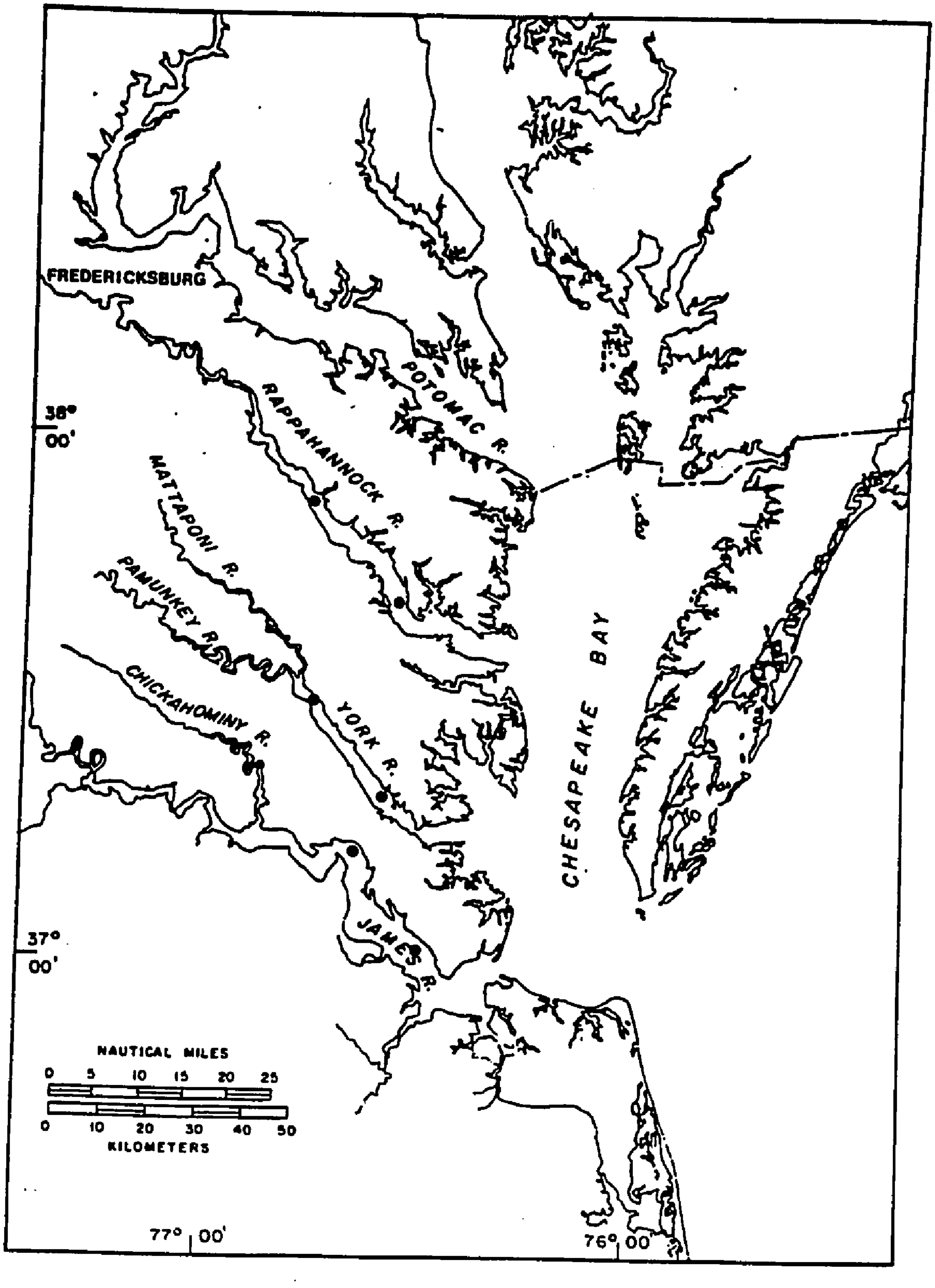
All field studies were conducted in three major tributaries of Chesapeake Bay: the James, York and Rappahannock Rivers. Chesapeake Bay, the largest estuary in the continental United States, is a partially mixed estuary with an average tidal range of approximately 0.6 m (Baird & Ulanowicz 1989). About 90 % of the freshwater entering the Bay comes from tributaries located along the northern and western sides (Davies & DeMoss 1982). The three rivers under investigation flow into the polyhaline (Baird & Ulanowicz 1989) portion constituting the lower Bay, and are characterized as partially mixed, coastal plain sub-estuaries (Kuo & Neilson 1987). Chesapeake Bay and its tributaries provide critical refuge, food, and habitats used in reproduction by the blue crab and a diverse assemblage of marine and estuarine vertebrates and invertebrates (Baird & Ulanowicz 1989, Hines et al. 1990).

Study sites in this investigation comprised six mid-channel stations, two of each located in the James (J), York (Y) and Rappahannock (R) Rivers. Each river contained single downriver (i.e., Y10, J13, R15) and upriver (Y25, J27, R30) stations located 16.1 (Y10), 20.93 (J13), 24.15 (R15), 40.25 (Y25), 43.47 (J27) and 48.3 km (R30) from the mouth of each river (Fig. 1). Sediments consisted of sand and shell (lower James), soft mud (lower York and Rappahannock), and mud-clay (upper Rappahannock, York and James). Abiotic parameters for each station-month combination are depicted separately for 1988 (Appendix 1) and 1989 (Appendix 2).

Blue Crab Abundance

Blue crabs were collected by trawling with a 9.14-m semi-balloon otter trawl fitted with a tickler chain, 3.8-cm mesh body and cod end lined with 1.3-cm stretch mesh. Two five-minute tows were taken at each

Figure 1. Sampling stations in 1988 and 1989 located in the James, York, and Rappahannock Rivers.


FREDERICKSBURG
POTOMAC R.
RAPPAHANNOCK R.
MATTAPONI R.
PAMUNKEY R.
CHICKAHOMINY R.
YORK R.
JAMES R.
CHESAPEAKE BAY
38° 00'
37° 00'
77° 00'
76° 00'
NAUTICAL MILES
0 5 10 15 20 25
0 10 20 30 40 50
KILOMETERS

of the six stations. Stations were sampled once per month from June through October, 1988 and 1989, in conjunction with The College of William and Mary, Virginia Institute of Marine Science (VIMS) trawl survey.

Variation in blue crab abundance was analyzed separately for each year as a function of river (James, York, Rappahannock), station location (upriver: J27, Y25, R30; downriver: J13, Y10, R15), and month (July-October in 1988, June-September in 1989) using full-factorial, fixed-effects analysis of variance (ANOVA) models. The dependent variable, number of crabs per tow, was obtained from each set of two monthly tows per station. Abundance was log-transformed to meet assumptions of normality and homogeneity of variance (Sokal & Rohlf 1981). In all cases, either the variances were homogeneous (Hartley's F-max test, Sokal & Rohlf 1981), or the null hypotheses were rejected at alpha values less than the P values of the test for homogeneity of variance (Underwood 1981). Where interaction effects were significant, main effects were examined within levels of the main factors (Underwood 1981) with ANOVA models and Ryan's Q test for multiple comparisons set at an experimentwise error rate of 0.05 (Day & Quinn 1989). Crab abundance was analyzed separately for all crabs and different year classes (< 50, ≤ 80 and > 80 mm CW) as determined by inspection of size-frequency histograms (see Results) or previous investigations (Eggleston 1990c, Hines et al. 1990, Smith 1990a). These size classes were selected because they represent (1) the new year class (i.e., < 50 mm CW, Lipcius & Van Engel 1990), (2) individuals most vulnerable to cannibalism (i.e., ≤ 80 mm CW, Smith 1990a), and (3) crabs of the previous year class and the most likely cannibals (i.e., > 80 mm CW, Smith 1990a).

Blue Crab Diet

Based on laboratory investigations of blue crabs feeding on bivalves (Eggleston 1990a,b,c), three size classes of male, mature female and immature female blue crabs were sampled: 60-99, 100-134 and

134-182 mm carapace width (CW) measured from point to point of the lateral spines. Upon capture, blue crabs were placed on ice, the dorsal portion of the carapace was removed, and the foregut was dissected out and individually preserved in 10% buffered formalin. Molt staging was accomplished by examination of the last two segments of the paddle fins for color changes associated with the formation of new shell (Oesterling 1988). Crabs were classified as hard intermolt, white sign indicating a molt within 2 wks, pink sign indicating a molt within 1 wk, red sign indicating a molt within 1 to 3 days (Oesterling 1988), and soft or paper shell (i.e., postmolt). Only hard intermolt crabs and non-berried females were used in diet analyses. Sexes were pooled for all analyses (Laughlin 1979, 1982).

The points method was chosen as the quantitative scoring method for stomach contents. This method is commonly used for describing gut contents of both fish and crabs, and adequately indicates the composition of the bulk of an animal's diet (Williams 1981, 1982, Hines 1982, Wassenberg and Hill 1989, Hines et al. 1990). In portunids, mastication of food by the mouth parts and gastric mill preclude counts of prey numbers in most cases and accurate determination of prey volume by traditional methods (Williams 1981, 1982). Methods used in stomach content analyses of fish and portunids have been assessed by Hynes (1950), Williams (1981) and Hyslop (1980).

The points method entails estimating the fullness of each stomach as a percent of the total volume occupied by the contents. Gut contents were dissected out, identified to 9 (1988) or 10 (1989) broad categories (Appendix 3), and the percentage by volume of each category was estimated. Two additional categories, digested and unknown/undigestible material (i.e., sand, worn shell fragments, pebble), were used only for sample size analysis. These categories, while providing no pertinent information on the diet of blue crabs, could limit subsequent food consumption and were commonly found in the guts of crabs.

The average diet composition for each size class was calculated using the fullness of the stomach as a weighting factor, so that the mean proportion of a food category in the diet was described by the equation (Hines 1982, Hines et al. 1990):

$$p_i = \frac{\Sigma\, x_{ij}\, y_j}{\Sigma\, \Sigma\, x_{ij}\, y_j}$$

where x_{ij} is the proportion of the contents of the ith food category of the jth crab, and y_j is the fullness of the stomach of the jth crab. Data were based on the number of stomachs that contained food, not on the total number of stomachs examined. Food items constituting less than 3 % (Stoner and Buchanan 1990) of the diet in more than 50 % of the cases were grouped into a miscellaneous category for graphical presentation, but not for analyses.

Dietary Diversity, Overlap and Selection

Relative diet similarity was analyzed using the Flexible Grouping (β=-0.25) clustering strategy (Boesch 1977, Laughlin 1979, 1982, SAS Inst. 1985) on the mean proportion of each food category in the diet. Analyses were performed by clustering size class, station, and month, or a combination of these variables. Groups were assigned by determining the point along each dendogram at which the branches were internally consistent when compared with the data matrices (Boesch 1973).

Diet diversity was calculated using the Shannon-Wiener diversity index (Zar 1984):

$$H' = n \log n - \Sigma\, f_i \log f_i\, /n.$$

This index was calculated both for groups identified after clustering, and to investigate overall patterns in diversity associated with size class, river, station and month.

Pairwise dietary overlap indicates the fraction of the diet in common between trophic groups (Hines et al. 1990). In this investigation, overlap between any two size classes i and h was calculated by (Hines 1982, Hines et al. 1990):

$$C_{ih} = 1 - 1/2\, \Sigma |p_{ij} - p_{hj}|$$

for the j diet categories.

Feeding preference was quantified with Chesson's (1978, 1983) α index:

$$\alpha = \frac{r_i/p_i}{\Sigma\ (r_i/p_i)}$$

where r_i is the proportion of food types in the diet, and p_i is the proportion of food types in the environment. The characteristics of α relative to other electivity indices have been thoroughly reviewed (Lechowicz 1982, Confer & Moore 1987). Although the relativized electivity index, E^* (Vanderploeg & Scavia 1979), is the most appropriate for field samples in which both the number and relative abundances of prey vary, the statistical properties of the index are not given (Lechowicz 1982, Chesson 1983, Confer & Moore 1987). In contrast, α is amenable to parametric statistical analyses (Chesson 1983). The index ranges from 0 to 1, is a function of n (i.e., the number of food types) and is symmetrical only when n=2 (Lechowicz 1982). Random feeding or neutral selection occurs when α equals 1/n, with values above and below 1/n indicating preference and avoidance, respectively (Chesson 1978, 1983, Lechowicz 1982, Confer & Moore 1987). Electivity (i.e., α) was calculated using the proportion of each food item in an individual crab gut and the mean proportion of that food in the benthos. Although Chesson (1983) suggested the use of multivariate techniques for $n > 2$, biases in gear selectivity (i.e., 1-mm sieve) under-estimated the abundance of infauna with small early developmental or juvenile stages, or that of species with extended reproductive periods and populations composed primarily of juveniles (e.g., spionid polychaetes; Table 2 in Holland et al. 1987). Therefore, α obtained for each food item was statistically compared to the value of 1/n for random feeding using two-tailed Student t-tests and individual crabs as replicates.

Graphical analysis of the 1988 data for large samples (i.e, upriver stations, see Results) provided estimates of the sample size ($n \geq 7$) and gut fullness (> 50%) required to include most food taxa, stabilize scoring methods for common food types, and reduce bias due to differing residency times of food items in the gut (Williams 1981). In 1989, an additional size class (10 - 59 mm CW) was sampled, and only guts that were at least 50 % full were retained for analysis.

Benthic Infaunal Abundance

Six (summer 1988) or eight (summer 1989) benthic samples were taken at each station with a Petersen grab (31 cm long X 21 cm deep X 21 cm wide), which sampled an area of 0.065 m^2 . Half of the samples each were taken at the start and end of a tow. Samples were immediately washed through a 1-mm sieve and preserved in 10 % buffered formalin. A flexible grouping ($\beta=-0.25$) clustering strategy (Boesch 1977, Laughlin 1979, 1982, SAS Inst. 1985) was run on the mean proportion of each prey category in the benthos. Analyses were performed by clustering station, month and river, or a combination of these factors. Groups were assigned by determining the point along each dendogram at which the branches were internally consistent when compared with the data matrices (Boesch 1973).

Variation in benthic abundance was analyzed separately for each year as a function of river, station, and month with full-factorial, fixed-effects analysis of variance (ANOVA) models, as for crab abundance. The dependent variable, density for each of the most abundant prey types (i.e., bivalves, polychaetes and crustaceans), was log-transformed to meet assumptions of normality and homogeneity of variance (Sokal & Rohlf 1981). In all cases, the variances were homogeneous as determined by Hartley's F-max test (Sokal & Rohlf 1981). Significant interaction effects necessitated examination of effects within levels of the main factors (Underwood 1981) using ANOVA models and Ryan's Q test for multiple comparisons set at an experimentwise error rate of 0.05 (Day & Quinn 1989).

Correlations Between Predator and Prey Abundance

Multiple regression analyses were run to determine the relationship between predator and prey abundance. The dependent variable, crab abundance per tow for three size classes of crabs (i.e., < 50 mm, ≤ 80 mm and > 80 mm CW), was regressed against prey abundance (i.e. crab abundance, bivalve, polychaete, and crustacean density), and the indicator variables station (i.e., downriver, upriver) and year (i.e., 1988, 1989). The prey categories selected for analyses represent the dominant dietary and benthic components. Abundance data were log-transformed to meet assumptions of normality and homogeneity of variance (Chatterjee & Price 1977, Zar 1984). Standardized residuals were plotted against the fitted values and against the various independent variables to determine whether violations of model assumptions or misspecification of the model occurred (Chatterjee & Price 1977). Violations would be reflected by a systematic pattern of variation to the residuals rather than random scatter.

The full regression model was:

$$Y_i = \beta_o + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_4 + \Gamma_1 S + \delta_1 Y$$

where Y_i = crab abundance with each size class analyzed separately

$\beta o, \beta 1 \ldots \beta 6$, $\Gamma 1$, $\delta 1$ = the model partial regression coefficients

X_1 = crab abundance for each size class so that when the dependent variable was abundance of crabs > 80 mm CW, this independent variable was either abundance of crabs ≤ 80 mm or < 50 mm. Similarly, for Y_i = abundance of crabs < 50 or ≤ 80 mm CW, X_1 = large crab (i.e., > 80 mm CW) abundance. Therefore, analyses were run for each possible crab size class combination in conjunction with prey density and indicator variables.

X_2, X_3, X_4 = mean bivalve, polychaete, and crustacean density, respectively

S & Y = dummy variables with one of two possible values each: downriver=1, upriver=0; 1988=1, 1989=0

The best model was subsequently determined using stepwise regression with backwards elimination until the minimum t-ratio was greater than 1 (Chatterjee & Price 1977). Residual plots were inspected as above to evaluate the fit of the models.

Cannibalism

Morphological cues used to differentiate blue crabs were lateral spines, claw parts, the distal portion of the walking legs, and paddle fins. Results for the incidence of cannibalism are presented as percent frequency of occurrence of blue crabs in the diet. Frequency of occurrence is a measure of the regularity of inclusion of a food item in the diet of a sample or population. Occurrence was recorded as presence or absence, and calculated by the equation (Williams 1981):

$$\% F_i = \frac{b_i}{n} X 100$$

where $\% F_i$ is the percent frequency of occurrence of cannibalism, b_i is the number of crabs whose gastric mills contained conspecifics, and n is the number of crabs in the sample without empty guts. Log-likelihood analysis was used to analyze cannibalism as a function of year, river, month, and size class (G-test: Sokal & Rohlf 1981). Due to differences in sampling associated with size class and month in the two years, comparisons were made for three size classes (i.e., 60-99, 100-134, > 134 mm CW) and three months (July through September). A further analysis to include the main effect of station was conducted, but the occurrence of frequencies less than 5 or equal to 0 (Sokal & Rohlf 1981) limited comparisons to July and August.

Multiple regression analysis was run to determine the relationship between cannibalism and crab abundance. The dependent variable, percent frequency of occurrence of cannibalism, was regressed against mean abundance of new juvenile recruits (i.e., crabs < 50 mm CW) or the combined mean abundance of new recruits and older juveniles (i.e., crabs ≤ 80 mm CW), and the indicator variables River (i.e., James, York, Rappahannock), Month (i.e., July, August, September) and Year (i.e., 1988, 1989). Cannibalism data were arcsin square-root transformed while abundance data were log-transformed to meet assumptions of normality and homogeneity of variance (Zar 1984). The full regression model was:

$$Y_i = \beta_o + \beta_1 X_1 + \Gamma_1 R_1 + \Gamma_2 R_2 + \delta_1 M_1 + \delta_2 M_2 + \alpha_1 Y$$

where Y_i = percent frequency of occurrence of cannibalism

β_o, β_1, Γ_1, Γ_2, δ_1, δ_2, α_1 = the model partial regression coefficients

X_1 = abundance of either new juvenile recruits or new recruits and older juveniles (i.e., < 50 mm & ≤ 80 mm CW crabs, respectively).

R_1, R_2, M_1, M_2, Y = dummy variables representing River, Month and Year, respectively, and having the values: $R_1=1$ $R_2=0$ for James, $R_1=0$ $R_2=1$ for York, $R_1=0$ $R_2=0$ for Rappahannock; $M_1=1$ $M_2=0$ for July, $M_1=0$ $M_2=1$ for August, $M_1=0$ $M_2=0$ for September; $Y=1$ for 1988, $Y=0$ for 1989.

The best fit was determined with stepwise multiple regression using backwards elimination until the minimum t-ratio was greater than 1 (Chatterjee & Price 1977). Residuals were examined after all analyses, outliers were deleted and the regression equation was reestimated (Chatterjee & Price 1977).

RESULTS

Blue Crab Abundance

Summer 1988

Seasonal population structure of blue crabs collected in 1988 is depicted in Fig. 2. The 1988 year class juveniles (i.e., crabs < 50 mm CW) recruited in September, and by October the population primarily consisted of new juvenile recruits.

Total crab abundance varied significantly among stations (Table 1a). Though River and Month were significant, there was a significant interaction (i.e., River X Month, Table 1a). Most of the variation in abundance was associated with Station (21.3 %, Table 1a). Crabs were most abundant at upriver stations (Fig. 2). Relatively high variation in abundance was due to the River X Month interaction (13.3 %, Table 1a). Crab abundance in the three rivers was similar in July (ANOVA: F=2.86, df=2,9, $P < 0.1095$), August (F=1.17, df=2,9, $P < 0.3546$) and September (F=0.51, df=2,9, $P < 0.6181$), but not in October (F=9.67, df=2,9, $P < 0.0057$): crabs were most abundant in the Rappahannock (Table 1b). Analyses of Month within each level of River indicated no seasonal effects in the James (ANOVA: F=3.48, df=3,12, $P < 0.0503$), York (F=1.77, df=3,12, $P < 0.2054$) or Rappahannock (F=0.82, df=3,12, $P < 0.5059$). As in most analyses, variation due to error was relatively high (20.8 %, Table 1a), indicating a need to increase the number of tows per station.

Most of the variation in the abundance of large juveniles and adults (i.e., > 80 mm CW) was associated with Month (27.4 %, Table 2a). Crabs were more abundant in August than September or October, and more abundant in July than October (Table 2c). Stations differed such that crabs were most abundant upriver (Table 2a). Crabs were more abundant in the Rappahannock than York (Table 2b), and the order of river

Figure 2. Population size structure of blue crabs collected at downriver and upriver stations from June through October, 1988. Rivers were pooled. Solid bars = males, Cross-hatched bars = juvenile females, Stippled bars = adult females. Numbers above the bars represent total sample size if greater than 100.

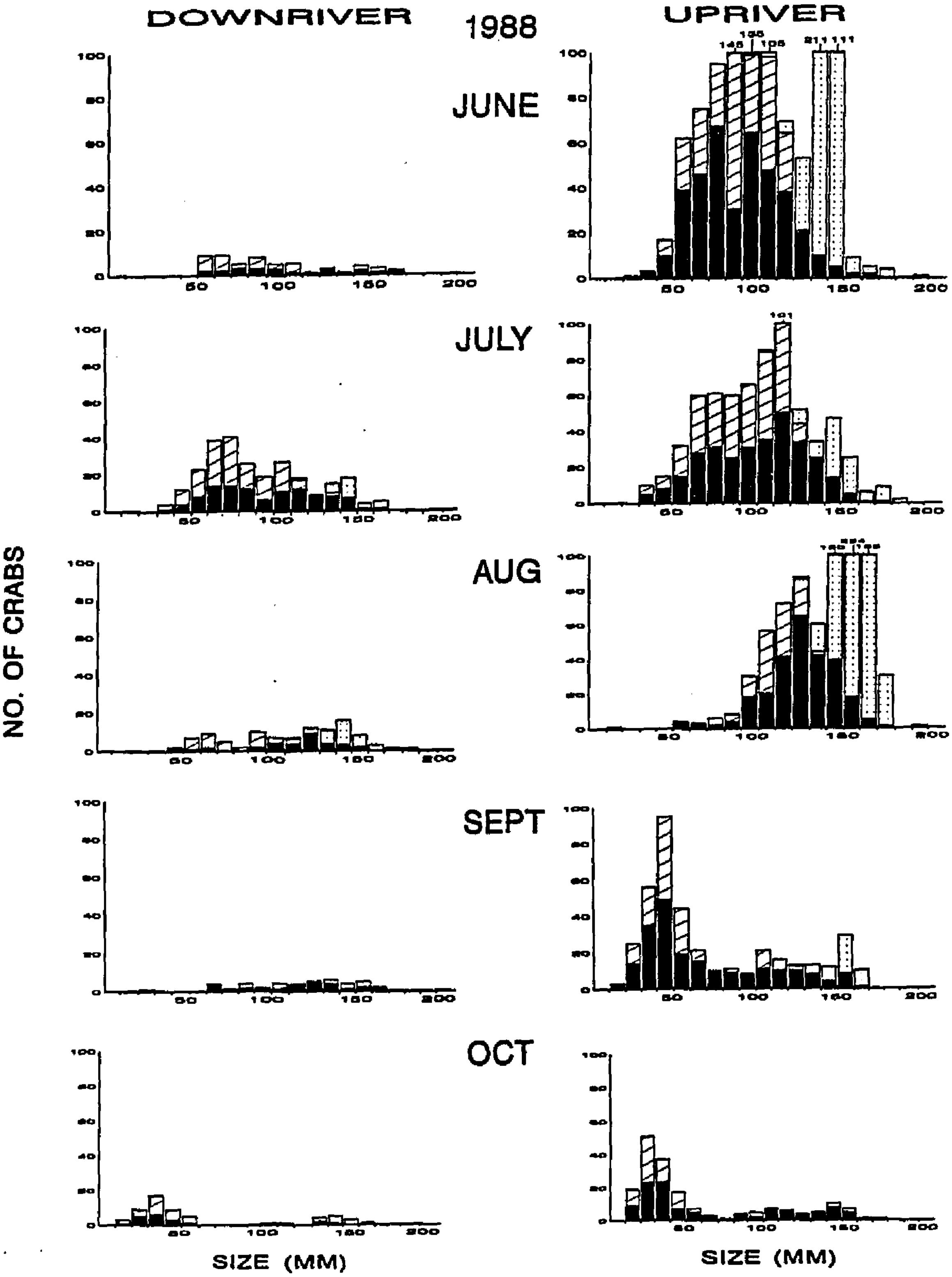

DOWNRIVER
1988
UPRIVER
JUNE
JULY
AUG
SEPT
OCT
NO. OF CRABS
SIZE (MM)
SIZE (MM)
0
20
40
60
80
100
50
100
150
200
145
185
105
211
111
101
150
224
185

Table 1. (a) Three-way analysis of variance with river, station and month as factors, and the dependent variable, log-transformed total crab abundance for each set of two monthly tows per station in 1988.

SOURCE OF VARIATION	DF	SS	PERCENTAGE OF VARIATION	MS	F	P<
RIVER	2	3.9723	18.3%	1.9861	10.49	0.0005
STATION	1	4.6348	21.3%	4.6348	24.48	0.0001
MONTH	3	2.9729	13.7%	0.9910	5.23	0.0064
RIVERxSTATION	2	0.1340	0.6%	0.0670	0.35	0.7055
RIVERxMONTH	6	2.8954	13.3%	0.4826	2.55	0.0471
STATIONxMONTH	3	0.7613	3.5%	0.2538	1.34	0.2847
RIVERxSTATIONxMONTH	6	1.8396	8.5%	0.3066	1.62	0.1850
ERROR	24	4.5436	20.8%	0.1893		

(b) Ryan's Q results for rivers in October, 1988. Means sharing the same line are not significantly different. * P < 0.05

YORK	JAMES		RAPPAHANNOCK
0.43	0.75	*	1.64

abundance, from greatest to least was: Rappahannock, James, York (Table 2b).

Variation in abundance of juveniles ≤ 80 mm CW produced significant interactions (i.e., River X Month and Station X Month; Table 3a). Most variation occurred with the River X Month interaction (23.3 %, Table 3a). Examination of Month within each level of River indicated seasonal effects in the Rappahannock (ANOVA: F=7.40, df=3,12, $P < 0.0046$) and James (F=5.16, df=3,12, $P < 0.0161$), but not in the York (F=0.93, df=3,12, $P < 0.4565$). More crabs occurred in the Rappahannock in October than in August or September (Table 3b). Crabs were also more abundant in July than August (Table 3b). Abundances in August and September were equally low (Table 3b). Juvenile crabs were most abundant in the James in July (Table 3b). Rivers, compared within each level of Month, were significantly different in July (ANOVA: F=8.79, df=2,9, $P < 0.0076$) and October (F=27.18, df=2,9, $P < 0.0002$). Lowest abundance occurred in the York in July, while abundances in the James and Rappahannock were comparably high (Table 3c). Crabs were most abundant in the Rappahannock in October (Table 3c).

The significant Station X Month interaction effect accounted for 13.3 % of the variation in crab abundance (Table 3a). Analyses of Month within each level of Station indicated no significant seasonal differences in crab abundance at either downriver (F=2.21, df=3,20, $P < 0.1179$) or upriver (F=3.07, df=3,20, $P < 0.0515$) stations. Analysis of Station within each level of Month was significant only in September (ANOVA: F=21.72, df=1,10, $P < 0.0009$): significantly more crabs were collected upriver.

In the analysis of abundance of the newly recruited 1988 year class (i.e., < 50 mm CW), the River X Month and Station X Month interaction effects were highly significant (Table 4a). The River X Month effect accounted for most variation in abundance (26.8%, Table 4a). Analysis of abundance between months within each level of River indicated significant seasonal effects in the Rappahannock (ANOVA:

Table 2. (a) Three-way analysis of variance with river, station and month as factors, and the dependent variable, log-transformed crab abundance for each set of two monthly tows per station and crabs > 80 mm CW in 1988.

SOURCE OF VARIATION	DF	SS	PERCENTAGE OF VARIATION	MS	F	P <
RIVER	2	2.1113	11.6 %	1.0557	6.23	0.0066
STATION	1	3.3306	18.3 %	3.3306	19.66	0.0002
MONTH	3	4.9853	27.4 %	1.6618	9.81	0.0002
RIVERXSTATION	2	0.4818	2.6 %	0.2409	1.42	0.2609
RIVERXMONTH	6	0.9354	5.1 %	0.1559	0.92	0.4979
STATIONXMONTH	3	0.2923	1.6 %	0.0974	0.57	0.6370
RIVERXSTATIONXMONTH	6	1.9819	10.9 %	0.3303	1.95	0.1135
ERROR	24	4.0667	22.4 %	0.1694		

(b) Ryan's Q results for river, months and stations pooled. Means sharing the same line are not significantly different.

YORK	JAMES	RAPPAHANNOCK
0.88	1.10	1.40

(c) Ryan's Q results for months, stations and rivers pooled. Means sharing the same line are not significantly different.

OCTOBER	SEPTEMBER	JULY	AUGUST
0.65	1.01	1.38	1.46

Table 3. (a) Three-way analysis of variance with river, station and month as factors, and the dependent variable, log-transformed crab abundance for each set of two monthly tows per station and crabs ≤ 80 mm CW in 1988.

SOURCE OF VARIATION	DF	SS	PERCENTAGE OF VARIATION	MS	F	P<
RIVER	2	3.7657	18.5%	1.8828	14.58	0.0001
STATION	1	2.4744	12.2%	2.4744	19.16	0.0002
MONTH	3	2.4232	11.9%	0.8077	6.25	0.0027
RIVERxSTATION	2	0.3612	1.8%	0.1806	1.40	0.2665
RIVERxMONTH	6	4.7404	23.3%	0.7901	6.12	0.0005
STATIONxMONTH	3	2.7069	13.3%	0.9023	6.99	0.0015
RIVERxSTATIONxMONTH	6	0.7387	3.6%	0.1231	0.95	0.4768
ERROR	24	3.0997	15.3%	0.1292		

(b) Ryan's Q results for months in the Rappahannock and James rivers. Means sharing the same line are not significantly different.

Rappahannock:	AUGUST	SEPTEMBER	JULY	OCTOBER
	0.70	0.93	1.47	1.57
	———	———	———	———
		———	———	

James:	OCTOBER	AUGUST	SEPTEMBER	JULY
	0.24	0.49	0.53	1.52
	———	———	——— *	———

Table 3 (cont).

(c) Ryan's Q results for river comparisons in July and October, 1988. Means sharing the same line are not significantly different. * $P < 0.05$

July:	YORK		RAPPAHANNOCK	JAMES		
	0.41	*	1.47	1.52		
	———		———————	———————		
October:	JAMES	YORK		RAPPAHANNOCK		
	0.24	0.25	*	1.57		
	———————	———————		———————		

F=10.86, df=3,12, $P < 0.0010$): relatively more new recruits were collected in October than in July, August or September (Table 4b). Rivers compared within each level of Month were significantly different in July (ANOVA: F=11.19, df=2,9, $P < 0.0036$), August (F=9.00, df=2,9, $P < 0.0071$) and October (F=38.52, df=2,9, $P < 0.0001$). In July, juveniles were least abundant in the York (Table 4c). Newly recruited crabs did not occur at sampling stations in the York or James in August. New recruits were most abundant in the Rappahannock in October (Table 4c). The significant Station X Month interaction effect accounted for 15.4 % of the variation in new recruit abundance (Table 4a). Analysis of monthly abundance within each level of Station was significant for upriver (ANOVA: F=4.33, df=3,20, $P < 0.0166$), but not downriver (F=1.68, df=3,20, $P < 0.2043$) stations. New recruits were more abundant in September than August (Table 4d). Comparisons of Station within each level of Month were significant in September (ANOVA: F=15.92, df=1,10, $P < 0.0026$): highest abundances occurred upriver.

In summary, juvenile crab recruitment began in September, and by October the population consisted primarily of new juvenile recruits. Juveniles and newly recruited crabs were usually more abundant at upriver sites, particularly in the fall. The analysis further indicated: (1) Crabs were generally more abundant at upriver stations; (2) Differences between rivers sometimes occurred such that crabs were most abundant in the Rappahannock; (3) Seasonal trends within rivers were usually associated with the influx of newly-recruited 1988 year-class juveniles in the fall.

Summer 1989

Seasonal population structure of blue crabs in 1989 is depicted in Fig. 3. More juvenile crabs (< 50 mm CW) were collected in June, 1989 (Fig. 3), reflecting recruitment of the 1988 year class (Hines et al. 1990, Lipcius & Van Engel 1990). The 1989 year class began recruiting as early as August, and by October the population primarily consisted of juvenile crabs < 50 mm CW (Fig. 3).

Table 4. (a) Three-way analysis of variance with river, station and month as factors, and the dependent variable, log-transformed crab abundance for each set of two monthly tows per station and crabs < 50 mm CW in 1988.

SOURCE OF VARIATION	DF	SS	PERCENTAGE OF VARIATION	MS	F	P<
RIVER	2	2.4888	15.2%	1.2444	14.93	0.0001
STATION	1	1.8744	11.4%	1.8744	22.48	0.0001
MONTH	3	2.4094	14.7%	0.8031	9.63	0.0002
RIVERxSTATION	2	0.1799	1.1%	0.0899	1.08	0.3558
RIVERxMONTH	6	4.3945	26.8%	0.7324	8.78	0.0001
STATIONxMONTH	3	2.5252	15.4%	0.8417	10.10	0.0002
RIVERxSTATIONxMONTH	6	0.5115	3.1%	0.0853	1.02	0.4347
ERROR	24	2.0010	12.2%	0.0834		

(b) Ryan's Q results for months in the Rappahannock river in 1988. Means sharing the same line are not significantly different. * P < 0.05

AUGUST	SEPTEMBER	JULY		OCTOBER
0.23	0.58	0.77		1.54
────────	────────	────────	*	────────

(c) Ryan's Q results for rivers in July and October, 1988. Means sharing the same line are not significantly different. * P < 0.05

July:

YORK		JAMES	RAPPAHANNOCK
0.08		0.69	0.77
────	*	────────	────────

October:

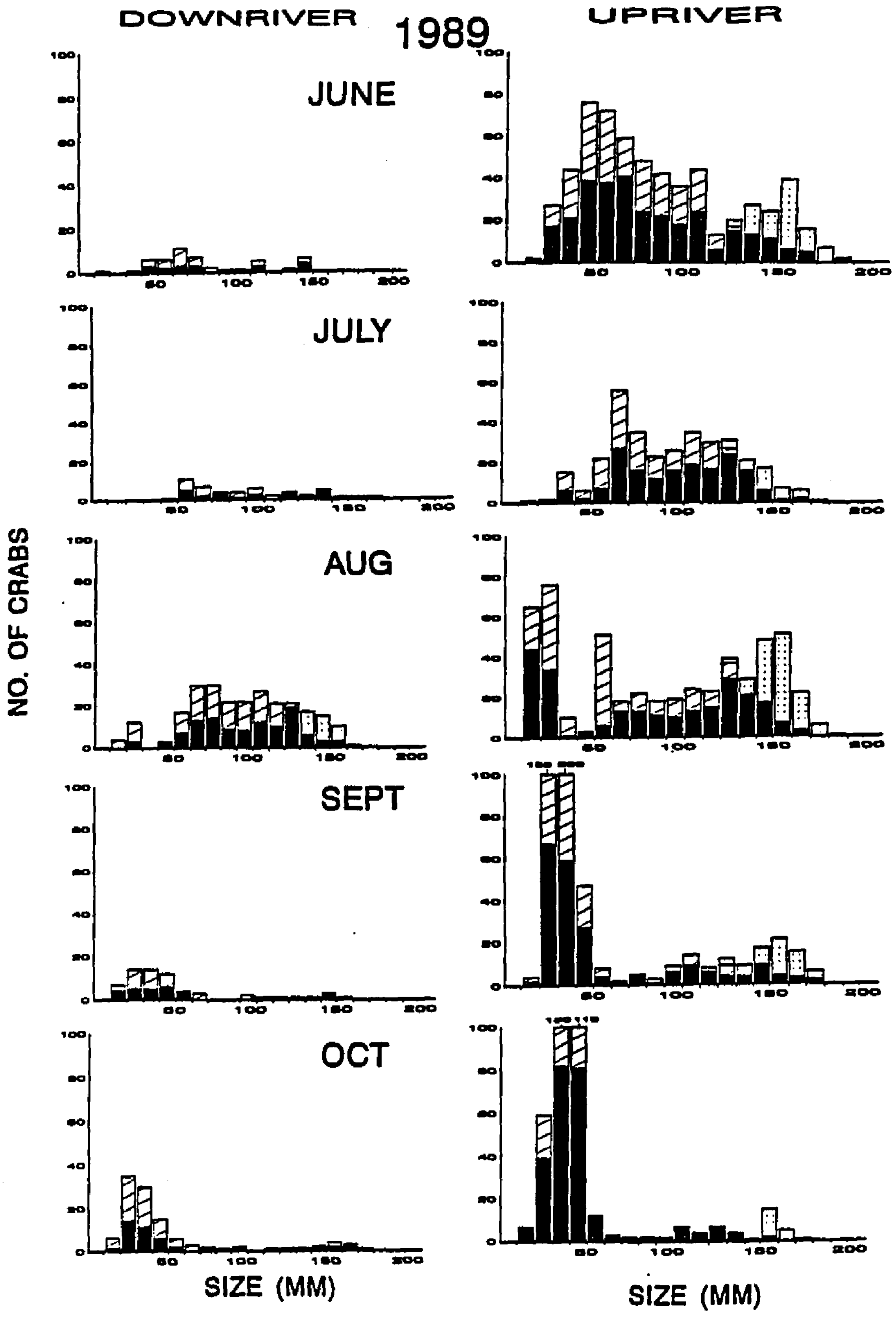
JAMES	YORK		RAPPAHANNOCK
0.15	0.15		1.54
────────	────────	*	────────

Table 4 (cont).

(d) Ryan's Q results for months at upriver sampling sites in 1988. Means sharing the same line are not significantly different.

AUGUST	JULY	OCTOBER	SEPTEMBER
0.05	0.57	0.79	1.20
———	———	———	
	———	———	———

Figure 3. Population size structure of blue crabs collected at downriver and upriver stations from June through October, 1989. Rivers were pooled. Solid bars = males, Cross-hatched bars = juvenile females, Stippled bars = adult females. Numbers above the bars represent total sample size if greater than 100.

DOWNRIVER
1989
UPRIVER
JUNE
JULY
AUG
SEPT
OCT
NO. OF CRABS
0
20
40
60
80
100
50
100
150
200
150 200
120 119
SIZE (MM)
SIZE (MM)

In the analysis of total blue crab abundance (Table 5a), the River X Month and Station X Month interaction effects were significant (Table 5a). The River X Month interaction effect accounted for 10.9 % of the variation in crab abundance (Table 5a). Analysis of Month within each level of River indicated no seasonal differences in any river (ANOVA: James: F=0.15, df=3,12, $P < 0.9289$; York: F=2.08, df=3,12, $P < 0.1569$; Rappahannock: F=1.15, df=3,12, $P < 0.3677$). Similarly, there were no significant differences in crab abundance between rivers for any month (ANOVA: June: F=0.34, df=2,9, $P < 0.7197$; July: F=0.46, df=2,9, $P < 0.6471$; August: F=1.32, df=2,9, $P < 0.3133$; September: F=1.28, df=2,9, $P < 0.3231$). Thus, the River X Month interaction effect was not due to distinct patterns in abundance, but likely due to differing trends in abundance.

The Station X Month interaction effect accounted for 6.8 % of the variation in crab abundance (Table 5a). Seasonal effects occurred at downriver (ANOVA: F=7.06, df=3,20, $P < 0.0020$), but not upriver stations (F=0.88, df=3,20 $P < 0.4675$): crabs were most abundant downriver in August (Table 5b, Fig. 3). Analysis for Station within each level of Month indicated significant differences throughout the sampling period (ANOVA: June: F=31.96, df=1,10, $P < 0.0002$; July: F=18.42, df=1,10, $P < 0.0016$; August: F=6.97, df=1,10, $P < 0.0248$; September: F=15.79, df=1,10, $P < 0.0026$): crabs were always more abundant upriver.

The River X Station X Month interaction effect was significant in the analysis of large juvenile and adult blue crab abundance (i.e., > 80 mm CW, Table 6). Analysis of River and Station within each level of Month indicated significant Station, but not River, effects in June and September (Table 7a): crabs were most abundant upriver. The River X Station interaction effect was significant in July and August (Table 7a), necessitating examination of effects within each level of the main factors (Table 7b). Stations differed in the Rappahannock in July, and in the James and Rappahannock in August (Table 7b(i)): crabs were

Table 5. (a) Three-way analysis of variance with river, station and month as factors, and the dependent variable, log-transformed total crab abundance for each set of two monthly tows per station in 1989.

SOURCE OF VARIATION	DF	SS	PERCENTAGE OF VARIATION	MS	F	P<
RIVER	2	0.0481	0.4%	0.0240	0.43	0.653
STATION	1	6.6961	52.4%	6.6961	120.90	0.0001
MONTH	3	1.4457	11.3%	0.4819	8.70	0.0004
RIVERxSTATION	2	0.1972	1.5%	0.0986	1.78	0.1902
RIVERxMONTH	6	1.3970	10.9%	0.2328	4.20	0.0050
STATIONxMONTH	3	0.8647	6.8%	0.2882	5.20	0.0065
RIVERxSTATIONxMONTH	6	0.7975	6.2%	0.1329	2.40	0.0585
ERROR	24	1.3293	10.4%	0.0554		

(b) Ryan's Q results for months at downriver stations in 1989. Means sharing the same line are not significantly different. * P < 0.05

JULY	JUNE	SEPTEMBER	AUGUST
0.86	0.87	0.98	1.57
———	———	———	* ———

Table 6. Three-way analysis of variance with river, station and month as factors, and the dependent variable, log-transformed crab abundance for each set of two monthly tows per station and crabs > 80 mm CW in 1989.

SOURCE OF VARIATION	DF	SS	PERCENTAGE OF VARIATION	MS	F	P<
RIVER	2	0.1818	1.2 %	0.0909	1.83	0.1818
STATION	1	7.7851	50.2 %	7.7851	156.91	0.0001
MONTH	3	3.1533	20.3 %	1.0511	21.18	0.0001
RIVERxSTATION	2	0.4926	3.2 %	0.2463	4.96	0.0157
RIVERxMONTH	6	0.9090	5.9 %	0.1515	3.05	0.0230
STATIONxMONTH	3	1.0451	6.7 %	0.3484	7.02	0.0015
RIVERxSTATIONxMONTH	6	0.7486	4.8 %	0.1248	2.51	0.0495
ERROR	24	1.1908	7.7 %	0.0496		

Table 7. (a) Two-way analysis of variance for river and station within each level of month, and the dependent variable, log-transformed crab abundance for each set of two monthly tows per station and crabs > 80 mm CW in 1989.

MONTH	SOURCE OF VARIATION	DF	SS	MS	F	P <
JUNE	RIVER	2	0.0746	0.0373	0.37	0.7043
	STATION	1	3.7241	3.7241	37.11	0.0009
	RIVERXSTATION	2	0.1489	0.0745	0.74	0.5154
	ERROR	6	0.6021	0.1004		
JULY	RIVER	2	0.0465	0.0233	0.49	0.6344
	STATION	1	2.0559	2.0559	43.41	0.0006
	RIVERXSTATION	2	0.7575	0.3788	8.00	0.0203
	ERROR	6	0.2842	0.0474		
AUGUST	RIVER	2	0.5309	0.2655	42.21	0.0003
	STATION	1	0.3178	0.3178	50.52	0.0004
	RIVERXSTATION	2	0.0754	0.0377	5.99	0.0371
	ERROR	6	0.0377	0.0063		
SEPTEMBER	RIVER	2	0.4387	0.2194	4.93	0.0541
	STATION	1	2.7324	2.7324	61.47	0.0002
	RIVERXSTATION	2	0.2593	0.1297	2.92	0.1303
	ERROR	6	0.2667	0.0445		

Table 7 (cont).

(b) Lower-level (i.e., one-way) analysis of variance for (i) station within each level of river and (ii) river within each level of station in July and August.

(i)

MONTH	RIVER	SOURCE OF VARIATION	DF	SS	MS	F	P <
JULY	JAMES	STATION	1	0.4171	0.4171	10.47	0.0837
		ERROR	2	0.0796	0.0398		
	YORK	STATION	1	0.1049	0.1049	2.69	0.2424
		ERROR	2	0.0779	0.0389		
	RAPP	STATION	1	2.2914	2.2914	36.18	0.0265
		ERROR	2	0.1267			
AUGUST	JAMES	STATION	1	0.2028	0.2028	35.13	0.0273
		ERROR	2	0.0115	0.0058		
	YORK	STATION	1	0.1800	0.1800	14.13	0.0640
		ERROR	2	0.0255	0.0127		
	RAPP	STATION	1	0.0104	0.0104	29.07	0.0327
		ERROR	2	0.0007			

Table 7 (cont).

(ii)

MONTH	STATION	SOURCE OF VARIATION	DF	SS	MS	F	P <
JULY	DOWNRIVER	RIVER	2	0.4419	0.2210	2.94	0.1964
		ERROR	3	0.2255	0.0752		
	UPRIVER	RIVER	2	0.3622	0.1811	9.26	0.0520
		ERROR	3	0.0586	0.0195		
AUGUST	DOWNRIVER	RIVER	2	0.4908	0.2454	36.33	0.0079
		ERROR	3	0.0203	0.0068		
	UPRIVER	RIVER	2	0.1155	0.0577	9.92	0.0476
		ERROR	3	0.0175	0.0058		

(c) Ryan's Q results for river, downriver and upriver in August. Means sharing the same line are not significantly different. * P < 0.05

Downriver:	JAMES	YORK		RAPPAHANNOCK
	1.02	1.24		1.71
			*	

Upriver:	JAMES	YORK	RAPPAHANNOCK
	1.47	1.67	1.81

always more abundant upriver. Rivers differed downriver and upriver in August (Table 7b(ii)): crabs were generally most abundant in the Rappahannock (Table 7c).

The analysis of River and Month within each level of Station (Table 8a) indicated significant River and Month effects upriver. Crabs were most abundant in the Rappahannock, and densities were higher in June and August than September (Table 8e). A significant River X Month interaction occurred downriver (Table 8a). Examination of factors within each level of the main effects indicated significant river differences in August (Table 7c) and September (Table 8b(i)): crabs were most abundant in the Rappahannock in August and in the James in September (Table 8c). Months differed downriver in the Rappahannock (Table 8b(ii)): crabs were most abundant in August (Table 8d).

The analysis of Station and Month within each level of River indicated significant Station differences in the James and York (Table 9a): crabs were most abundant upriver. Months differed in the York (Table 9a): crabs were more abundant in August than September (Table 9c). The Station X Month interaction effect was significant in the Rappahannock (Table 9a). Lower-level ANOVA indicated significant Station differences in all months (Table 9b(i)): crabs were always more abundant upriver. Months differed downriver and upriver in the Rappahannock (Table 9b(ii),d) as described above (Table 8d,e).

Most of the variation in abundance of juvenile crabs $\leq$ 80 mm CW was associated with station location (27.7 %, Table 10a). Crabs were always more abundant at upriver locations (Fig. 3). A significant River X Month interaction effect accounted for 23.6 % of the variation (Table 10a). Analysis of seasonal abundance within each level of River was significant for the York (ANOVA: $F=5.39$, $df=3,12$, $P < 0.0140$): more crabs occurred in August and September than in July (Table 10b). Comparisons between rivers within each level of Month were not significant (ANOVA: June: $F=0.81$, $df=2,9$, $P < 0.4738$; July: $F=2.06$, $df=2,9$, $P < 0.1834$; August: $F=0.83$, $df=2,9$, $P < 0.466$; September:

Table 8. (a) Two-way analysis of variance for river and month within each level of station, and the dependent variable, log-transformed crab abundance for each set of two monthly tows per station and crabs > 80 mm CW.

STATION	SOURCE OF VARIATION	DF	SS	MS	F	P <
DOWNRIVER	RIVER	2	0.1660	0.0830	1.26	0.3183
	MONTH	3	3.6215	1.2072	18.35	0.0001
	RIVERXMONTH	6	1.4159	0.2360	3.59	0.0284
	ERROR	12	0.7896	0.0658		
UPRIVER	RIVER	2	0.5084	0.2542	7.60	0.0074
	MONTH	3	0.5769	0.1923	5.75	0.0112
	RIVERXMONTH	6	0.2417	0.0403	1.21	0.3675
	ERROR	12	0.4012	0.0334		

(b) Lower-level (i.e., one-way) analysis of variance for (i) river within each level of month, downriver and (ii) month within each level of river, downriver.

(i)

MONTH	SOURCE OF VARIATION	DF	SS	MS	F	P <
JUNE	RIVER	2	0.0398	0.0199	0.12	0.8906
	ERROR	3	0.4954	0.1651		
JULY	RIVER	2	0.4419	0.2210	2.94	0.1964
	ERROR	3	0.2255	0.0752		
AUGUST	RIVER	2	0.4908	0.2454	36.33	0.0079
	ERROR	3	0.0203	0.0068		
SEPTEMBER	RIVER	2	0.6094	0.3047	18.87	0.0200
	ERROR	3	0.0484	0.0161		

Table 8 (cont).

(ii)

RIVER	SOURCE OF VARIATION	DF	SS	MS	F	P <
JAMES	MONTH	3	0.1935	0.0645	2.39	0.2091
	ERROR	4	0.1078	0.0269		
YORK	MONTH	3	1.3226	0.4409	3.19	0.1458
	ERROR	4	0.5524	0.1381		
RAPP	MONTH	3	3.5213	1.1738	36.27	0.0023
	ERROR	4	0.1295	0.0324		

(c) Ryan's Q results for rivers, downriver in September. Means sharing the same line are not significantly different. * P < 0.05

September:	RAPPAHANNOCK	YORK		JAMES
	0.00	0.15		0.74
	————	————	*	————

(d) Ryan's Q results for months, downriver in the Rappahannock. Means sharing the same line are not significantly different. * P < 0.05

SEPTEMBER	JULY	JUNE		AUGUST
0.00	0.24	0.39		1.71
————	————	————	*	————

(e) Ryan's Q results for rivers, upriver, months pooled and months, upriver, rivers pooled. Means sharing the same line are not significantly different. * P < 0.05

River:	YORK	JAMES		RAPPAHANNOCK
	1.32	1.47		1.68
	————	————	*	————

Month:	SEPTEMBER	JULY	JUNE	AUGUST
	1.25	1.45	1.60	1.65
	————	————		
		————	————	————

Table 9. (a) Two-way analysis of variance for station and month within each level of river, and the dependent variable, log-transformed crab abundance for each set of two monthly tows per station and crabs > 80 mm CW in 1989.

RIVER	SOURCE OF VARIATION	DF	SS	MS	F	P <
JAMES	STATION	1	1.8452	1.8452	99.75	0.0001
	MONTH	3	0.0893	0.0298	1.61	0.2621
	STATIONXMONTH	3	0.1699	0.0566	3.06	0.0914
	ERROR	8	0.1480	0.0185		
YORK	STATION	1	1.6685	1.6685	15.32	0.0045
	MONTH	3	1.4464	0.4821	4.43	0.0411
	STATIONXMONTH	3	0.3007	0.1002	0.92	0.4736
	ERROR	8	0.8712	0.1089		
RAPPAHANNOCK	STATION	1	4.7640	4.7640	222.11	0.0001
	MONTH	3	2.5265	0.8422	39.26	0.0001
	STATIONXMONTH	3	1.3232	0.4411	20.56	0.0004
	ERROR	8	0.1716	0.0214		

Table 9 (cont).

(b) Lower-level (i.e., one-way) analysis of variance for (i) station within each level of month, and (ii) month within each level of station in the Rappahannock river.

(i)

MONTH	SOURCE OF VARIATION	DF	SS	MS	F	P <
JUNE	STATION	1	2.0255	2.0255	119.03	0.0083
	ERROR	2	0.0340	0.0170		
JULY	STATION	1	2.2914	2.2914	36.18	0.0265
	ERROR	2	0.1267	0.0633		
AUGUST	STATION	1	0.0104	0.0104	29.07	0.0327
	ERROR	2	0.0007	0.0004		
SEPTEMBER	STATION	1	1.7599	1.7599	346.18	0.0029
	ERROR	2	0.0102	0.0051		

(ii)

STATION	SOURCE OF VARIATION	DF	SS	MS	F	P <
DOWNRIVER	MONTH	3	3.5213	1.1738	36.27	0.0023
	ERROR	4	0.1295	0.0324		
UPRIVER	MONTH	3	0.3284	0.1095	10.40	0.0233
	ERROR	4	0.0421	0.0105		

Table 9 (cont).

(c) Ryan's Q results for months in the York river, stations pooled. Means sharing the same line are not significantly different.

SEPTEMBER	JUNE	JULY	AUGUST
0.61	0.93	0.99	1.46
———	———	———	
	———	———	———

(d) Ryan's Q results for months, upriver in the Rappahannock river. Means sharing the same line are not significantly different. * $P < 0.05$

Upriver:	SEPTEMBER		JULY	AUGUST	JUNE
	1.33		1.75	1.81	1.81
	———	*	———	———	———

Table 10. (a) Three-way analysis of variance with river, station and month as factors, and the dependent variable, log-transformed crab abundance for each set of two monthly tows per station and crabs ≤ 80 mm CW in 1989.

SOURCE OF VARIATION	DF	SS	PERCENTAGE OF VARIATION	MS	F	P<
RIVER	2	0.4217	3.0%	0.2108	1.84	0.1799
STATION	1	3.8721	27.7%	3.8721	33.87	0.0001
MONTH	3	0.9437	6.8%	0.3146	2.75	0.0647
RIVERxSTATION	2	0.2509	1.8%	0.1255	1.10	0.3499
RIVERxMONTH	6	3.3005	23.6%	0.5501	4.81	0.0024
STATIONxMONTH	3	0.8624	6.2%	0.2875	2.51	0.0824
RIVERxSTATIONxMONTH	6	1.5793	11.3%	0.2632	2.30	0.0675
ERROR	24	2.7437	19.6%	0.1143		

(b) Ryan's Q results for months in the York river in 1989. Means sharing the same line are not significantly different.

JULY	JUNE	AUGUST	SEPTEMBER
0.52	0.87	1.45	1.64

F=3.17, df=2,9, P < 0.0909).

Station location was highly significant and accounted for the most variation in abundance (32.9 %, Table 11a) of newly recruited 1988 or 1989 year-class crabs < 50 mm CW. These were more abundant at upriver locations (Fig. 3). There was a significant River X Month interaction (15.4 % of variation, Table 11a). Comparisons between rivers within each level of Month indicated no significant differences in abundance for any month (ANOVA: June: F=1.30, df=2,9, P < 0.3187; July: F=0.46, df=2,9, P < 0.6455; August: F=0.31, df=2,9, P < 0.7400; September: F=2.85, df=2,9, P < 0.1099). However, seasonal differences in abundance occurred in the York river (ANOVA: F=6.59, df=3,12, P < 0.0070): more new recruits occurred in September than in June or July (Table 11b).

In summary, recruitment of the 1989 year-class began as early as August, and by September and October the population was dominated by new juvenile recruits. In general there was: (1) greater abundance of all crab size classes at upriver stations, (2) seasonal trends in abundance within rivers due to recruitment of the new year class in the fall, and (3) similar abundance between rivers for older juveniles and new recruits, but generally greater abundance of adults in the Rappahannock river.

Similar patterns in blue crab abundance occurred in 1988 and 1989 such that crabs were most abundant upriver and in the Rappahannock river, and seasonal trends in abundance were associated with the influx of new recruits in the fall. However, recruitment occurred earlier in 1989, while small juveniles were generally less abundant in 1988.

Sampling Requirements for Diet Analysis

Most food items occurring in the guts of blue crabs were fragmented, but identifiable (Appendix 3). The percentage of identifiable prey types increased sharply to a mean of 64 % (7 of 11) at sample sizes of 3-7 crabs (Fig. 4a-c). Asymptotic maxima of the number of food types occurred at sample sizes of 7 (J27, small crabs, Fig. 4a) to 18 (Y25, medium crabs, Fig. 4b) crabs. Therefore, a minimum sample

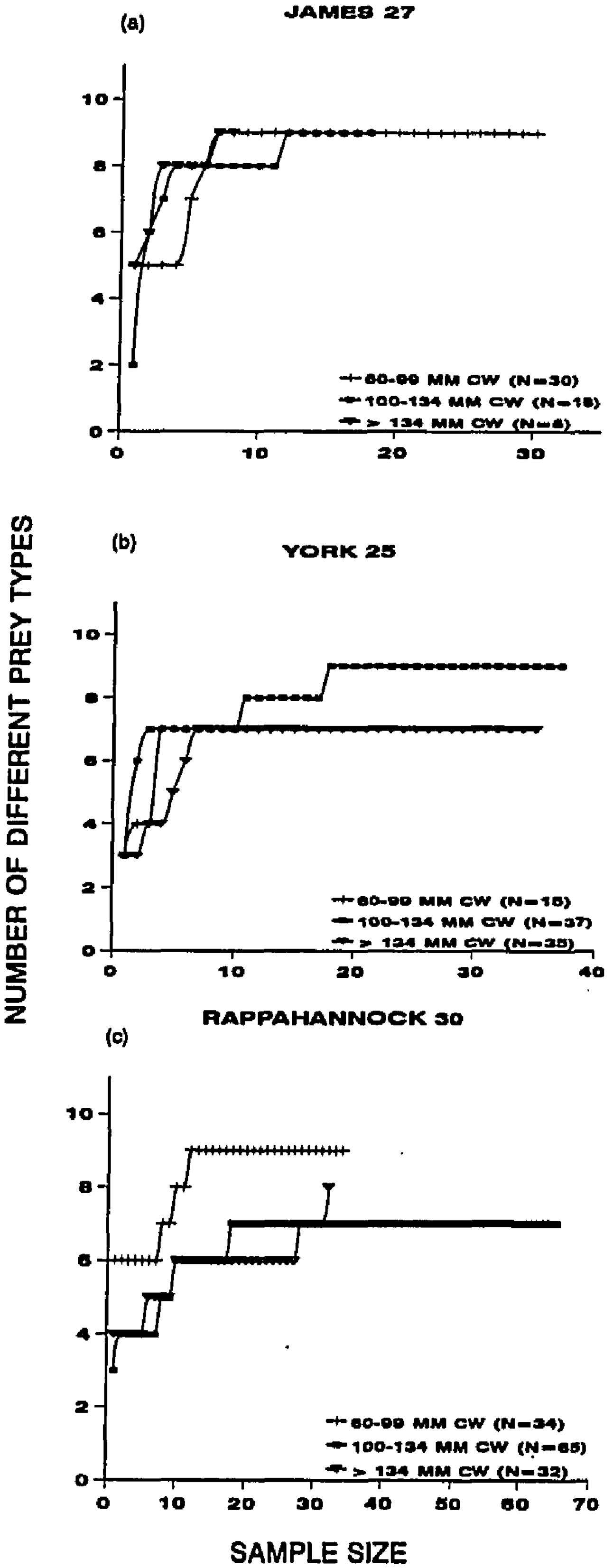
Table 11. (a) Three-way analysis of variance with river, station and month as factors, and the dependent variable, log-transformed crab abundance for each set of two monthly tows per station and crabs < 50 mm CW in 1989.

SOURCE OF VARIATION	DF	SS	PERCENTAGE OF VARIATION	MS	F	P<
RIVER	2	0.3830	2.3%	0.1915	1.67	0.2099
STATION	1	5.5162	32.9%	5.5162	48.02	0.0001
MONTH	3	3.4329	20.5%	1.1443	9.96	0.0002
RIVERxSTATION	2	0.6657	4.0%	0.3329	2.90	0.0746
RIVERxMONTH	6	2.5976	15.4%	0.4329	3.77	0.0087
STATIONxMONTH	3	0.1787	1.1%	0.0596	0.52	0.6734
RIVERxSTATIONxMONTH	6	1.2279	7.3%	0.2047	1.78	0.1456
ERROR	24	2.7569	16.5%	0.1149		

(b) Ryan's Q results for months in the York river in 1989. Means sharing the same line are not significantly different.

JULY	JUNE	AUGUST	SEPTEMBER
0.23	0.42	0.98	1.60
———	———	———	
		———	———

Figure 4. Cumulative numbers of food types in the foreguts of three size classes of blue crabs in relation to sample size for crabs collected in 1988 from the three upriver stations: (a) James, (b) York and (c) Rappahannock Rivers.

(a)
JAMES 27
10
8
6
4
2
0
0
10
20
30
60-99 MM CW (N=30)
100-134 MM CW (N=18)
> 134 MM CW (N=6)
(b)
YORK 25
10
8
6
4
2
0
0
10
20
30
40
60-99 MM CW (N=15)
100-134 MM CW (N=37)
> 134 MM CW (N=35)
RAPPAHANNOCK 30
(c)
10
8
6
4
2
0
0
10
20
30
40
50
60
70
60-99 MM CW (N=34)
100-134 MM CW (N=65)
> 134 MM CW (N=32)
NUMBER OF DIFFERENT PREY TYPES
SAMPLE SIZE

size of 7 foreguts was required to quantify gut contents of blue crabs. The mean number of food types per crab increased with gut fullness (Fig. 5). In general, asymptotes were reached at 25-50 % gut fullness.

Blue Crab Diet: Spatial and Temporal Patterns

Summer 1988

The strategy in the multivariate (i.e., cluster) analysis of diet entailed two components. First, samples, meeting a minimum sample size of 7, were partitioned by all factor combinations jointly (i.e., river, month, station, and size) to determine general features of the blue crab diet. Second, particular factors or factor combinations were collapsed to assess the specific effects of non-collapsed factors upon diet. In the fully-partitioned analysis, the data clustered into 5 groups (Fig. 6a), which were used to examine dietary differences between these groups (Fig. 6b). The major food items consumed by all blue crabs, regardless of grouping, were bivalves and crabs, with minor consumption of polychaetes and miscellaneous prey consisting of hydroids, gastropods, insects, crustaceans, fish and plants (Fig. 6b). In general, the groups could be separated by the proportions of bivalve, crab and polychaete prey in the diet (Fig. 6b). Some groupings were distinguished by their very high (group 2: 0.87 - 0.99) and very low (group 5: 0) proportions of bivalves. Similarly, crab consumption ranged from 0.79 (group 5) to low levels (groups 1-3). Diet diversity was equally variable with lowest values for group 2 (Fig. 6a) which reflected the almost exclusive consumption of bivalves (Fig. 6b). One group (i.e., group 4) had a moderate proportion of bivalves (0.30-0.68) and high proportion of crabs (0.12-0.52). Most crabs in group 4 were large (i.e., > 134 mm). Blue crabs occurred in 17.8 % of the guts, with the remainder consisting of xanthids, one spider crab, and unknown species. The polychaete fraction was needed to differentiate group 3 from groups 1 and 4, such that group 3 had the highest proportion of polychaetes (0.53) in the diet (Fig. 6b).

Figure 5. Mean number (± S.E.) of food types per crab in relation to percent gut fullness for three size classes of blue crabs collected in July, 1988 from the three upriver stations in the James (JA27), York (YK25) and Rappahannock (RA30) Rivers. Numbers in parentheses represent sample size.

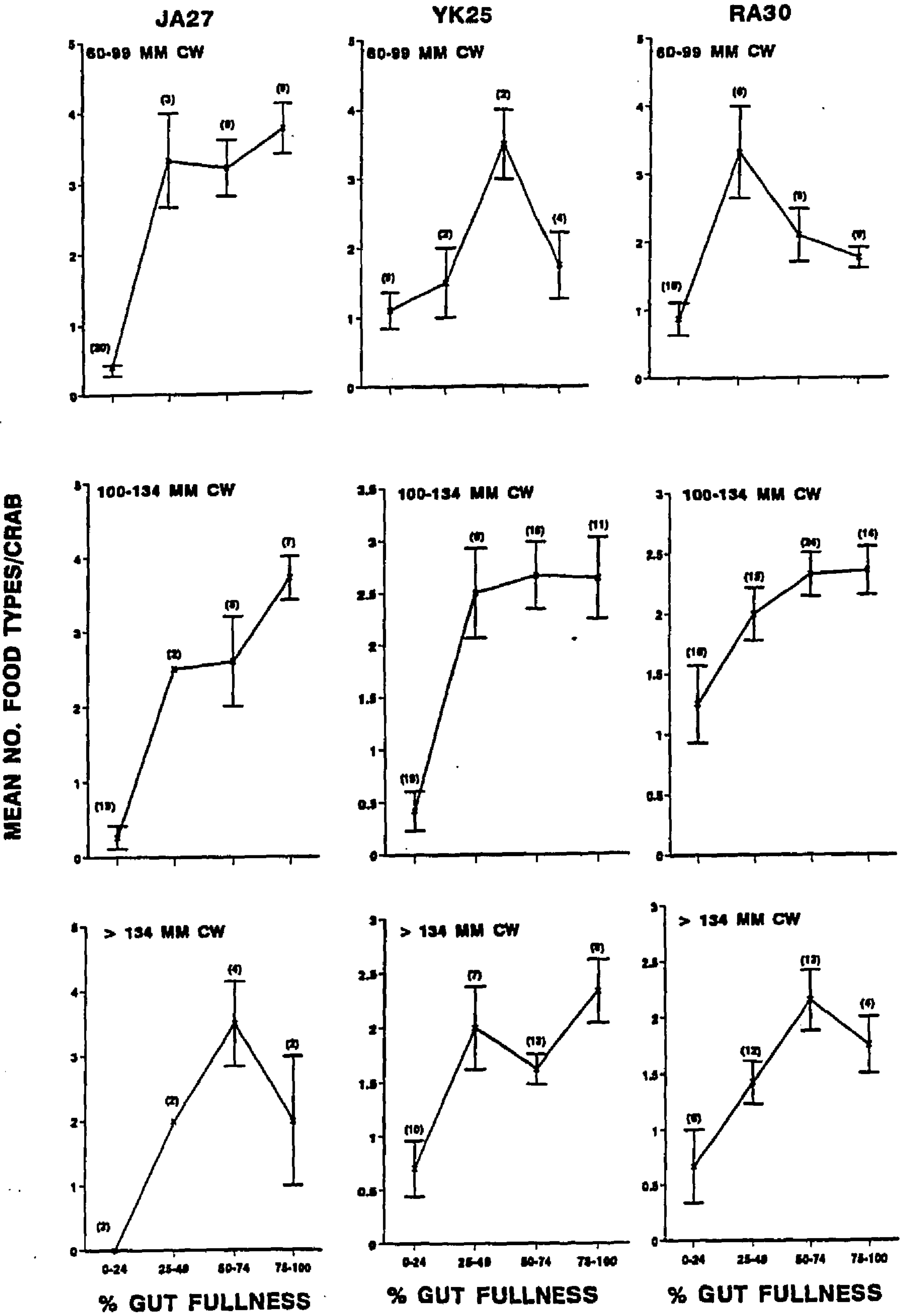
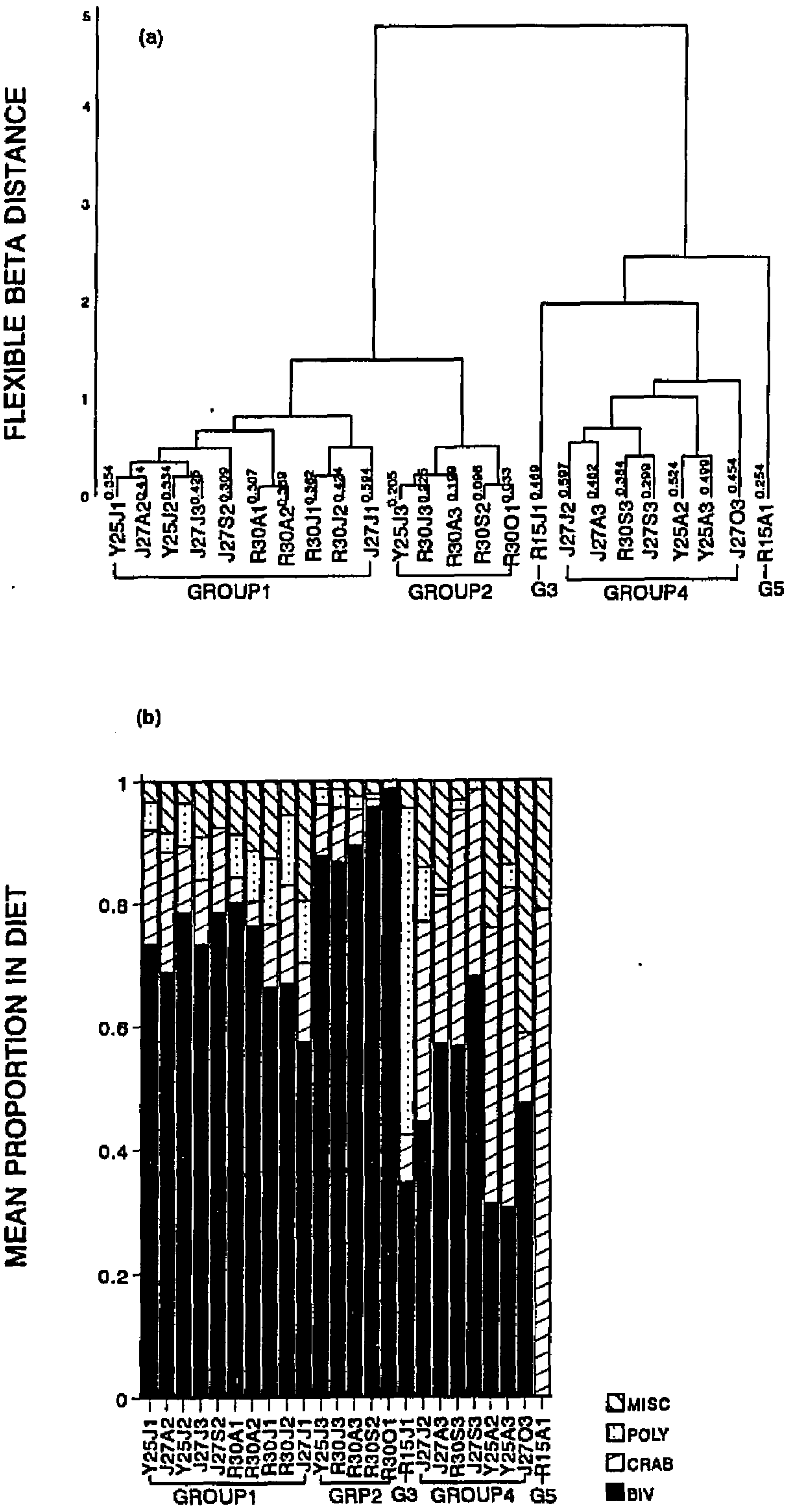

JA27
YK25
RA30
60-99 MM CW
100-134 MM CW
> 134 MM CW
MEAN NO. FOOD TYPES/CRAB
0-24
25-49
50-74
75-100
% GUT FULLNESS

Figure 6. (a) Cluster diagram representing diet similarity in 1988 for the station (Y25=York25, J27=James27, R15=Rappahannock15, R30=Rappahannock30), month (J=July, A=August, S=September, O=October), and size class (1=60-99 mm, 2=100-134 mm, 3≥134 mm) combinations with a minimum sample size of 7 crabs. The Shannon-Weiner diversity index is given at the root of each branch. Sample sizes were: Group 1 = 293, Group 2 = 144, Group 3 = 21, Group 4 = 73, Group 5 = 8. (b) Diet composition in blue crabs illustrated as proportion in the diet for the station-month-size class combinations described in (a). Major food items in the diet were bivalves, crabs and polychaetes. Minor items (see text for definition) were pooled into miscellaneous (i.e., hydroids, gastropods, insects, crustaceans, fish, plants).


(a)
FLEXIBLE BETA DISTANCE
0
1
2
3
4
5
Y25J1
J27A2
Y25J2
J27J3
J27S2
R30A1
R30A2
R30J1
R30J2
J27J1
Y25J3
R30J3
R30A3
R30S2
R30O1
R15J1
J27J2
J27A3
R30S3
J27S3
Y25A2
Y25A3
J27O3
R15A1
GROUP1
GROUP2
G3
GROUP4
G5
(b)
MEAN PROPORTION IN DIET
0
0.2
0.4
0.6
0.8
1
GROUP1
GRP2
G3
GROUP4
G5
▨MISC
☐POLY
☐CRAB
■BIV

To examine the effects of river, station and crab size, diets were pooled across month; five groupings were apparent (Fig. 7a). Group 1 primarily comprised upriver stations, where the major food item consumed was bivalves, followed by moderate consumption of crabs, and minor amounts of polychaetes, fish, crustaceans, hydroids, gastropods, insects, and plants (Fig. 7b). Group 2 consisted of all crab size classes at the R30 station (Fig. 7a). This group was unique in its almost exclusive consumption of bivalves (Fig. 7b) and low diet diversity (Fig. 7a). Although clustering into three groups (i.e., Groups 3-5, Fig. 7), the downriver stations were very similar in the low proportions of bivalves and the relatively higher proportion of crabs, polychaetes or fish (Fig. 7b).

To clarify the effects of river and station, diets were collapsed across month and size. The river stations clustered into two major groups: downriver stations (group 1) and upriver stations (group 2; Fig. 8a). Bivalves (Fig. 8b) were consumed in the greatest proportions upriver and diet diversity was relatively low (Fig. 8a). Crabs at downriver stations (Fig. 8b) consumed proportionally fewer bivalves and more crabs (Y10, 6.7 % blue crab), polychaetes (R15), fish (Y10, J13), or gastropods (J13). Diet diversity was correspondingly higher in this group (Fig. 8a).

Crab size effects were examined by collapsing diets across station and month. Three groupings were apparent (Fig. 9a). The first group consisted of small crabs in all three rivers (i.e., 60-99 mm CW, Fig. 9a) and was characterized by a moderate consumption of bivalves, low consumption of crabs, and relatively high consumption of polychaetes (Fig. 9b). Group 2 comprised medium and large crabs in the York and James Rivers; these consumed proportionally more crabs and fish (Fig. 9b). Group 3 consisted of medium and large crabs in the Rappahannock. This group was unique in its high consumption of bivalves (Fig. 9b) and low diet diversity (Fig. 9a). The difference among rivers was only evident in larger crabs (medium and large): the James and York Rivers

Figure 7. (a) Cluster diagram representing diet similarity among three size classes of crabs collected from six stations in 1988. Months were pooled. The Shannon-Weiner diversity index is given at the root of each branch. Sample sizes were: Group 1 = 248, Group 2 = 313, Group 3 = 32, Group 4 = 15, Group 5 = 9. (b) Station differences in diet composition of three size classes of blue crabs illustrated as proportion in the diet for station-size combinations described in (a). Major food items in the diet were bivalves, crabs, polychaetes and fish. Minor items (see text for definition) were pooled into miscellaneous (i.e., hydroids, gastropods, insects, crustaceans, plants).

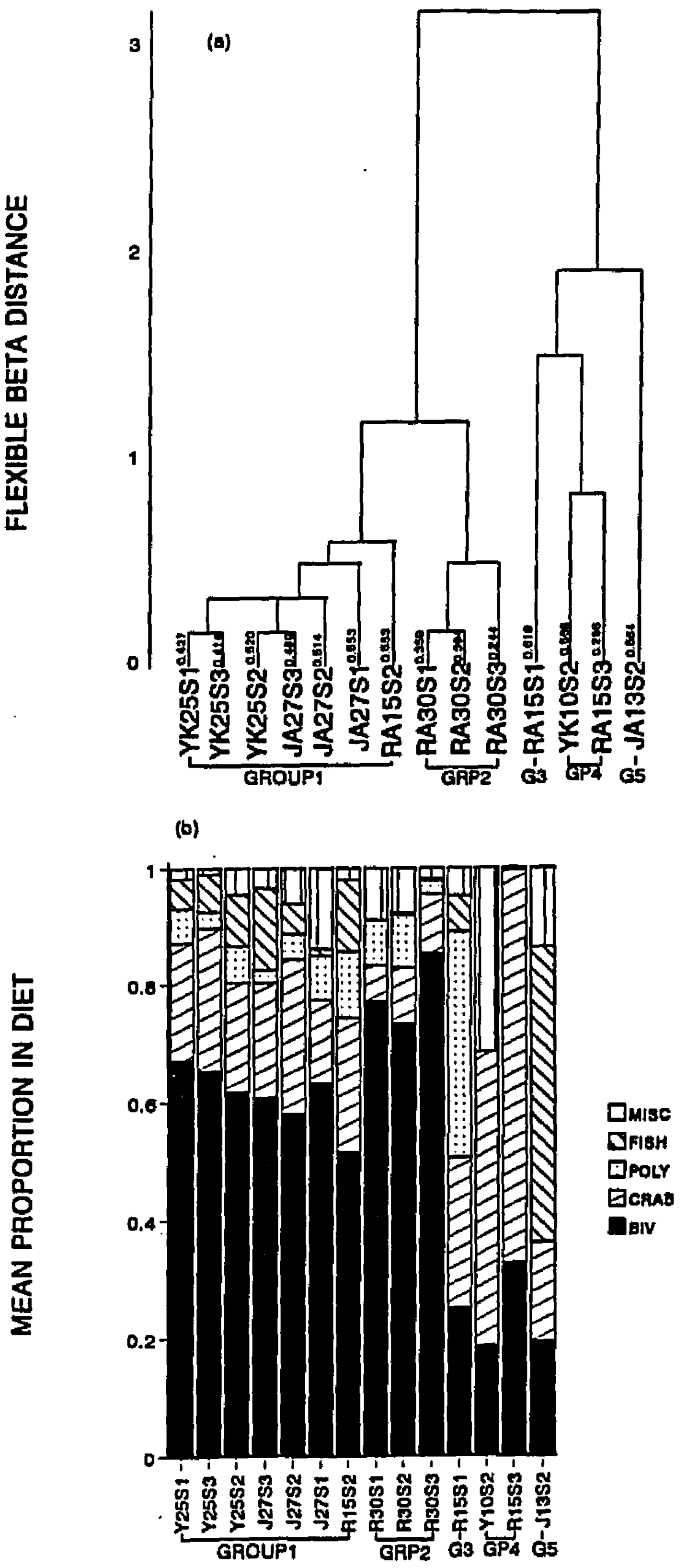
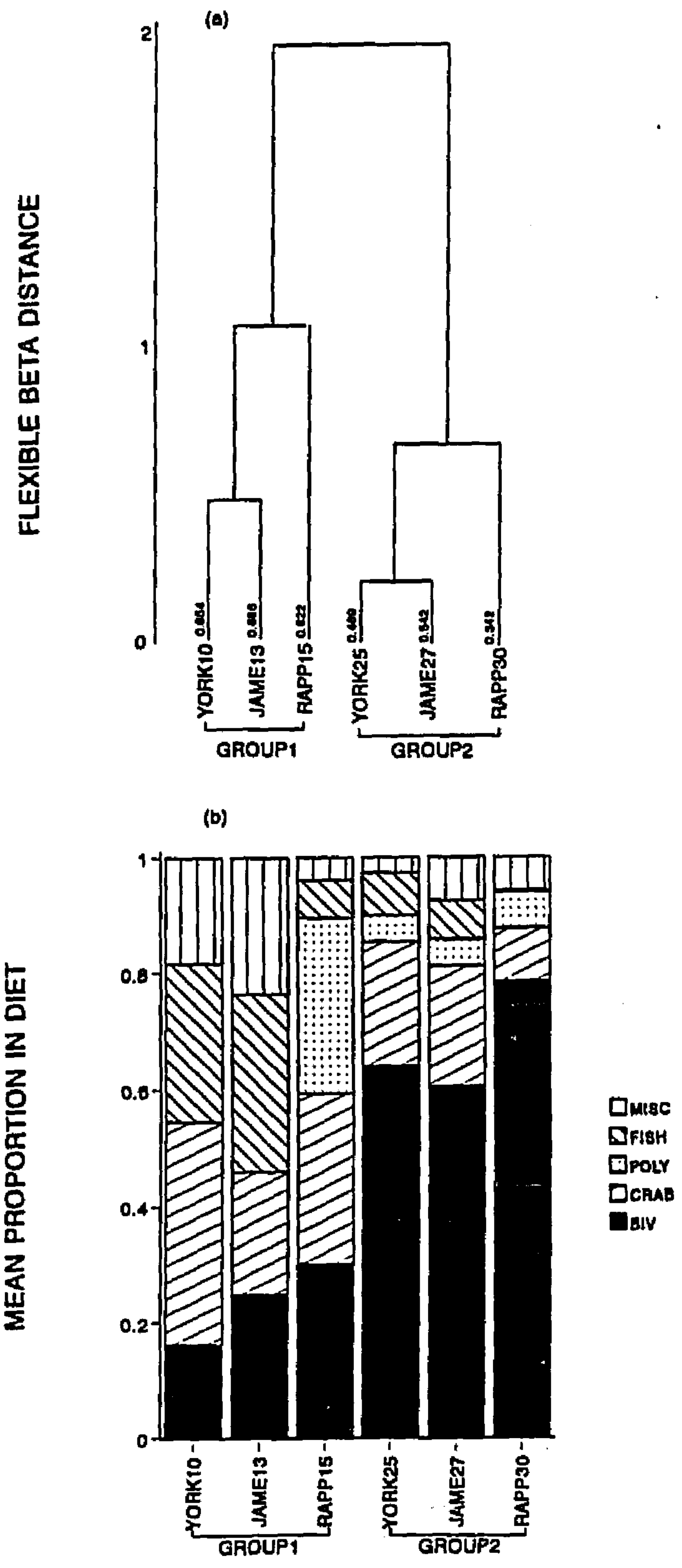
(a)
FLEXIBLE BETA DISTANCE
0
1
2
3
YK25S1 0.427
YK25S3
YK25S2 0.520
JA27S3
JA27S2 0.514
JA27S1 0.553
RA15S2 0.553
RA30S1 0.356
RA30S2
RA30S3 0.244
G-RA15S1 0.619
YK10S2
RA15S3 0.296
G-JA13S2 0.564
GROUP1
GRP2
G3
GP4
G5
(b)
MEAN PROPORTION IN DIET
0
0.2
0.4
0.6
0.8
1
Y25S1
Y25S3
Y25S2
J27S3
J27S2
J27S1
R15S2
R30S1
R30S2
R30S3
G-R15S1
Y10S2
R15S3
G-J13S2
GROUP1
GRP2
G3
GP4
G5
MISC
FISH
POLY
CRAB
BIV

Figure 8. (a) Cluster diagram representing diet similarity among crabs collected from six stations in 1988. Months and size classes were pooled. The Shannon-Weiner diversity index is given at the root of each branch. Sample sizes were: Group 1 = 76, Group 2 = 553. (b) Diet composition of blue crabs illustrated as proportion in the diet for the stations described in (a). Major food items in the diet were bivalves, crabs, polychaetes and fish. Minor items (see text for definition) were pooled into miscellaneous (i.e., hydroids, gastropods, insects, crustaceans, plants).


(a)
FLEXIBLE BETA DISTANCE
2
1
0
YORK10 0.654
JAME13 0.686
RAPP15 0.622
YORK25 0.469
JAME27 0.542
RAPP30 0.342
GROUP1
GROUP2
(b)
MEAN PROPORTION IN DIET
1
0.8
0.6
0.4
0.2
0
YORK10
JAME13
RAPP15
YORK25
JAME27
RAPP30
GROUP1
GROUP2
MISC
FISH
POLY
CRAB
BIV

separated from the Rappahannock River such that diet diversity was lowest in the Rappahannock (Fig. 9a), where crabs consumed the greatest proportion of bivalves (Fig. 9b).

There were no obvious seasonal effects on blue crab diet when rivers and stations were pooled (Fig. 10a). Although five groups differed in the relative proportions of bivalves, crabs, polychaetes and fish in the diet (Fig. 10b), there were no clear seasonal patterns.

In summary, the analysis of 1988 diets indicated the following major patterns: (1) Blue crab diets were separable on the basis of proportional consumption of bivalves, crabs and polychaetes, the dominant dietary components (Fig. 6); other dietary components, such as fish, hydroids, gastropods, insects, crustaceans other than crabs, and plants had little influence in cluster analysis within the Chesapeake Bay system. (2) Diets of crabs collected upriver differed from those of crabs collected downriver, such that upriver crabs consumed proportionally more bivalves and fewer crabs, polychaetes and fish (Figs. 7 & 8). (3) Diets of juveniles (60-99 mm CW) differed from those of larger juveniles and adult crabs (100-134 & > 134 mm CW) such that smaller juveniles generally ate proportionately more polychaetes, and fewer crabs and fish (Fig. 9). Large juveniles and adults in the Rappahannock River ate proportionately more bivalves than those in the York and James, where more crabs and fish were eaten (Fig. 9). (4) Some stations were uniquely separable from other stations; for instance, the upriver Rappahannock station (R30) had the highest proportions of bivalves in the diet (Figs. 7 & 8). (5) Neither seasonal (Fig. 10) nor broad inter-river patterns were apparent (e.g., Fig. 9).

Summer 1989

In 1989, analyses were similar except that a smaller size class of crabs (10-59 mm CW) was added. In the complete analysis, diets clustered into 7 groups (Fig. 11a). The major food item consumed by all crabs was bivalves, followed by crabs and polychaetes, and then minor consumption of hydroids, gastropods, insects, crustaceans, fish,

Figure 9. (a) Cluster diagram representing diet similarity among the three size classes of crabs collected in 1988 within the three rivers. Months and stations were pooled. The Shannon-Weiner diversity index is given at the root of each branch. Sample sizes were: Group 1 = 162, Group 2 = 205, Group 3 = 262. (b) Diet composition of blue crabs illustrated as proportion in the diet for the three rivers described in (a). Major food items in the diet were bivalves, crabs, polychaetes and fish. Minor items (see text for definition) were pooled into miscellaneous (i.e., hydroids, gastropods, insects, crustaceans, plants).

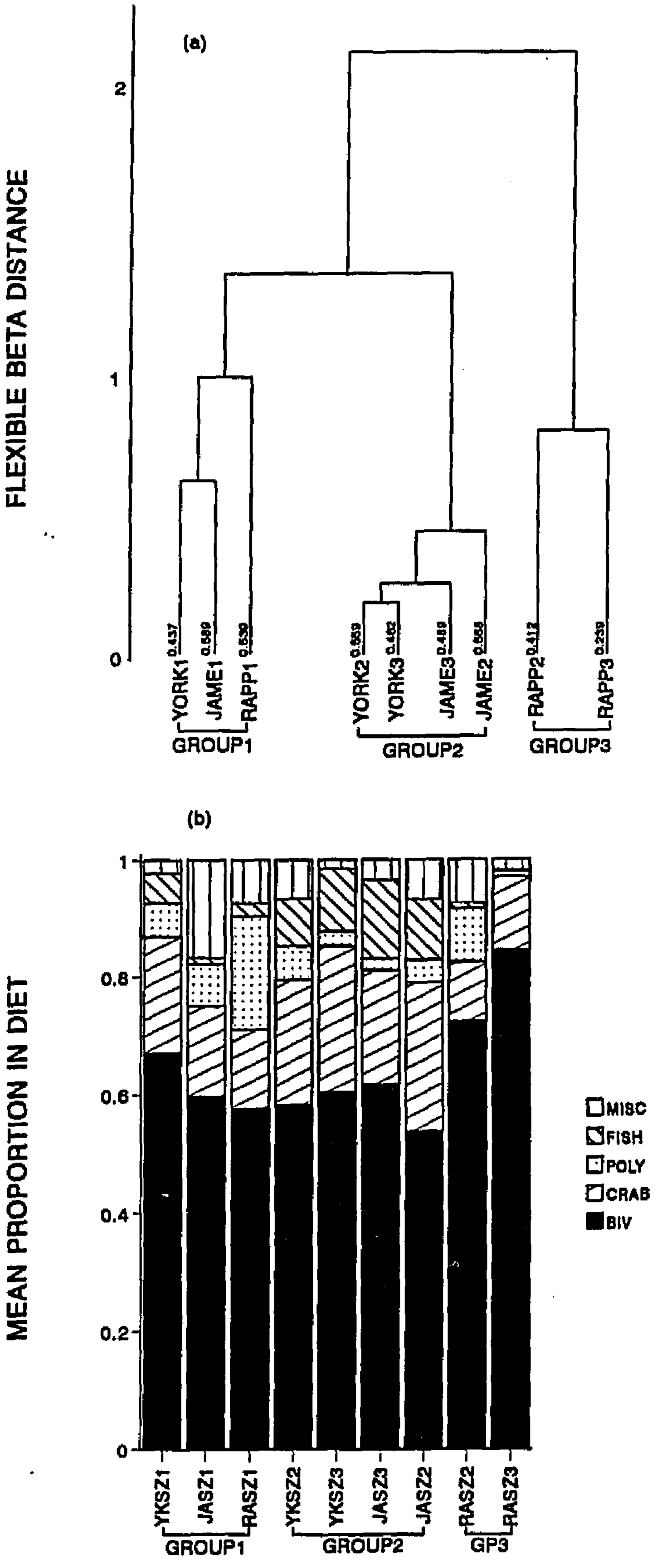
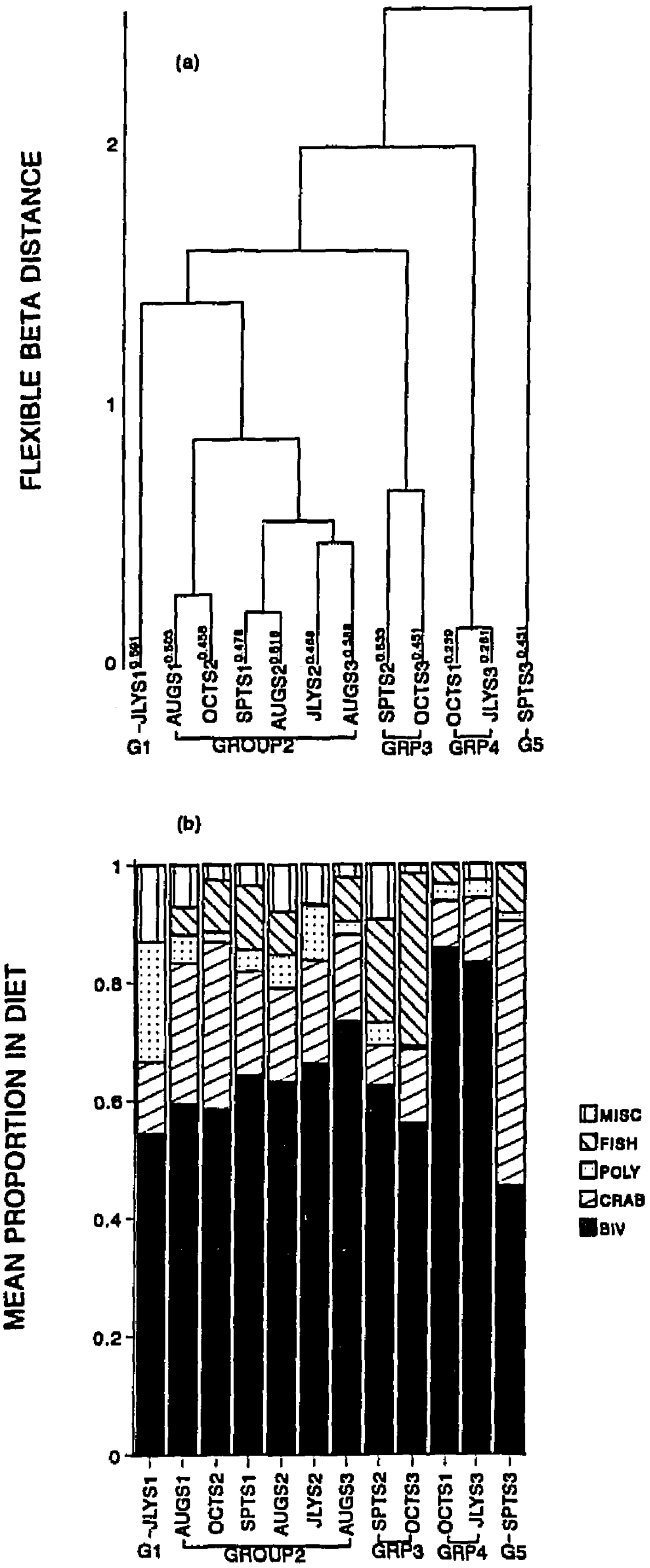

(a)
FLEXIBLE BETA DISTANCE
2
1
0
YORK1 0.437
JAME1 0.589
RAPP1 0.539
YORK2 0.559
YORK3 0.462
JAME3 0.489
JAME2 0.588
RAPP2 0.412
RAPP3 0.239
GROUP1
GROUP2
GROUP3
(b)
MEAN PROPORTION IN DIET
1
0.8
0.6
0.4
0.2
0
YKSZ1
JASZ1
RASZ1
YKSZ2
YKSZ3
JASZ3
JASZ2
RASZ2
RASZ3
GROUP1
GROUP2
GP3
MISC
FISH
POLY
CRAB
BIV

Figure 10. (a) Cluster diagram of food similarity among months for the three size classes of crabs collected in 1988. Rivers and stations were pooled. The Shannon-Weiner diversity index is given at the root of each branch. Sample sizes were: Group 1 = 104, Group 2 = 362, Group 3 = 43, Group 4 = 94, Group 5 = 26. (b) Diet composition of blue crabs illustrated as proportion in the diet for the four months described in (a). Major food items in the diet were bivalves, crabs, polychaetes and fish. Minor items (see text for definition) were pooled into miscellaneous (i.e., hydroids, gastropods, insects, crustaceans, plants).

(a)
FLEXIBLE BETA DISTANCE
0
1
2
JLYS1 0.591
AUGS1 0.553
OCTS2 0.456
SPTS1 0.478
AUGS2 0.518
JLYS2 0.468
AUGS3
SPTS2 0.533
OCTS3 0.451
OCTS1 0.259
JLYS3 0.261
SPTS3 0.431
G1
GROUP2
GRP3
GRP4
G5
(b)
MEAN PROPORTION IN DIET
0
0.2
0.4
0.6
0.8
1
JLYS1
AUGS1
OCTS2
SPTS1
AUGS2
JLYS2
AUGS3
SPTS2
OCTS3
OCTS1
JLYS3
SPTS3
G1
GROUP2
GRP3
GRP4
G5
MISC
FISH
POLY
CRAB
BIV

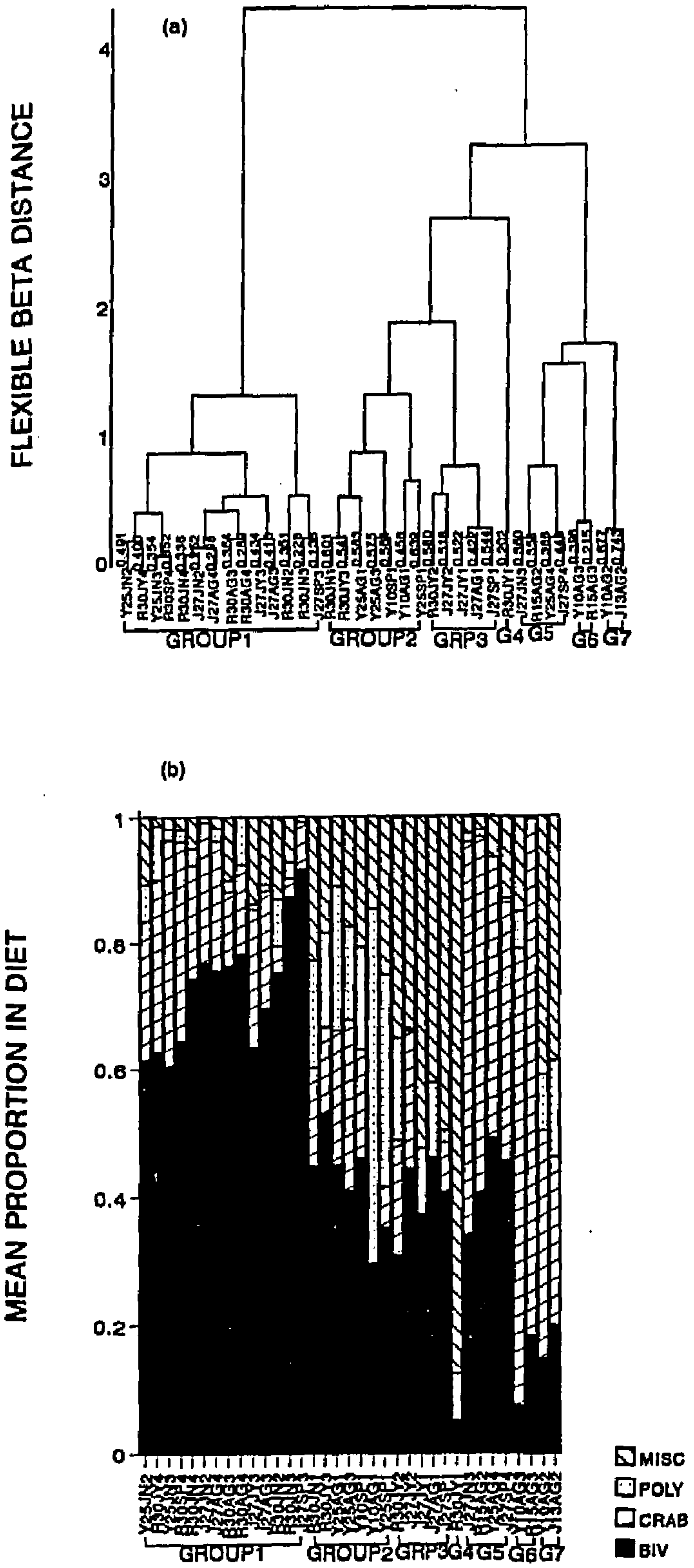
ophiuroids and plants (Fig. 11b). Although bivalves were consumed by all groups, the proportions in the diet again varied substantially from 0.05 - 0.92 (Fig. 11b). As in 1988, groups were separable based on their proportional consumption of bivalves, crabs and polychaetes (Fig. 11a,b). Some crabs (groups 1 and 4) were unique in their extremely high and low proportional consumption of bivalves (Fig. 11b). Crabs in group 1 were all large juveniles or adults (≥ 60 mm CW) from upriver stations. Blue crab remains occurred in 25.8 % of their guts (Fig. 11b). Diet diversity was relatively low (Fig. 11a). Group 4 (Fig. 11a) consisted of young juveniles < 60 mm CW collected at R30 in July. These crabs almost exclusively consumed small crustaceans other than crabs (Fig. 11b). Their diet diversity was the lowest of all groups (Fig. 11a).

Three groups (5, 6 & 7) were distinguishable based on their bivalve and crab consumption. All three groups were larger crabs (≥ 60 mm CW) that ate either low (groups 6 & 7) or moderate (group 5) amounts of bivalves and a moderate (groups 5 & 7) to high (group 6) proportion of crabs (Fig. 11b). Percent occurrence of blue crabs in the guts was 50 %, 46.7 % and 12.5 % for groups 5, 6 and 7 respectively. Within groups, blue crabs occurred most frequently in the diets of adults and very large juveniles > 99 mm CW (i.e., group 5: 47.9 % for crabs > 99 mm and 2.1 % for crabs 60-99 mm). A significant proportion of the diet of group 7 crabs consisted of gastropods (Fig. 11b), which also had the highest diet diversity (Fig. 11a).

The remaining groups (groups 2 & 3; Fig. 11a) were characterized by their moderate consumption of bivalves, crabs, and polychaetes. These groups were not separable on any single factor or combination thereof, although in group 3 crustaceans made up the major proportion of the diet (Fig. 11b).

To differentiate the combined effects of river, station and size, the data were pooled across month. Three groupings were apparent (Fig. 12a). Group 1 primarily comprised young juveniles (i.e., < 60 mm CW) whether upriver or downriver. Diet diversity was relatively high (Fig.

Figure 11. (a) Cluster diagram representing diet similarity in 1989 for the station (Y10=York10, Y25=York25, J13=James13, J27=James27, R15=Rappahannock 15, R30=Rappahannock30), month (JN=June, JY=July, AG=August, SP=September), and size class (1≤60 mm, 2=60-99 mm, 3=100-134 mm, 4≥134 mm) combinations with a minimal sample size of 7 crabs. The Shannon-Weiner diversity index is given at the root of each branch. Sample sizes were: Group 1 = 145, Group 2 = 100, Group 3 = 78, Group 4 = 12, Group 5 = 87, Group 6 = 15, Group 7 = 24.
(b) Diet composition in blue crabs illustrated as proportion in the diet for the station-month-size class combinations described in (a). Major food items in the diet were bivalves, crabs, and polychaetes. Minor items (see text for definition) were pooled into miscellaneous (i.e., hydroids, gastropods, insects, crustaceans, fish, ophiuroids, plants).


(a)
FLEXIBLE BETA DISTANCE
0
1
2
3
4
Y25JN2 0.491
R30JY4 0.409
Y25JN3 0.354
R30SP4 0.352
R30JN4 0.336
J27JN2 0.162
J27AG4 0.258
R30AG3 0.364
R30AG4 0.280
J27JY3 0.434
J27AG3 0.410
R30JN2 0.361
R30JN3 0.229
J27SP3 0.135
R30JN1 0.601
R30JY3 0.541
Y25AG1 0.563
Y25AG3 0.575
Y10SP1 0.558
Y10AG1 0.458
Y25SP1 0.639
R30JY2 0.580
J27JY2 0.518
J27JY1 0.522
J27AG1 0.427
J27SP1 0.544
R30JY1 0.202
J27JN3 0.560
R15AG2 0.334
Y25AG4 0.388
J27SP4 0.449
Y10AG3 0.398
R15AG3 0.215
Y10AG2 0.672
J13AG2 0.743
GROUP1
GROUP2
GRP3
G4
G5
G6
G7
(b)
MEAN PROPORTION IN DIET
0
0.2
0.4
0.6
0.8
1
GROUP1
GROUP2
GRP3
G4
G5
G6
G7
MISC
POLY
CRAB
BIV

12a), with moderate consumption of bivalves, high consumption of polychaetes and crustaceans, and low consumption of crabs (Fig. 12b). Groups 2 and 3 consisted of large juveniles and adults that consumed a relatively high proportion of crabs (Fig. 12b). Group 2 occurred only at downriver stations (Fig. 12a), where bivalve consumption was low (Fig. 12b), while diet diversity was generally high (Fig. 12a). This group consumed the most crabs (16.7 % blue crab) and gastropods (Fig.12b). Large crabs in group 3 were mostly from upriver stations (Fig. 12a). These crabs consumed the most bivalves and moderate to high quantities of crabs (Fig. 12b, 2.8 % blue crabs). Their diet diversity was the lowest of all groups (Fig. 12a).

To define river and station effects clearly, diets were collapsed across month and size. As in 1988, diets clustered into downriver (group 1) and upriver (group 2) sites (Fig. 13a). Crabs from downriver stations consumed fewer bivalves and more polychaetes, fish and gastropods (Fig. 13b). With the exception of R15 which had a high proportion of crabs (24 % blue crab remains), diet diversity was higher for this group (Fig. 13a). Crabs at upriver stations predominantly consumed bivalves and crustaceans (Fig. 13b).

When crab diets were lumped by rivers and stations (Fig. 14a) the data clustered into four groups indicating differences by crab size: groups 1 and 2 consisted of small juveniles, usually < 60 mm CW, whereas groups 3 and 4 crabs were all larger juveniles and adults ≥ 60 mm CW (Fig. 14a). Small juveniles consumed fewer bivalves and crabs, but proportionally more polychaetes and crustaceans (Fig. 14b). Diet diversity was generally higher for these crabs (Fig. 14a). Blue crabs occurred in 4.1 % of the guts of small juveniles (groups 1 & 2), with 2.6 % in crabs 60-99 mm CW and 1.5 % in crabs < 60 mm CW. In contrast, blue crabs occurred in 27.6 % of the guts of larger crabs (groups 3 & 4). Again there were no major seasonal differences in diet composition (Fig. 14).

The analysis of 1989 diets indicated the following major patterns:

Figure 12. (a) Cluster diagram representing diet similarity among four size classes of crabs collected from six stations in 1989. Months were pooled. The Shannon-Weiner diversity index is given at the root of each branch. Sample sizes were: Group 1 = 180, Group 2 = 55, Group 3 = 281. (b) Station differences in diet composition of four size classes of blue crabs illustrated as proportion in the diet for station-size combinations described in (a). Major food items in the diet were bivalves, crabs, polychaetes and crustaceans. Minor items (see text for definition) were pooled into miscellaneous (i.e., hydroids, gastropods, insects, fish, ophiuroids, plants).

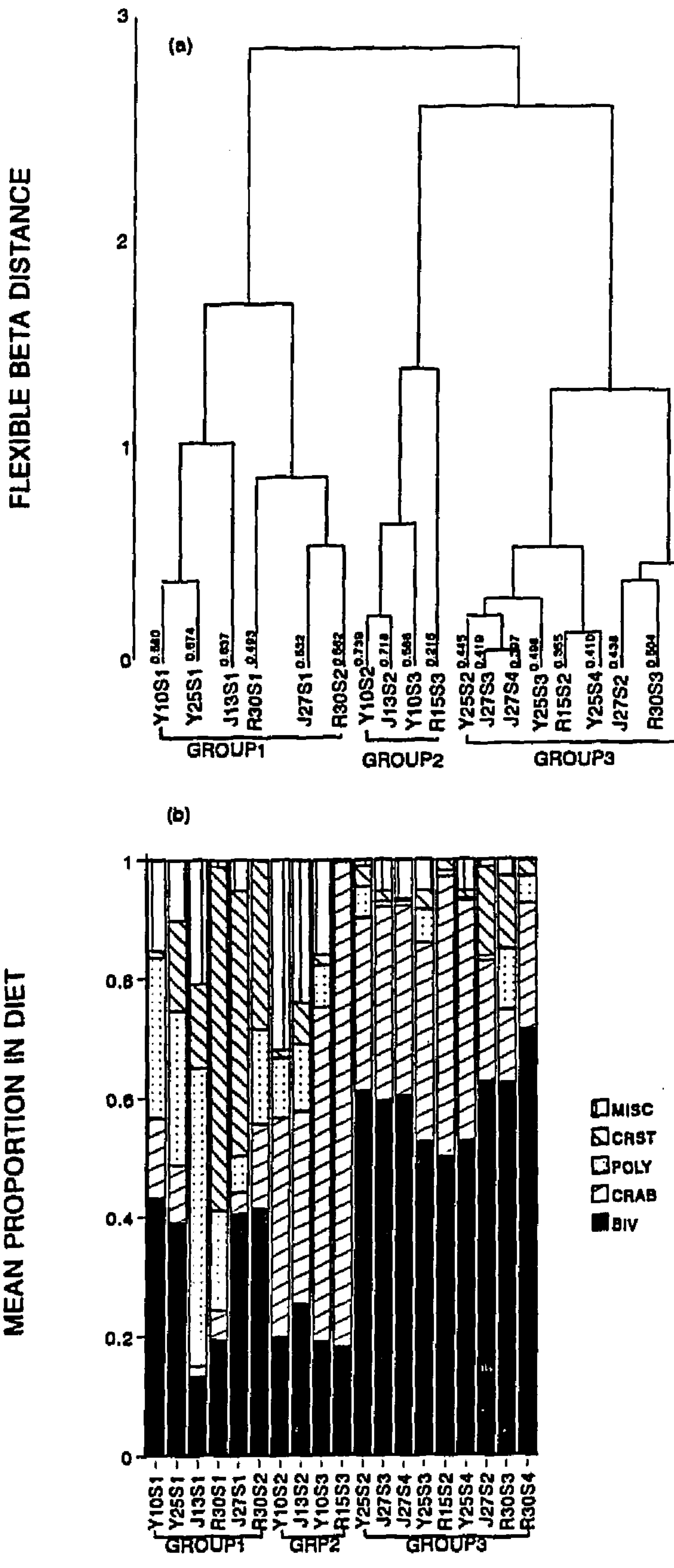

(a)
FLEXIBLE BETA DISTANCE
0
1
2
3
Y10S1 0.580
Y25S1 0.674
J13S1 0.637
R30S1 0.493
J27S1 0.532
R30S2 0.562
Y10S2 0.739
J13S2 0.718
Y10S3 0.566
R15S3 0.216
Y25S2 0.445
J27S3 0.419
J27S4 0.357
Y25S3 0.494
R15S2 0.365
Y25S4 0.410
J27S2 0.438
R30S3 0.504
R30S4 0.368
GROUP1
GROUP2
GROUP3
(b)
MEAN PROPORTION IN DIET
0
0.2
0.4
0.6
0.8
1
Y10S1
Y25S1
J13S1
R30S1
J27S1
R30S2
Y10S2
J13S2
Y10S3
R15S3
Y25S2
J27S3
J27S4
Y25S3
R15S2
Y25S4
J27S2
R30S3
R30S4
GROUP1
GRP2
GROUP3
MISC
CRST
POLY
CRAB
BIV

Figure 13. (a) Cluster diagram representing diet similarity among crabs collected from six stations in 1989. Months and size classes were pooled. The Shannon-Weiner diversity index is given at the root of each branch. Sample sizes were: Group 1 = 110, Group 2 = 413. (b) Diet composition of blue crabs illustrated as proportion in the diet for the stations described in (a). Major food items in the diet were bivalves, crabs, polychaetes, crustaceans and fish. Minor items (see text for definition) were pooled into miscellaneous (i.e., hydroids, gastropods, insects, ophiuroids, plants).

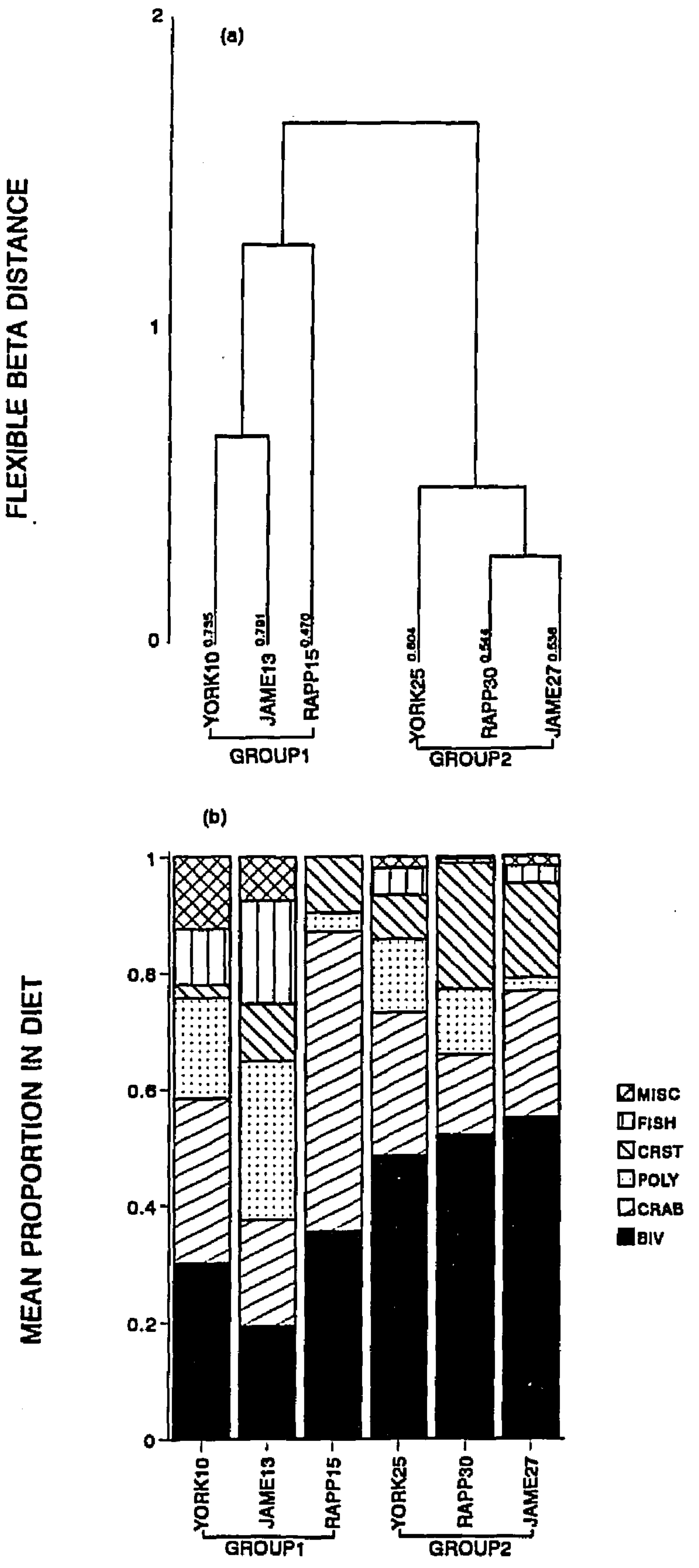
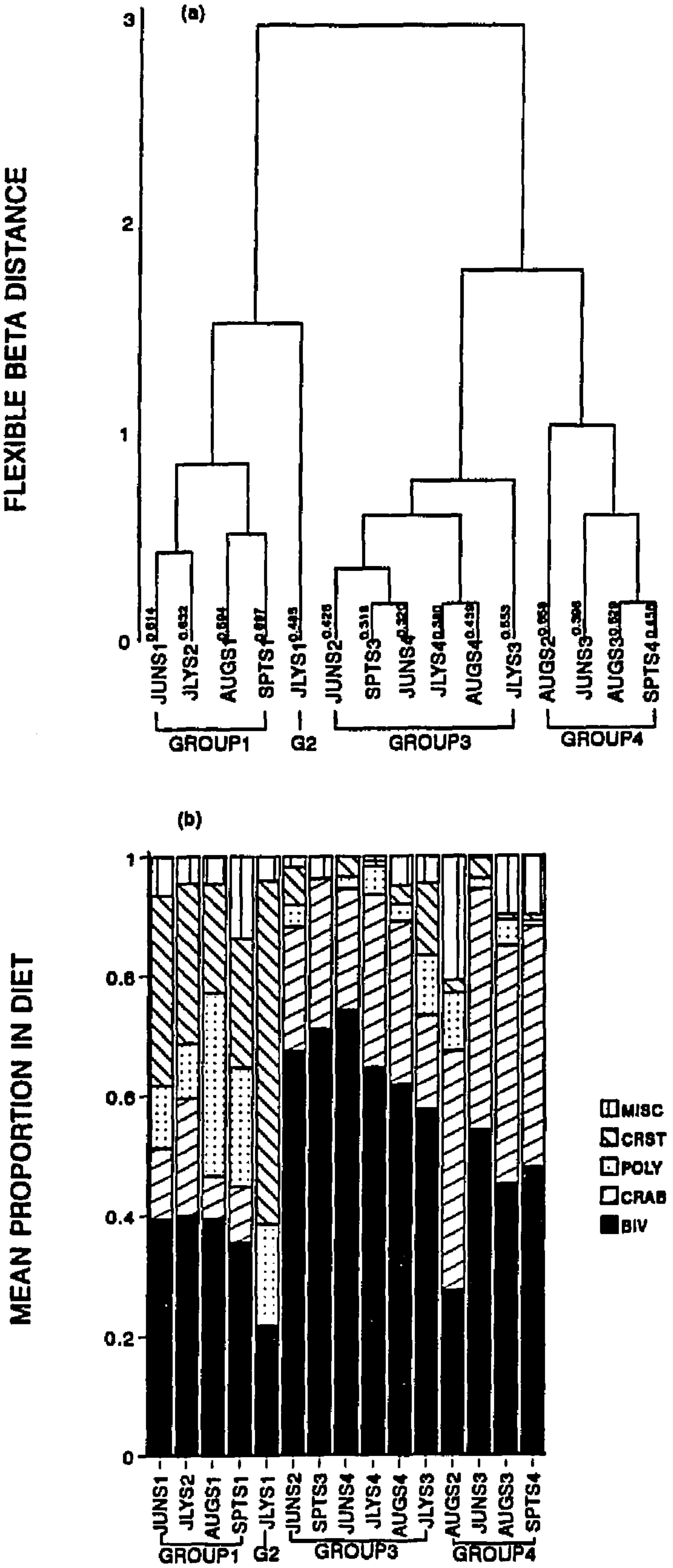
(a)
FLEXIBLE BETA DISTANCE
2
1
0
YORK10 0.735
JAME13 0.781
RAPP15 0.470
YORK25 0.604
RAPP30 0.544
JAME27 0.536
GROUP1
GROUP2
(b)
MEAN PROPORTION IN DIET
1
0.8
0.6
0.4
0.2
0
YORK10
JAME13
RAPP15
YORK25
RAPP30
JAME27
GROUP1
GROUP2
MISC
FISH
CRST
POLY
CRAB
BIV

Figure 14. (a) Cluster diagram of food similarity among months (i.e., June-September) for the four size classes of crabs collected in 1989. Rivers and stations were pooled. The Shannon-Weiner diversity index is given at the root of each branch. Sample sizes were: Group 1 = 167, Group 2 = 27, Group 3 = 180, Group 4 = 143. (b) Diet composition of blue crabs illustrated as proportion in the diet for the four months described in (a). Major food items in the diet were bivalves, crabs, polychaetes and crustaceans. Minor items (see text for definition) were pooled into miscellaneous (i.e., hydroids, gastropods, insects, fish, ophiuroids, plants).

(a)
FLEXIBLE BETA DISTANCE
3
2
1
0
JUNS1 0.614
JLYS2 0.632
AUGS1 0.594
SPTS1 0.697
JLYS1 0.485
JUNS2 0.426
SPTS3 0.318
JUNS4 0.320
JLYS4 0.380
AUGS4 0.439
JLYS3 0.553
AUGS2 0.658
JUNS3 0.306
AUGS3 0.528
SPTS4 0.456
GROUP1
G2
GROUP3
GROUP4
(b)
MEAN PROPORTION IN DIET
1
0.8
0.6
0.4
0.2
0
MISC
CRST
POLY
CRAB
BIV
JUNS1
JLYS2
AUGS1
SPTS1
JLYS1
JUNS2
SPTS3
JUNS4
JLYS4
AUGS4
JLYS3
AUGS2
JUNS3
AUGS3
SPTS4
GROUP1
G2
GROUP3
GROUP4

(1) Blue crab diets were again separable on the basis of bivalve, crab and polychaete fractions, which dominated the diet (Fig. 11). (2) Diets of crabs from upriver stations again differed from those downriver, whereby upriver crabs ate relatively more bivalves, and fewer crabs, polychaetes and other categories (Fig. 13). (3) Even with the addition of a smaller size class (10-59 mm CW), size-related patterns were similar to 1988, such that large juveniles and adults ate relatively more crabs and bivalves than small juveniles, which ate more polychaetes and small crustaceans, and had a more diverse diet (Figs. 12 & 14). The smallest juveniles were unique in their high consumption of polychaetes and crustaceans and relatively low consumption of bivalves and crabs (Figs. 12 & 14). Large crabs in the Rappahannock River again ate relatively more bivalves and less crabs than those in the York and James Rivers (Fig. 12), though the difference was not as great as in 1988. (4) As in 1988, some stations were uniquely separable on the basis of diet; for example, small crabs at the upriver Rappahannock station were unique in their low consumption of bivalves and high consumption of small crustaceans (Fig. 12). (5) Seasonal and river-specific patterns again were inconsistent (e.g., Fig. 14).

Blue Crab Diet: Diversity

1988

Diet diversity was negatively correlated with crab size (Table 12a), though there were exceptions (e.g., in the York River) where larger juveniles (i.e., 100-134 mm CW) consumed the greatest variety of prey (Table 12b). Furthermore, diet diversity was relatively higher downriver in all rivers where polychaetes, crustaceans and other miscellaneous prey were consumed in addition to the dominant dietary constituents - bivalves and crabs (Table 12c). The overall seasonal pattern indicated highest diversity in September (Table 12d), and low values in July, August and October.

1989

Diet diversity again correlated negatively with crab size (Table

12a). However, diet diversity of new recruits in the Rappahannock river was lower than that of larger juveniles and small adults (Table 12b). As in 1988, diet diversity was generally higher downriver (Table 12c). The overall seasonal pattern indicated highest diet diversity in August followed by September and July, and lowest diversity in June (Table 12d).

In summary, the generalized conclusions for both years indicated: (1) diet diversity correlated negatively with crab size, and (2) higher diversity at downriver stations due to consumption of various prey such as crustaceans, polychaetes and fish in addition to bivalves and crabs.

Blue Crab Diet: Cannibalism

The incidence of cannibalism increased with crab size (Fig. 15a; Table 13a), and frequency differed significantly between all size classes comparable in 1988 and 1989 (Table 13c(iii)). River differences occurred (Fig. 15b; Table 13a) such that cannibalism was most frequent in the James and York and significantly lower in the Rappahannock (Table 13c(ii)). A significant Year X Month interaction effect necessitated examination within levels of the main factors (Table 13a). Months compared within each level of Year were significantly different in 1988 and 1989 (Table 13b(i)). Cannibalism occurred more frequently in September than August in 1988, but there were no differences in July and August, and July and September (Fig. 15c; Table 13c(i)). In 1989, cannibalism occurred more frequently in August and September than July (Fig. 15c; Table 13c(i)). The frequency of occurrence of cannibalism was higher in 1989 in all months (i.e., July through September, Table 13b(ii)).

The analysis for cannibalism as a function of Year, River, Month (i.e., July & August), Size and Station also indicated a highly significant size effect (Table 14a): cannibalism increased with size class (Table 14c(ii)). Significant Year X Month and River X Station interaction effects occurred (Table 14a) necessitating examination within levels of the main factors (Table 14b,c). Stations

Table 12. (a) Diet diversity of blue crabs by size class in 1988 and 1989. Stations, rivers and months were pooled. Numbers in parentheses represent sample size.

SIZE CLASS (MM)	1988	1989
< 60	-	0.670 (140)
60-99	0.570 (162)	0.651 (139)
100-134	0.514 (261)	0.528 (135)
> 134	0.386 (206)	0.419 (109)

(b) Diet diversity of blue crabs by size class and river in 1988 and 1989. Months and stations are pooled. Numbers in parentheses represent sample size.

SIZE	JAMES		YORK		RAPPAHANNOCK	
CLASS (MM)	1988	1989	1988	1989	1988	1989
< 60	-	0.619 (47)	-	0.658 (66)	-	0.485 (27)
60-99	0.589 (43)	0.578 (39)	0.437 (21)	0.688 (45)	0.539 (98)	0.561 (55)
100-134	0.568 (54)	0.419 (45)	0.559 (61)	0.565 (32)	0.412 (146)	0.526 (58)
> 134	0.489 (34)	0.413 (32)	0.462 (56)	0.449 (25)	0.239 (116)	0.360 (52)

(c) Diet diversity of blue crabs by station in 1988 and 1989. Months and size classes are pooled. Numbers in parentheses represent sample size.

STATION	1988	1989
J13	0.686 (14)	0.791 (19)
J27	0.542 (117)	0.536 (144)
Y10	0.654 (15)	0.735 (66)
Y25	0.469 (123)	0.604 (102)
R15	0.622 (47)	0.470 (25)
R30	0.342 (313)	0.544 (167)

Table 12 (cont).

(d) Diet diversity of blue crabs by month in 1988 and 1989. Rivers, stations and size classes are pooled. Numbers in parentheses represent sample size.

MONTH	1988	1989
JUNE	-	0.475 (123)
JULY	0.473 (316)	0.617 (150)
AUGUST	0.468 (212)	0.731 (147)
SEPTEMBER	0.524 (60)	0.661 (103)
OCTOBER	0.424 (41)	-

Figure 15. Percent frequency occurrence of cannibalism in 1988 and 1989 as a function of (a) Size Class, rivers and months (i.e., July - September) pooled, (b) River, size classes (i.e., 60-99, 100-134, > 134 mm CW) and months (i.e., July - September) pooled, and (c) Month, rivers and size classes (i.e., 60-99, 100-134, > 134 mm CW) pooled. Stations were pooled for all figures.

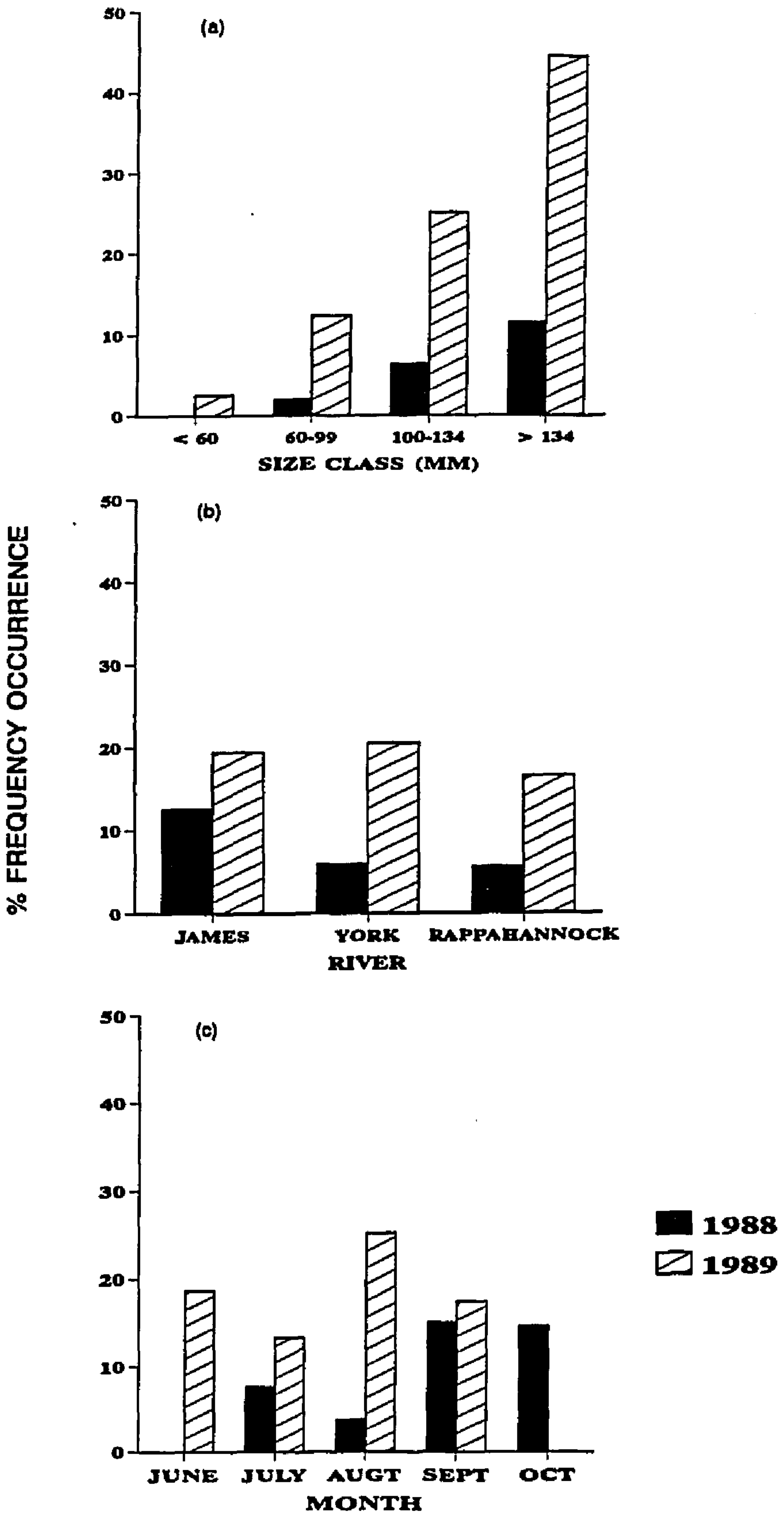

% FREQUENCY OCCURRENCE
(a)
0
10
20
30
40
50
< 60
60-99
100-134
> 134
SIZE CLASS (MM)
(b)
0
10
20
30
40
50
JAMES
YORK
RAPPAHANNOCK
RIVER
(c)
0
10
20
30
40
50
JUNE
JULY
AUGT
SEPT
OCT
MONTH
■ 1988
▨ 1989

Table 13. (a) G-test of cannibalism as a function of Year, River, Month, and Size Class. Analyses were run only for comparable months (i.e., July, August and September) and size classes (i.e., 60-99, 100-134, > 134 mm) in the two years, and to insure minimal occurrence of frequencies < 5 or = 0 (Sokal & Rohlf 1981).

SOURCE OF VARIATION	DF	X^2	P <
YEAR	1	55.206	0.00005
RIVER	2	6.263	0.0436
MONTH	2	2.377	0.3047
SIZE	2	31.184	0.00005
YEAR X RIVER	2	5.410	0.0669
YEAR X MONTH	2	6.829	0.0329
YEAR X SIZE	2	1.606	0.4479
RIVER X MONTH	4	3.465	0.4832
RIVER X SIZE	4	3.269	0.5139
MONTH X SIZE	4	1.197	0.8786
YEAR X RIVER X MONTH	4	5.045	0.2827
YEAR X MONTH X SIZE	4	3.442	0.4868
YEAR X RIVER X SIZE	4	1.401	0.8440
RIVER X MONTH X SIZE	8	6.822	0.5560
YEAR X RIVER X MONTH X SIZE	4	4.369	0.3583

(b) Lower-level G-tests for the Year X Month interaction to evaluate (i) Month within each level of Year, and (ii) Year within each level of Month.

(i)

YEAR	SOURCE OF VARIATION	DF	X^2	P <
1988	MONTH	2	9 494	0.0087
1989	MONTH	2	11.310	0.0035

Table 13 (cont).

(ii)

MONTH	SOURCE OF VARIATION	DF	X^2	P <
JULY	YEAR	1	7.372	0.0066
AUGUST	YEAR	1	45.869	0.00005
SEPTEMBER	YEAR	1	7.990	0.0047

(c) Lower-level G-tests for (i) Month in 1988 and 1989, (ii) the main effect of River, and (iii) the main effect of Size.

(i)

YEAR	SOURCE OF VARIATION	DF	X^2	P <
1988	JULY V. AUGUST	1	3.254	0.0712
	AUGUST V. SEPTEMBER	1	10.059	0.0015
	JULY V. SEPTEMBER	1	3.454	0.0631
1989	JULY V. AUGUST	1	6.522	0.0107
	AUGUST V. SEPTEMBER	1	1.249	0.2637
	JULY V. SEPTEMBER	1	9.965	0.0016

Table 13 (cont).

(ii)

SOURCE OF VARIATION	DF	X^2	$P <$
JAMES V. YORK	1	0.898	0.3432
YORK V. RAPPAHANNOCK	1	6.223	0.0126
JAMES V. RAPPAHANNOCK	1	13.198	0.0003

(iii)

SOURCE OF VARIATION	DF	X^2	$P <$
60-99 V. 100-134	1	5.476	0.0193
60-99 V. > 134	1	23.454	0.00005
100-134 V. > 134	1	9.139	0.0025

compared within each level of River were not significantly different (Table 14b(iii)), while river differences occurred upriver (Table 14b(iv)): cannibalism was least frequent in the Rappahannock (Table 14c(i)). Months differed only in 1989 (Table 14b(i)), reflecting the results of previous analyses (i.e., greater frequency in August than July in 1989 and no differences in July and August in 1988). Annual differences occurred in both months (Table 14b(ii)) with higher frequencies in 1989.

Residual analysis indicated no violations of model assumptions or model misspecification after data transformation and removal of one extreme outlier in the analysis of cannibalism as a function of either new juvenile recruit (i.e., < 50 mm CW) or total juvenile (i.e., ≤ 80 mm CW) abundance. The following best fit regression equation is depicted for transformed data (see Methods). The frequency of cannibalism was independent of new recruit (Fig. 16a) or total juvenile (Fig. 16b) abundance and river, but was significantly affected by month (M_1: $t=-2.75$, $P < 0.017$; M_2: $t=-1.63$, $P < 0.128$) and Year ($t=-5.08$, $P < 0.0005$). The equation explained 63.9 % of the total variability in cannibalism frequency (ANOVA: $F=10.43$, $df= 3,13$, $P < 0.001$) and was:

$$Y_i = 0.809 - 0.238M_1 - 0.141M_2 - 0.353Y$$

In summary, these analyses indicated that cannibalism: (1) increased with crab size, (2) occurred with greatest frequencies in the James and York Rivers, (3) was most frequent during the period of new juvenile recruitment in the Fall in both years (i.e., September in 1988 and August and September in 1989), and (4) occurred with greater frequency in 1989, the year of higher new recruit abundance. Although regression analyses indicated that cannibalism was unrelated to juvenile blue crab abundance, there were significant seasonal and annual effects (i.e., greatest frequency in September and in 1989).

Figure 16. Percent frequency occurrence of cannibalism, *arcsin square-root transformed data, as a function of (a) mean new juvenile recruit abundance (i.e., crabs < 50 mm CW) and (b) mean abundance of juveniles ≤ 80 mm CW. Abundance data were log (X+1) transformed for analysis (N=17) and graphical presentation (N=18).

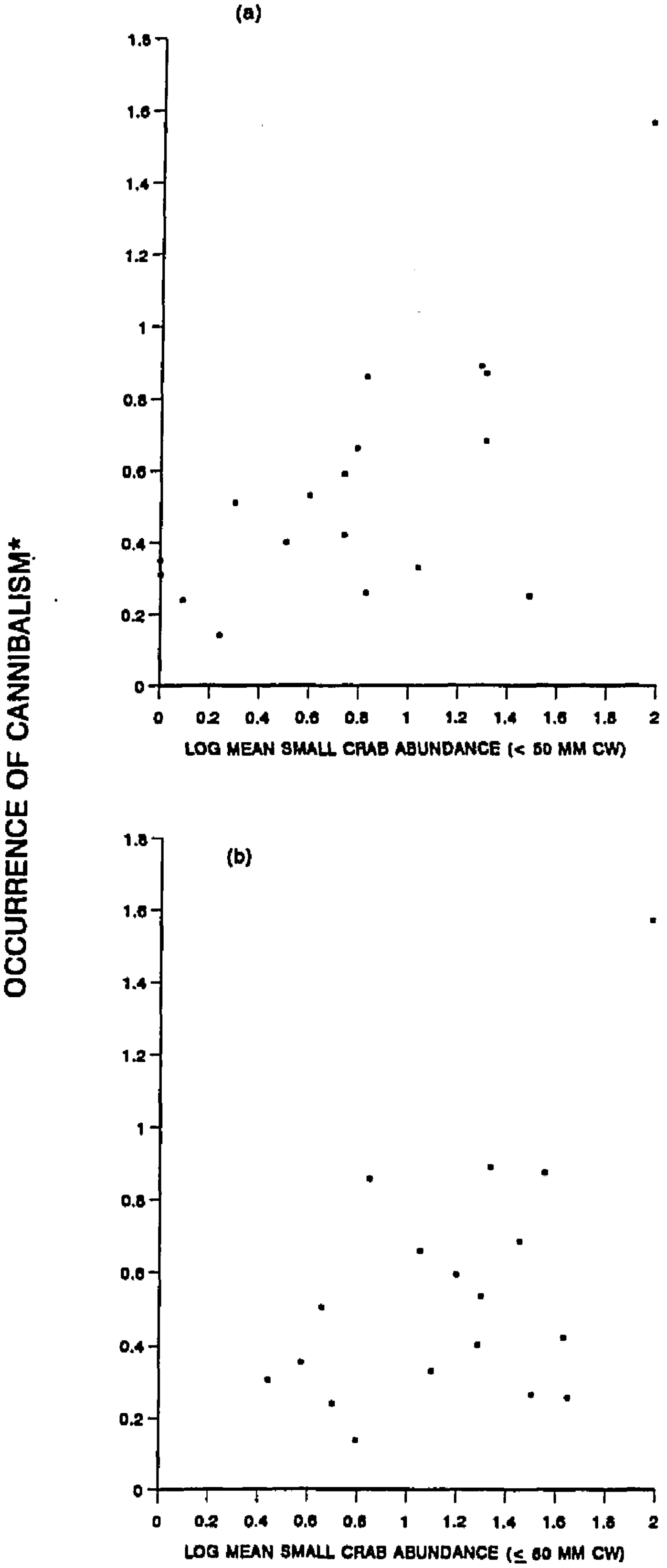
(a)
OCCURRENCE OF CANNIBALISM*
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
LOG MEAN SMALL CRAB ABUNDANCE (< 50 MM CW)
(b)
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
LOG MEAN SMALL CRAB ABUNDANCE (≤ 50 MM CW)

Table 14. (a) G-test of cannibalism as a function of Year, River, Month, Size Class and Station. Analyses were run only for comparable months (i.e., July and August) and size classes (i.e., 60-99, 100-134, > 134 mm) in the two years, and to insure minimal occurrence of frequencies < 5 or = 0 (Sokal & Rohlf 1981).

SOURCE OF VARIATION	DF	X^2	P <
YEAR	1	45.377	0.00005
RIVER	2	10.647	0.0049
MONTH	1	0.112	0.7378
STATION	1	0.057	0.8116
SIZE	2	21.709	0.00005
YEAR X RIVER	2	5.585	0.0613
YEAR X MONTH	1	6.950	0.0084
YEAR X STATION	1	0.000	1.0000
YEAR X SIZE	2	1.827	0.4010
RIVER X MONTH	2	4.104	0.1285
RIVER X STATION	2	7.740	0.0209
RIVER X SIZE	4	4.615	0.3291
MONTH X STATION	1	0.192	0.6613
MONTH X SIZE	2	0.253	0.8813
STATION X SIZE	2	0.315	0.8544
YEAR X RIVER X MONTH	2	1.127	0.5692
YEAR X RIVER X STATION	2	0.000	1.0000
YEAR X MONTH X STATION	1	0.000	1.0000
YEAR X MONTH X SIZE	2	3.645	0.1616
YEAR X RIVER X SIZE	4	2.227	0.6941
YEAR X STATION X SIZE	2	0.025	0.9876
RIVER X MONTH X STATION	2	0.155	0.9256
RIVER X MONTH X SIZE	4	8.195	0.0847
RIVER X STATION X SIZE	4	2.772	0.5967
MONTH X STATION X SIZE	2	0.077	0.9621
YEAR X RIVER X MONTH X STATION	2	0.000	0.9999
YEAR X RIVER X MONTH X SIZE	4	0.886	0.9265
YEAR X RIVER X STATION X SIZE	4	0.336	0.9874
YEAR X MONTH X STATION X SIZE	2	0.000	0.9999
RIVER X MONTH X STATION X SIZE	4	0.212	0.9948
YEAR X RIVER X MONTH X STATION X SIZE CLASS	3	0.000	1.0000

Table 14 (cont).

(b) Lower-level G-tests for the Year X Month and River X Station interactions to evaluate (i) Month within each level of Year, (ii) Year within each level of Month, (iii) Station within each level of River, and (iv) River within each level of Station.

(i)

YEAR	SOURCE OF VARIATION	DF	X^2	P <
1988	MONTH	1	3.254	0.0712
1989	MONTH	1	7.502	0.0062

(ii)

MONTH	SOURCE OF VARIATION	DF	X^2	P <
JULY	YEAR	1	4.911	0.0267
AUGUST	YEAR	1	45.869	0.00005

(iii)

RIVER	SOURCE OF VARIATION	DF	X^2	P <
JAMES	STATION	1	0.993	0.3190
YORK	STATION	1	0.301	0.5835
RAPP	STATION	1	2.049	0.1523

(iv)

STATION	SOURCE OF VARIATION	DF	X^2	P <
DOWNRIVER	RIVER	2	0.087	0.9573
UPRIVER	RIVER	2	15.864	0.0004

Table 14 (cont).

(c) Lower-level G-tests for (i) River, upriver and (ii) the main effect of Size.

(i)

SOURCE OF VARIATION	DF	X^2	P <
JAMES V. YORK	1	0.623	0.4300
JAMES V. RAPPAHANNOCK	1	14.307	0.0002
YORK V. RAPPAHANNOCK	1	7.864	0.0050

(ii)

SOURCE OF VARIATION	DF	X^2	P <
60-99 V. 100-134	1	4.380	0.0364
60-99 V. > 134	1	23.454	0.00005
100-134 V. > 134	1	10.474	0.0012

Benthic Infaunal Abundance

Summer 1988

Abundance.-- Bivalves and polychaetes dominated benthic samples in density and relative abundance (Fig. 17, Appendix 4). Significant three-way interactions, River X Station X Month, in the analyses of bivalve (Table 15) and polychaete (Table 19) densities precluded singular conclusions about main effects, and necessitated analyses with lower-level ANOVA models.

First, bivalve abundance was examined for Station and Month effects within each level of River. Bivalve abundance differed significantly between stations in both the James and York (Table 16a): bivalve densities were greater upriver. For the Rappahannock, a significant Station X Month interaction (Table 16a) necessitated examination of main effects within each level of Station and Month. In the ANOVA for Station within each level of Month for the Rappahannock, bivalve densities were significantly higher upriver only in September and October (Table 16b(ii)). Seasonal differences in bivalve abundance occurred at the downriver (R15) station, but not upriver at R30 (Table 16b(i)): densities in July and August were significantly greater than those in September (no bivalves collected in six grabs, Table 16c). Significant seasonal differences in bivalve density occurred in the York, but not in the James (Table 16a). The order of mean abundance, from greatest to least, was July, August, October, September in the York (Table 16d).

Second, bivalve abundance was examined for River and Station effects within each level of Month (Table 17a). Significant differences between stations occurred in July and August (Table 17a): bivalve densities were greatest upriver. Neither the main effect of River nor the interaction effect (i.e., River X Station) were significant in these months (Table 17a). The River X Station interaction effect was significant in September and October (Table 17a), necessitating examination of main effects within levels of the main factors (Table

Figure 17. Mean density of prey types collected through benthic sampling downriver and upriver in the James (i.e., J13 & J27), York (i.e., Y10, Y25) and Rappahannock (i.e., R15, R30) Rivers from July through October, 1988. Numbers in parentheses represent sample size defined as grabs in which at least one living animal was recovered. The Miscellaneous category includes ophiuroids, fish, tunicates, anemones, sponges, and bryozoans. The Poly* category includes polychaetes, nemerteans and phoronids (Appendix 4).

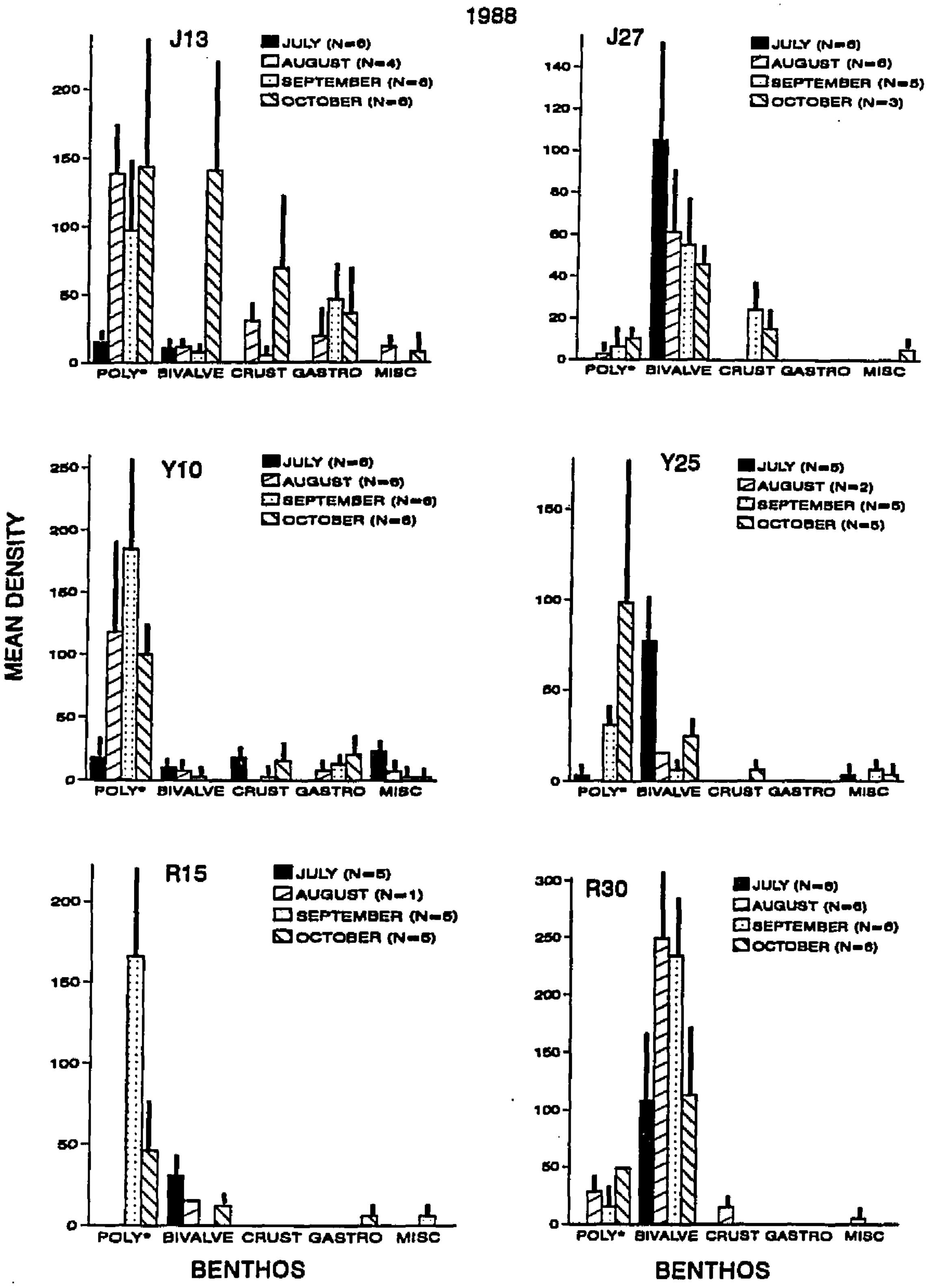

1988
MEAN DENSITY
J13
JULY (N=6)
AUGUST (N=4)
SEPTEMBER (N=6)
OCTOBER (N=6)
0
50
100
150
200
POLY* BIVALVE CRUST GASTRO MISC
J27
JULY (N=6)
AUGUST (N=6)
SEPTEMBER (N=5)
OCTOBER (N=3)
0
20
40
60
80
100
120
140
POLY* BIVALVE CRUST GASTRO MISC
Y10
JULY (N=6)
AUGUST (N=6)
SEPTEMBER (N=6)
OCTOBER (N=6)
0
50
100
150
200
250
POLY* BIVALVE CRUST GASTRO MISC
Y25
JULY (N=5)
AUGUST (N=2)
SEPTEMBER (N=5)
OCTOBER (N=5)
0
50
100
150
POLY* BIVALVE CRUST GASTRO MISC
R15
JULY (N=5)
AUGUST (N=1)
SEPTEMBER (N=5)
OCTOBER (N=5)
0
50
100
150
200
POLY* BIVALVE CRUST GASTRO MISC
BENTHOS
R30
JULY (N=6)
AUGUST (N=6)
SEPTEMBER (N=6)
OCTOBER (N=6)
0
50
100
150
200
250
300
POLY* BIVALVE CRUST GASTRO MISC
BENTHOS

Table 15. Three-way analysis of variance with river, station and month as factors, and the dependent variable, log-transformed bivalve density, for each set of six benthic grabs per station in 1988. In cases of n=1, the mean for benthic densities which grouped similarly in cluster analysis was substituted to insure a minimum sample size of two within all treatment combinations.

SOURCE OF VARIATION	DF	SS	PERCENTAGE OF VARIATION	MS	F	P<
RIVER	2	11.5572	13.7%	5.7786	16.21	0.0001
STATION	1	21.7744	25.8%	21.7744	61.10	0.0001
MONTH	3	5.1696	6.1%	1.7232	4.84	0.0035
RIVERxSTATION	2	0.3549	0.4%	0.1774	0.50	0.6093
RIVERxMONTH	6	2.3460	2.8%	0.3910	1.10	0.3695
STATIONxMONTH	3	0.6038	0.7%	0.2013	0.56	0.6395
RIVERxSTATIONxMONTH	6	6.9178	8.2%	1.1530	3.24	0.0060
ERROR	100	35.6399	42.2%	0.3564		

Table 16. (a) Two-way analysis of variance for Station and Month within each level of River, and the dependent variable, log-transformed bivalve density in 1988.

RIVER	SOURCE OF VARIATION	DF	SS	MS	F	P <
JAMES	STATION	1	5.7327	5.7327	15.02	0.0005
	MONTH	3	3.2951	1.0984	2.88	0.0503
	STATIONXMONTH	3	1.2307	0.4102	1.07	0.3729
	ERROR	34	12.9795	0.3817		
YORK	STATION	1	6.5266	6.5266	18.68	0.0001
	MONTH	3	3.0413	1.0138	2.90	0.0495
	STATIONXMONTH	3	1.6049	0.5350	1.53	0.2247
	ERROR	33	11.5293	0.3494		
RAPP	STATION	1	9.8700	9.8700	29.26	0.0001
	MONTH	3	1.1792	0.3931	1.17	0.3377
	STATIONXMONTH	3	4.6861	1.5620	4.63	0.0082
	ERROR	33	11.1311	0.3373		

(b) Lower-level (i.e., one-way) analysis of variance for (i) Month within each level of Station, and (ii) Station within each level of Month in the Rappahannock river.

(i)

STATION	SOURCE OF VARIATION	DF	SS	MS	F	P <
DOWNRIVER	MONTH	3	5.4124	1.8041	9.77	0.0012
	ERROR	13	2.3994	0.1846		
UPRIVER	MONTH	3	0.4528	0.1509	0.35	0.7926
	ERROR	20	8.7317	0.4366		

Table 16 (cont).

(ii)

MONTH	SOURCE OF VARIATION	DF	SS	MS	F	P <
JULY	STATION	1	0.0620	0.0620	0.43	0.5301
	ERROR	9	1.3081	0.1453		
AUGUST	STATION	1	0.6367	0.6367	0.74	0.4231
	ERROR	6	5.1725	0.8621		
SEPT	STATION	1	10.5110	10.5110	66.14	0.0001
	ERROR	9	1.4302	0.1589		
OCT	STATION	1	3.0164	3.0164	8.43	0.0175
	ERROR	9	3,2203	0.3578		

(c) Ryan's Q results for months at R15 in 1988. Means sharing the same line are not significantly different.

SEPTEMBER	OCTOBER	AUGUST	JULY
0.00	0.79	1.06	1.45

(d) Ryan's Q results for months in the York river, stations pooled. Means sharing the same line are not significantly different.

SEPTEMBER	OCTOBER	AUGUST	JULY
0.33	0.62	0.64	1.05

Table 17. (a) Two-way analysis of variance for River and Station within each level of Month, and the dependent variable, log-transformed bivalve density in 1988.

MONTH	SOURCE OF VARIATION	DF	SS	MS	F	P<
JULY	RIVER	2	1.2386	0.6193	1.68	0.2045
	STATION	1	3.9768	3.9768	10.79	0.0027
	RIVERXSTATION	2	1.1738	0.5869	1.59	0.2212
	ERROR	28	10.3167	0.3685		
AUGUST	RIVER	2	3.4302	1.7151	3.31	0.0575
	STATION	1	3.6330	3.6330	7.00	0.0155
	RIVERXSTATION	2	0.0965	0.0483	0.09	0.9116
	ERROR	20	10.3776	0.5189		
SEPT	RIVER	2	3.2524	1.6262	4.48	0.0209
	STATION	1	9.2682	9.2682	25.53	0.0001
	RIVERXSTATION	2	3.9050	1.9525	5.38	0.0108
	ERROR	27	9.8024	0.3631		
OCT	RIVER	2	5.3365	2.6683	12.97	0.0001
	STATION	1	6.1654	6.1654	29.97	0.0001
	RIVERXSTATION	2	1.9405	0.9703	4.72	0.0183
	ERROR	25	5.1432	0.2057		

Table 17 (cont).

(b) Lower-level (i.e., one-way) analysis of variance for (i) Station within each level of River, and (ii) River within each level of Station in September and October.

(i)

MONTH	RIVER	SOURCE OF VARIATION	DF	SS	MS	F	P <
SEPT	JAMES	STATION	1	2.4434	2.4434	4.09	0.0738
		ERROR	9	5.3755	0.5973		
	YORK	STATION	1	0.2188	0.2188	0.66	0.4385
		ERROR	9	2.9967	0.3330		
	RAPP	STATION	1	10.5110	10.5110	66.14	0.0001
		ERROR	9	1.4302	0.1589		
OCT	JAMES	STATION	1	0.0185	0.0185	0.07	0.7929
		ERROR	7	1.7403	0.2486		
	YORK	STATION	1	5.0711	5.0711	249.89	0.0001
		ERROR	9	0.1826	0.0203		
	RAPP	STATION	1	3.0164	3.0164	8.43	0.0175
		ERROR	9	3.2203	0.3578		

Table 17 (cont).

(ii)

MONTH	STATION	SOURCE OF VARIATION	DF	SS	MS	F	P <
SEPT	DOWNRIVER	RIVER	2	0.5666	0.2833	1.06	0.3715
		ERROR	14	3.7285	0.2663		
	UPRIVER	RIVER	2	5.9940	2.9970	6.41	0.0115
		ERROR	13	6.0739	0.4672		
OCT	DOWNRIVER	RIVER	2	7.3118	3.6559	13.43	0.0006
		ERROR	14	3.8112	0.2722		
	UPRIVER	RIVER	2	0.6158	0.3079	2.54	0.1237
		ERROR	11	1.3319	0.1211		

(c) Ryan's Q results for rivers compared upriver in September and downriver in October. Means sharing the same line are not significantly different. * $p < 0.05$

Upriver in September:	YORK		JAMES	RAPPAHANNOCK
	0.49		1.40	1.96
	——	*	————	————

Downriver in October:	YORK		RAPPAHANNOCK		JAMES
	0.00		0.79		1.56
	——	*	————	*	——

17b). Station was significant in the Rappahannock in September (Table 17b(i)): highest bivalve densities occurred upriver. Rivers compared within each level of Station in September were significantly different at upriver sampling sites (Table 17b(ii)): bivalves were least abundant in the York (Table 17c). Stations differed in the York and Rappahannock (Table 17b(i)) in October: bivalves were most abundant upriver. Rivers compared within each level of Station differed downriver in October (Table 17b(ii)) with greatest abundance in the James followed by the Rappahannock then York (no bivalves collected in 6 grabs; Table 17c).

Third, bivalve abundance was analyzed for River and Month effects within each level of Station (Table 18a). River was significant at upriver stations (Table 18a): bivalves were least abundant in the York (Table 18c). Month and the River X Month interaction effect were not significant (Table 18a). However, for downriver stations, the River X Month interaction was significant (Table 18a). The analysis of River within Month downriver was significant in October (Table 18b(i)): abundance was greatest in the James followed by the Rappahannock then York (Table 18c). Month compared within River was significant for the Rappahannock (Table 18b(ii)): bivalves were more abundant in July and August than September (no clams collected in 6 grabs; Table 18d).

The analyses for polychaete abundance progressed similarly to those for bivalve abundance (Fig. 17; Table 19). First, Station and Month were analyzed within each level of River (Table 20a). Polychaete abundance differed significantly between stations in the York and James (Table 20a), and between months in the York (Table 20a).

Polychaetes were most abundant downriver in the York and James. A pronounced seasonal effect occurred in the York (Table 20a): polychaete densities were greater in September and October than July (Table 20c). A seasonal effect also occurred in the lower Rappahannock (Table 20b(i)); however, multiple comparisons were precluded by low abundances.

A significant Station X Month (Table 20a) interaction effect occurred for the Rappahannock, requiring examination of effects within

Table 18. (a) Two-way analysis of variance for River and Month within each level of Station, and the dependent variable, log-transformed bivalve density in 1988.

STATION	SOURCE OF VARIATION	DF	SS	MS	F	P <
DOWNRIVER	RIVER	2	4.0904	2.0452	6.21	0.0039
	MONTH	3	4.7494	1.5831	4.80	0.0051
	RIVERXMONTH	6	6.2053	1.0342	3.14	0.0107
	ERROR	51	16.8050	0.3295		
UPRIVER	RIVER	2	4.2673	2.1337	5.55	0.0067
	MONTH	3	1.0854	0.3618	0.94	0.4280
	RIVERXMONTH	6	2.9971	0.4995	1.30	0.2751
	ERROR	49	18.8348	0.3844		

(b) Lower-level (i.e., one-way) analysis of variance for (i) River within each level of Month, and (ii) Month within each level of River, downriver.

(i)

MONTH	SOURCE OF VARIATION	DF	SS	MS	F	P <
JULY	RIVER	2	1.8678	0.9339	2.71	0.1014
	ERROR	14	4.8309	0.3451		
AUGUST	RIVER	2	0.5655	0.2828	0.57	0.5827
	ERROR	9	4.4344	0.4927		
SEPTEMBER	RIVER	2	0.5666	0.2833	1.06	0.3715
	ERROR	14	3.7285	0.2663		
OCTOBER	RIVER	2	7.3118	3.6559	13.43	0.0006
	ERROR	14	3.8112	0.2722		

Table 18 (cont).

(ii)

RIVER	SOURCE OF VARIATION	DF	SS	MS	F	P <
JAMES	MONTH	3	4.0672	1.3557	3.03	0.0561
	ERROR	18	8.0477	0.4471		
YORK	MONTH	3	1.4751	0.4917	1.55	0.2334
	ERROR	20	6.3580	0.3179		
RAPP	MONTH	3	5.4124	1.8041	9.77	0.0012
	ERROR	13	2.3994	0.1846		

(c) Ryan's Q results for rivers upriver, months pooled, and downriver in October. Means sharing the same line are not significantly different.
* $P < 0.05$

Upriver, months pooled:	YORK		JAMES	RAPPAHANNOCK
	1.14		1.63	1.78
	———	*	———	———

Downriver in October:	YORK		RAPPAHANNOCK		JAMES
	0.00		0.79		1.56
	———	*	———	*	———

(d) Ryan's Q results for months downriver in the Rappahannock. Means sharing the same line are not significantly different.

SEPTEMBER	OCTOBER	AUGUST	JULY
0.00	0.79	1.06	1.45
———	———		
	———	———	———

Table 19. Three-way analysis of variance with river, station and month as factors, and the dependent variable, log-transformed polychaete density, for each set of six benthic grabs per station in 1988. In cases of n=1, the mean for benthic densities which grouped similarly in cluster analysis was substituted to insure a minimum sample size of two within all treatment combinations.

SOURCE OF VARIATION	DF	SS	PERCENTAGE OF VARIATION	MS	F	P<
RIVER	2	3.5411	3.7%	1.7706	4.06	0.0202
STATION	1	13.7184	14.3%	13.7184	31.46	0.0001
MONTH	3	19.4946	20.3%	6.4982	14.90	0.0001
RIVERxSTATION	2	2.7579	2.9%	1.3789	3.16	0.0466
RIVERxMONTH	6	3.0859	3.2%	0.5143	1.18	0.3233
STATIONxMONTH	3	1.7786	1.9%	0.5929	1.36	0.2595
RIVERxSTATIONxMONTH	6	7.8724	8.2%	1.3121	3.01	0.0096
ERROR	100	43.6037	45.4%	0.4360		

Table 20. (a) Two-way analysis of variance for Station and Month within each level of River, and the dependent variable, log-transformed polychaete density in 1988.

RIVER	SOURCE OF VARIATION	DF	SS	MS	F	P <
JAMES	STATION	1	12.0499	12.0499	26.36	0.0001
	MONTH	3	3.4238	1.1413	2.50	0.0763
	STATIONXMONTH	3	1.2927	0.4309	0.94	0.4309
	ERROR	34	15.5441	0.4518		
YORK	STATION	1	3.1178	3.1178	6.79	0.0136
	MONTH	3	8.8617	2.9539	6.44	0.0015
	STATIONXMONTH	3	0.9030	0.3010	0.66	0.5849
	ERROR	33	15.1421	0.4589		
RAPP	STATION	1	1.3087	1.3087	3.34	0.0765
	MONTH	3	10.2950	3.4317	8.77	0.0002
	STATIONXMONTH	3	7.4553	2.4851	6.35	0.0016
	ERROR	33	12.9175	0.3914		

(b) Lower-level (i.e., one-way) analysis of variance for (i) Month within each level of Station, and (ii) Station within each level of Month in the Rappahannock river.

(i)

STATION	SOURCE OF VARIATION	DF	SS	MS	F	P <
DOWNRIVER	MONTH	3	13.6120	4.5373	19.25	0.0001
	ERROR	13	3.0640	0.2357		
UPRIVER	MONTH	3	4.1384	1.3795	2.80	0.0664
	ERROR	20	9.8536	0.4927		

Table 20 (cont).

(ii)

MONTH	SOURCE OF VARIATION	DF	SS	MS	F	P <
JULY	STATION		no polychaetes collected			
	ERROR					
AUGUST	STATION	1	1.7734	1.7734	2.98	0.1350
	ERROR	6	3.5691	0.5948		
SEPT	STATION	1	6.6826	6.6826	14.44	0.0042
	ERROR	9	4.1652	0.4628		
OCT	STATION	1	0.3799	0.3799	0.66	0.4376
	ERROR	9	5.1833	0.5759		

(c) Ryan's Q results for months in the York in 1988. Means sharing the same line are not significantly different.

JULY	AUGUST	SEPTEMBER	OCTOBER
0.50	0.99	1.50	1.60
————	————		
	————	————	————

each level of the main factors. Rappahannock stations compared within each level of Month differed significantly in September (Table 20b(ii)): greatest densities occurred at R15.

In the analysis of River and Station effects for polychaete density within each level of Month, significant differences occurred between stations, but not rivers, in July and September (Table 21a): polychaetes were most abundant downriver. A significant River X Station interaction occurred in August (Table 21a). Examination of Station within each level of River in August indicated significantly greater densities in the lower James (Table 21b(i)), but no differences in the York or Rappahannock (Table 21b(i)). River differences did not occur at either station in August (Table 21b(ii)). Polychaetes were similarly abundant in all rivers and stations in October (Table 21a).

In the analysis of polychaete abundance for River and Month within each level of Station, there were significant River and Month (Table22a) differences upriver. The River X Month interaction effect was not significant (Table 22a). Polychaetes were least abundant in the James river (Table 22c). Abundance was also greater in September and October than July (Table 22d). The River X Month interaction was marginally significant in the analysis for downriver sites (Table 22a). River differences did not occur in any month (Table 22b(i)). Months differed in the Rappahannock (Table 22b(ii)): polychaetes were not collected in July or August, but occurred in high densities in September and October (Table 22e).

In summary bivalves were generally more abundant (1) at upriver stations, (2) in the Rappahannock, and (3) in summer (i.e., July & August). Polychaete densities were generally higher (1) downriver, (2) in the York, and (3) in Fall (i.e., September & October).

<u>Benthic Similarity</u>. -- Benthic abundance clustered into three groups (Fig. 18a) separable primarily by the proportion of polychaetes and bivalves in the benthos (Fig. 18b). With the exception of Y25 in September and October (i.e., group 2), groups 1 and 2 were downriver

Table 21. (a) Two-way analysis of variance for River and Station within each level of Month, and the dependent variable, log-transformed polychaete density in 1988.

MONTH	SOURCE OF VARIATION	DF	SS	MS	F	P<
JULY	RIVER	2	1.5114	0.7557	2.65	0.0882
	STATION	1	1.4944	1.4944	5.24	0.0298
	RIVERXSTATION	2	0.8187	0.4094	1.44	0.2548
	ERROR	28	7.9799	0.2850		
AUGUST	RIVER	2	0.1304	0.0652	0.11	0.8941
	STATION	1	3.4025	3.4025	5.87	0.0250
	RIVERXSTATION	2	7.4467	3.7234	6.43	0.0070
	ERROR	20	11.5869	0.5793		
SEPT	RIVER	2	2.2577	1.1289	2.58	0.0944
	STATION	1	8.6664	8.6664	19.80	0.0001
	RIVERXSTATION	2	1.5949	0.7975	1.82	0.1811
	ERROR	27	11.8187	0.4377		
OCT	RIVER	2	1.5355	0.7678	1.57	0.2277
	STATION	1	1.9037	1.9037	3.90	0.0596
	RIVERXSTATION	2	0.1698	0.0849	0.17	0.8416
	ERROR	25	12.2182	0.4887		

Table 21 (cont).

(b) Lower-level (i.e, one-way) analysis of variance for (i) Station within each level of River, and (ii) River within each level of Station in August.

(i)

RIVER	SOURCE OF VARIATION	DF	SS	MS	F	P <
JAMES	STATION	1	6.4721	6.4721	33.02	0.0004
	ERROR	8	1.5679	0.1960		
YORK	STATION	1	2.6037	2.6037	2.42	0.1706
	ERROR	6	6.4498	1.0750		
RAPP	STATION	1	1.7734	1.7734	2.98	0.1350
	ERROR	6	3.5690	0.5948		

(ii)

STATION	SOURCE OF VARIATION	DF	SS	MS	F	P <
DOWNRIVER	RIVER	2	4.5594	2.2797	3.02	0.0991
	ERROR	9	6.7896	0.7544		
UPRIVER	RIVER	2	3.0625	1.5312	3.51	0.0662
	ERROR	11	4.7972	0.4361		

Table 22. (a) Two-way analysis of variance for River and Month within each level of Station, and the dependent variable, log-transformed polychaete density in 1988.

STATION	SOURCE OF VARIATION	DF	SS	MS	F	P <
DOWNRIVER	RIVER	2	1.6899	0.8450	1.64	0.2043
	MONTH	3	14.2631	4.7544	9.22	0.0001
	RIVERXMONTH	6	7.1888	1.1981	2.32	0.0465
	ERROR	51	26.2971	0.5156		
UPRIVER	RIVER	2	3.2419	1.6210	4.59	0.0149
	MONTH	3	6.8166	2.2722	6.43	0.0009
	RIVERXMONTH	6	3.9631	0.6605	1.87	0.1050
	ERROR	49	17.3066	0.3532		

(b) Lower-level (i.e., one-way) analysis of variance for (i) River within each level of Month, and (ii) Month within each level of River, downriver.

(i)

MONTH	SOURCE OF VARIATION	DF	SS	MS	F	P <
JULY	RIVER	2	1.9122	0.9561	1.97	0.1765
	ERROR	14	6.8009	0.4858		
AUGUST	RIVER	2	4.5594	2.2797	3.02	0.0991
	ERROR	9	6.7896	0.7544		
SEPTEMBER	RIVER	2	1.6471	0.8236	2.72	0.1006
	ERROR	14	4.2407	0.3029		
OCTOBER	RIVER	2	0.7751	0.3875	0.64	0.5416
	ERROR	14	8.4658	0.6047		

Table 22 (cont).

(ii)

RIVER	SOURCE OF VARIATION	DF	SS	MS	F	P <
JAMES	MONTH	3	3.3776	1.1259	1.76	0.1912
	ERROR	18	11.5286	0.6405		
YORK	MONTH	3	4.4622	1.4874	2.54	0.0853
	ERROR	20	11.7045	0.5852		
RAPP	MONTH	3	13.6120	4.5373	19.25	0.0001
	ERROR	13	3.0640	0.2357		

(c) Ryan's Q results for rivers, months pooled, upriver. Means sharing the same line are not significantly different. * P < 0.05

JAMES	RAPPAHANNOCK	YORK
0.26	0.64	0.83
———	* ———	———

(d) Ryan's Q results for months, rivers pooled, upriver. Means sharing the same line are not significantly different.

JULY	AUGUST	SEPTEMBER	OCTOBER
0.07	0.55	0.69	1.05
———	———		
	———	———	———

(e) Ryan's Q results for months downriver in the Rappahannock. Means sharing the same line are not significantly different. * P < 0.05

AUGUST	JULY	OCTOBER	SEPTEMBER
0.00	0.00	1.28	2.12
———	———	* ———	———

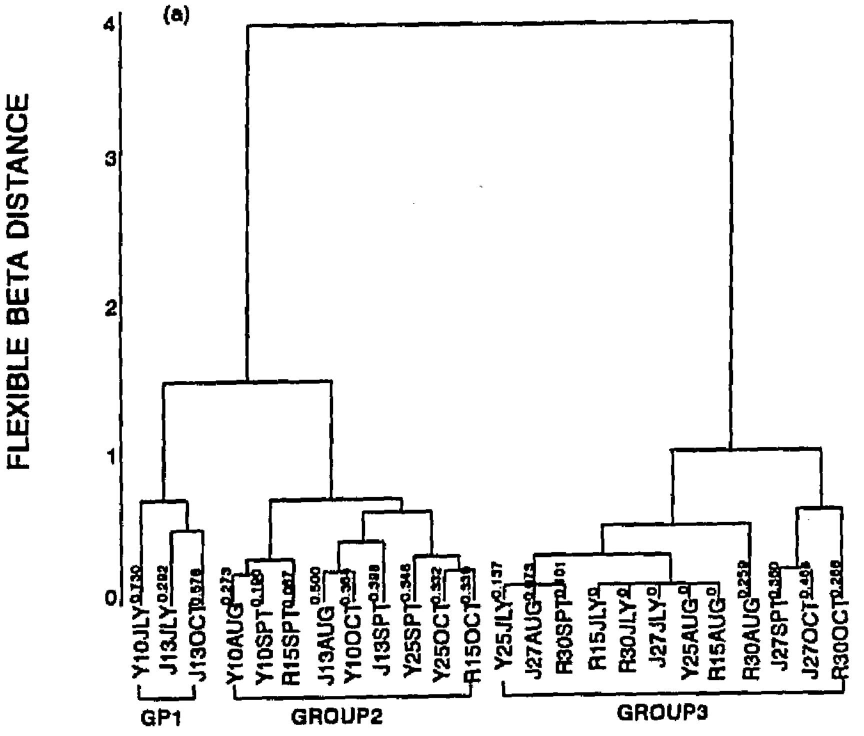
stations where polychaetes occurred in much greater proportions (0.26-0.96) than bivalves (0.0-0.40) or other species (Fig. 18b). Group 3, with the exception of R15 in July and August, consisted of upriver stations where bivalves (0.60-1.0) predominated (Fig. 18b) and benthic diversity was relatively low (Fig. 18a).

To clarify station and river groupings the data were collapsed across month (Fig. 19a). As above, group 1 primarily consisted of downriver stations (except for Y25) with relatively high benthic diversity (Fig. 19a). Group 2 consisted of the upriver stations, R30 and J27. Proportionally more polychaetes (0.48-0.78) occurred downriver, while bivalves (0.84-0.86, Fig. 19b) were dominant upriver. The York upriver station was similar to James and Rappahannock upriver stations in that bivalve densities were higher than those downriver, but the York densities differed in that these were not as high as those in the James and Rappahannock (Fig. 19b). Crustaceans occurred in greater proportions at James River stations, while gastropods only occurred downriver (Fig. 19b).

Months clustered into two groups collapsed across river and station (Fig. 20a): July (group 1) was separable from August, September and October (group 2). Benthic diversity was lowest in July (Fig. 20a) reflecting the relatively high proportion of bivalves (Fig. 20b). Proportionally more polychaetes, crustaceans and gastropods occurred from August through October (i.e., group 2), while more miscellaneous species (i.e., ophiuroids, fish, tunicates, anemones, sponges, bryozoans) occurred in July (Fig. 20b).

In summary, polychaetes and bivalves dominated the benthos in 1988 (Fig. 17). The results of cluster and abundance analyses similarly indicated differences in benthic composition associated with station location (Figs. 17-19: greater bivalve abundance upriver but greater polychaete abundance downriver) and season (i.e., a Summer/Fall pattern of highest bivalve densities in summer but highest polychaete densities in Fall). However, river-specific trends were suggested only by the

Figure 18. (a) Cluster diagram representing benthic similarity in 1988 for station (Y10, J13, R15, Y25, R30, J27) and month (July, August, September, October) combinations. The Shannon-Weiner diversity index is given at the root of each branch. (b) Benthic composition illustrated as proportion in the benthos for the station-month combinations described in (a). Animals predominating the benthos were bivalves and polychaetes. Rare benthic organisms were pooled into a miscellaneous category (i.e., crustaceans, ophiuroids, fish, gastropods, tunicates, anemones, sponges, bryozoans).


(a)
FLEXIBLE BETA DISTANCE
0
1
2
3
4
Y10JLY 0.730
J13JLY 0.282
J13OCT 0.576
Y10AUG 0.273
Y10SPT 0.186
R15SPT 0.067
J13AUG 0.500
Y10OCT 0.36
J13SPT 0.398
Y25SPT 0.346
Y25OCT 0.332
R15OCT 0.33
Y25JLY 0.157
J27AUG 0.073
R30SPT 0.101
R15JLY 0
R30JLY 0
J27JLY 0
Y25AUG 0
R15AUG 0
R30AUG 0.252
J27SPT 0.350
J27OCT 0.40
R30OCT 0.266
GP1
GROUP2
GROUP3

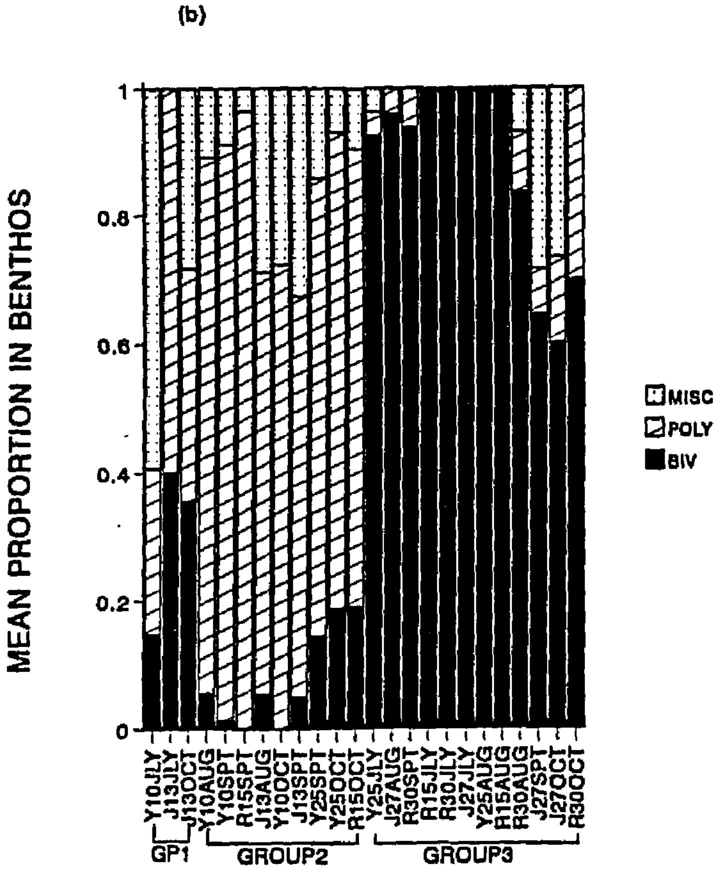

(b)
MEAN PROPORTION IN BENTHOS
0
0.2
0.4
0.6
0.8
1
MISC
POLY
BIV
Y10JLY
J13JLY
J13OCT
Y10AUG
Y10SPT
R15SPT
J13AUG
Y10OCT
J13SPT
Y25SPT
Y25OCT
R15OCT
Y25JLY
J27AUG
R30SPT
R15JLY
R30JLY
J27JLY
Y25AUG
R15AUG
R30AUG
J27SPT
J27OCT
R30OCT
GP1
GROUP2
GROUP3

Figure 19. (a) Cluster diagram representing benthic similarity in 1988 among the six stations sampled. Months were pooled. The Shannon-Weiner diversity index is given at the root of each branch. (b) Benthic composition illustrated as proportion in the benthos for the stations described in (a). Animals predominating the benthos were bivalves, polychaetes and crustaceans. Rare benthic organisms were pooled into a miscellaneous category (i.e., gastropods, ophiuroids, fish, tunicates, anemones, sponges, bryozoans).

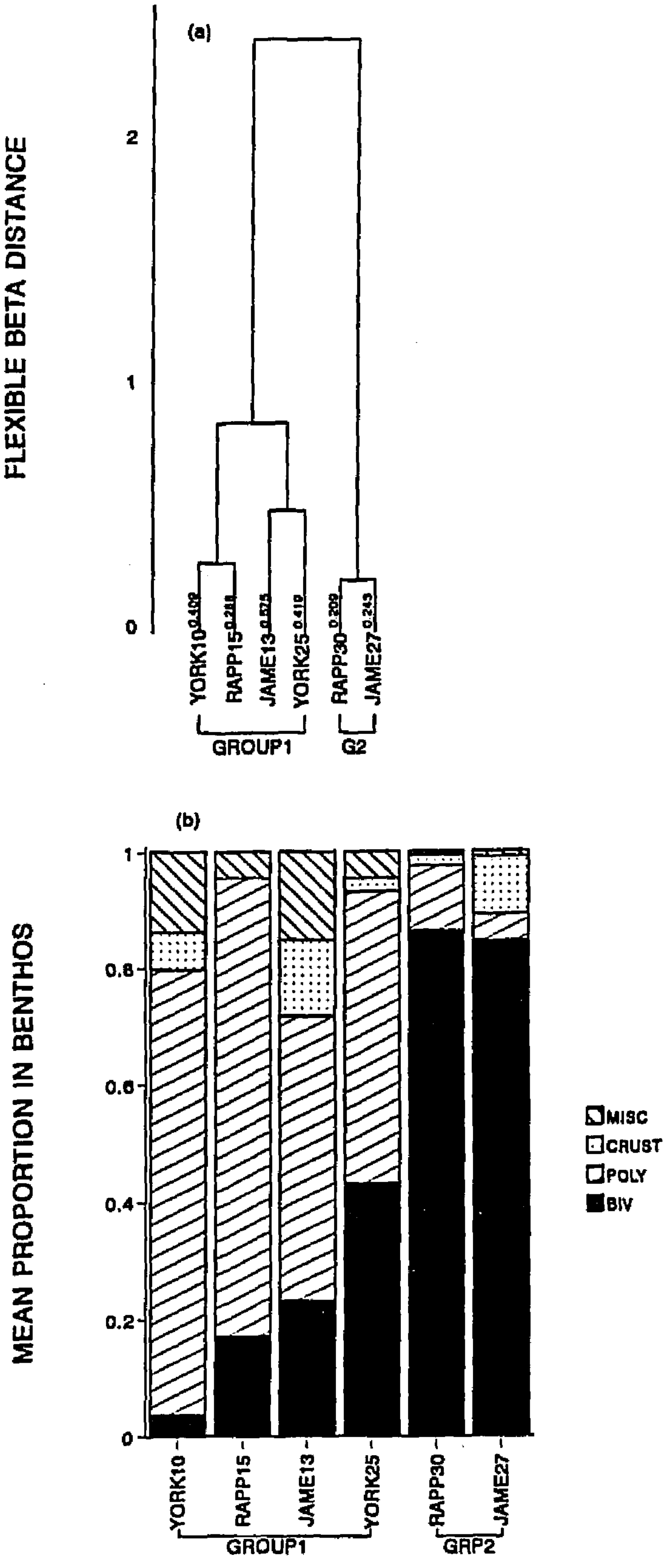
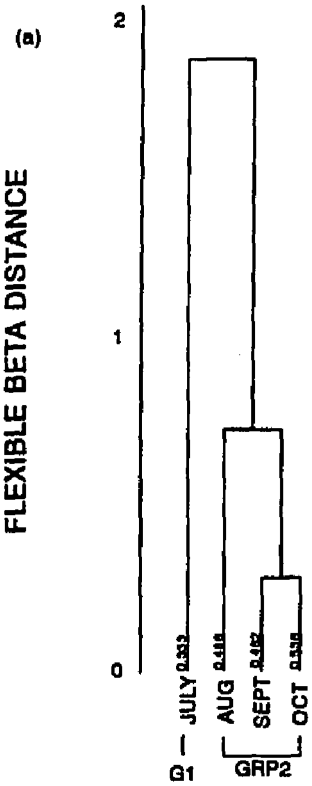
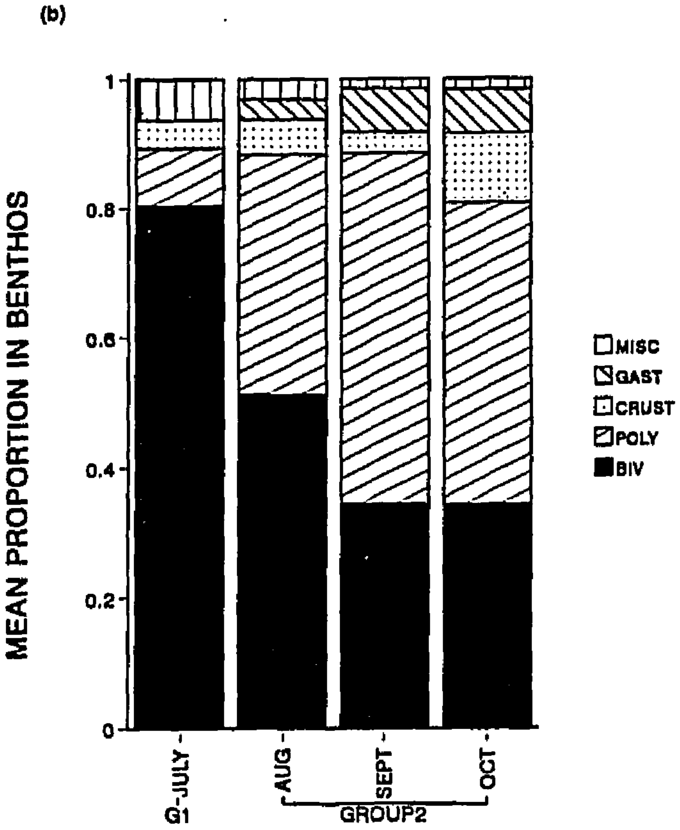
(a)
FLEXIBLE BETA DISTANCE
2
1
0
YORK10 0.409
RAPP15 0.288
JAME13 0.575
YORK25 0.419
RAPP30 0.209
JAME27 0.243
GROUP1
G2
(b)
MEAN PROPORTION IN BENTHOS
1
0.8
0.6
0.4
0.2
0
YORK10
RAPP15
JAME13
YORK25
RAPP30
JAME27
GROUP1
GRP2
MISC
CRUST
POLY
BIV

Figure 20. (a) Cluster diagram representing benthic similarity in 1988 among the four months sampled. Rivers and stations were pooled. The Shannon-Weiner diversity index is given at the root of each branch. (b) Benthic composition illustrated as proportion in the benthos for the months described in (a). Animals predominating the benthos were bivalves, polychaetes, crustaceans and gastropods. Rare benthic organisms were pooled into a miscellaneous category (i.e., ophiuroids, fish, tunicates, anemones, sponges, bryozoans).


(a)
FLEXIBLE BETA DISTANCE
2
1
0
JULY 0.333
AUG 0.486
SEPT 0.462
OCT 0.538
G1
GRP2


(b)
MEAN PROPORTION IN BENTHOS
1
0.8
0.6
0.4
0.2
0
G-JULY
G1
AUG
SEPT
OCT
GROUP2
MISC
GAST
CRUST
POLY
BIV

abundance analysis (Fig. 17).

Summer 1989

Benthic Abundance. -- Polychaetes and bivalves again dominated the benthos, with sporadically high crustacean densities (Fig. 21, Appendix 4). A significant River X Station interaction in the analysis of bivalve density (Table 23a) and significant River X Station X Month interaction in the analysis of polychaete (Table 24) and crustacean (Table 28) densities precluded singular conclusions about main effects. Thus, as for the 1988 data, lower-level ANOVA models were employed. In the analysis of Station within each level of River, there were significant differences for all rivers (Table 23b(i)): bivalves were always more abundant upriver. The analysis for River within each level of Station was significant at both downriver and upriver (Table 23b(ii)) stations. Bivalves were most abundant in the Rappahannock at downriver stations, and in the Rappahannock and York at upriver stations (Fig. 21, Table 23c).

Polychaete abundance (Fig. 21, Table 24) required ANOVA models within levels of each of the main factors. The analysis for Station and Month within each level of River indicated significant differences between stations and months in the York and James, but not in the Rappahannock (Table 25a). Polychaetes were more abundant downriver in both rivers. There were no obvious seasonal patterns in abundance in the York (Table 25b), while polychaetes were more abundant in the James in summer (i.e., relatively greater abundance in June and July than September; Table 25b). The Station X Month interaction effect was not significant in any analysis (Table 25a).

In the analysis of River and Station within each level of Month, there were significant station differences in June and September (Table 26a), and river differences in September (Table 26a). Polychaetes were most abundant downriver in both months, while the order of river abundance, from greatest to least in September was York, Rappahannock, and James (Table 26c). Significant River X Station interactions

Figure 21. Mean density of prey types collected through benthic sampling downriver and upriver in the James (i.e., J13, J27), York (i.e, Y10, Y25) and Rappahannock (i.e., R15, R30) Rivers from June through September, 1989. Numbers in parentheses represent sample size defined as grabs in which at least one living animal was recovered. The Miscellaneous category includes insects, ophiuroids, fish, tunicates, anemones, sponges, and bryozoans. The Poly* category includes polychaetes, nemerteans and phoronids (Appendix 4).

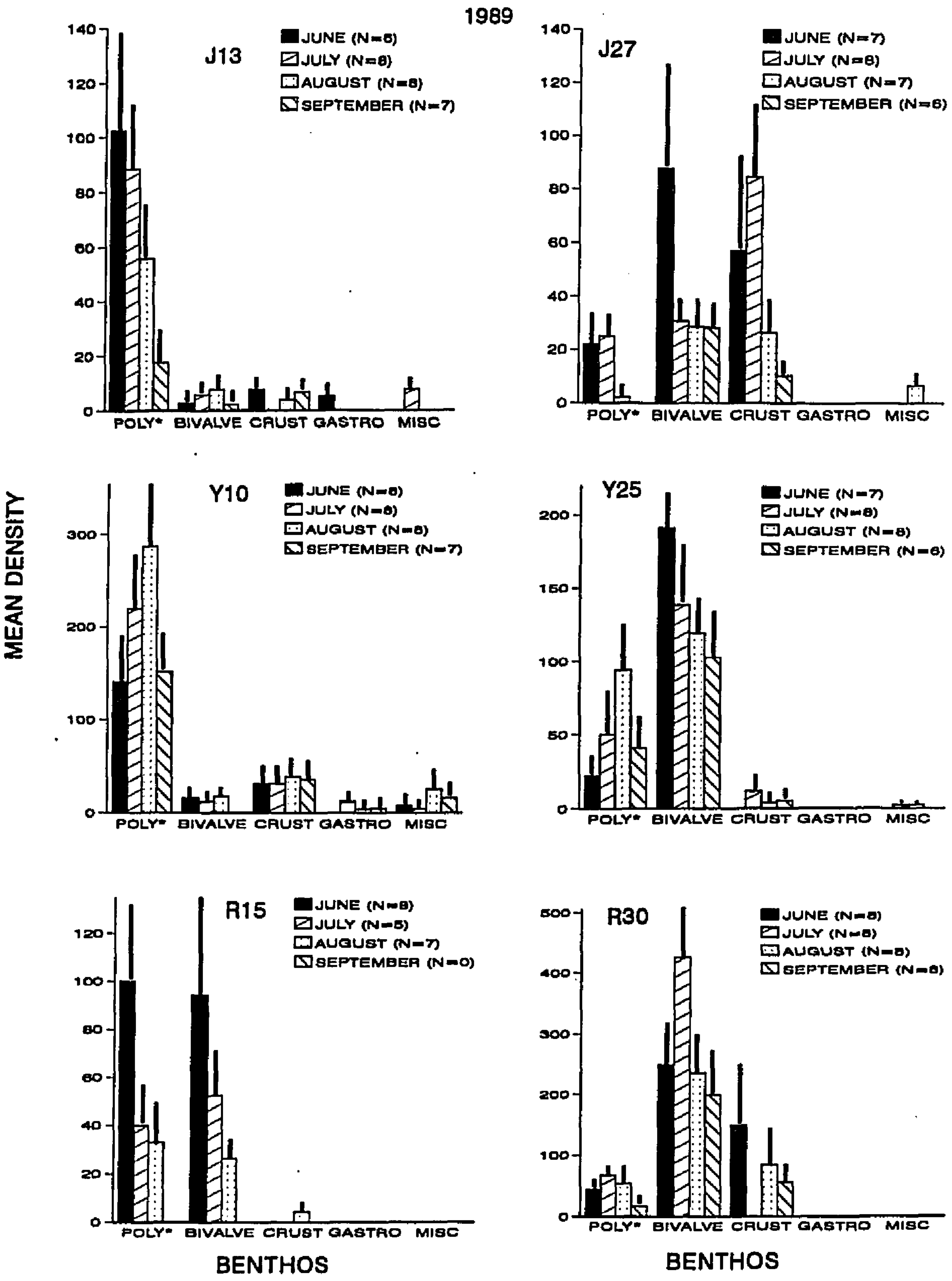

1989
MEAN DENSITY
J13
■ JUNE (N=6)
▨ JULY (N=8)
☐ AUGUST (N=8)
▧ SEPTEMBER (N=7)
0
20
40
60
80
100
120
140
POLY*
BIVALVE
CRUST
GASTRO
MISC
J27
■ JUNE (N=7)
▨ JULY (N=8)
☐ AUGUST (N=7)
▧ SEPTEMBER (N=6)
0
20
40
60
80
100
120
140
POLY*
BIVALVE
CRUST
GASTRO
MISC
Y10
■ JUNE (N=8)
▨ JULY (N=8)
☐ AUGUST (N=8)
▧ SEPTEMBER (N=7)
0
100
200
300
POLY*
BIVALVE
CRUST
GASTRO
MISC
Y25
■ JUNE (N=7)
▨ JULY (N=8)
☐ AUGUST (N=8)
▧ SEPTEMBER (N=6)
0
50
100
150
200
POLY*
BIVALVE
CRUST
GASTRO
MISC
R15
■ JUNE (N=8)
▨ JULY (N=5)
☐ AUGUST (N=7)
▧ SEPTEMBER (N=0)
0
20
40
60
80
100
120
POLY*
BIVALVE
CRUST
GASTRO
MISC
BENTHOS
R30
■ JUNE (N=8)
▨ JULY (N=8)
☐ AUGUST (N=8)
▧ SEPTEMBER (N=8)
0
100
200
300
400
500
POLY*
BIVALVE
CRUST
GASTRO
MISC
BENTHOS

Table 23. (a) Three-way analysis of variance with river, station and month as factors, and the dependent variable, log-transformed bivalve density, for each set of eight benthic grabs per station in 1989. In cases of n=0, the mean for benthic densities which grouped similarly in cluster analysis was substituted to insure a minimum sample size of two within all treatment combinations.

SOURCE OF VARIATION	DF	SS	PERCENTAGE OF VARIATION	MS	F	P<
RIVER	2	27.4769	21.0%	13.7384	34.80	0.0001
STATION	1	34.7911	26.6%	34.7911	88.13	0.0001
MONTH	3	1.9943	1.5%	0.6648	0.78	0.5852
RIVERxSTATION	2	3.4396	2.6%	1.7198	4.36	0.0145
RIVERxMONTH	6	1.8525	1.4%	0.3088	0.78	0.5852
STATIONxMONTH	3	0.7823	0.6%	0.2608	0.66	0.5776
RIVERxSTATIONxMONTH	6	2.3138	1.8%	0.3856	0.98	0.4431
ERROR	147	58.0302	44.4%	0.3948		

(b) Lower-level (i.e., one-way) analysis of variance for (i) Station within each level of River and (ii) River within each level of Station.

(i)

RIVER	SOURCE OF VARIATION	DF	SS	MS	F	P <
JAMES	STATION	1	13.0711	13.0711	34.38	0.0001
	ERROR	55	20.9129	0.3802		
YORK	STATION	1	21.7825	21.7825	50.15	0.0001
	ERROR	58	25.1932	0.4344		
RAPP	STATION	1	3.3771	3.3771	9.31	0.0036
	ERROR	52	18.8671	0.3628		

Table 23 (cont).

(ii)

STATION	SOURCE OF VARIATION	DF	SS	MS	F	P <
DOWNRIVER	RIVER	2	17.9537	8.9768	22.65	0.0001
	ERROR	79	31.3111	0.3963		
UPRIVER	RIVER	2	7.5729	3.7865	9.67	0.0002
	ERROR	86	33.6622	0.3914		

(c) Ryan's Q results for rivers compared within each level of station, months pooled. Means sharing the same line are not significantly different. * P < 0.05

Downriver: JAMES YORK RAPPAHANNOCK

0.31 0.54 1.46

____________ * ____________

Upriver: JAMES YORK RAPPAHANNOCK

1.27 1.75 1.97

______ * ________________

Table 24. Three-way analysis of variance with river, station and month as factors, and the dependent variable, log-transformed polychaete density, for each set of eight benthic grabs per station in 1989. In cases of n=0, the mean for benthic densities which grouped similarly in cluster analysis was substituted to insure a minimum sample size of two within all treatment combinations.

SOURCE OF VARIATION	DF	SS	PERCENTAGE OF VARIATION	MS	F	P<
RIVER	2	10.5439	9.7%	5.2720	13.81	0.0001
STATION	1	14.4714	13.3%	14.4714	37.92	0.0001
MONTH	3	3.1162	2.9%	1.0387	2.72	0.0466
RIVERxSTATION	2	8.4551	7.8%	4.2276	11.08	0.0001
RIVERxMONTH	6	9.1382	8.4%	1.5230	3.99	0.0010
STATIONxMONTH	3	1.2576	1.2%	0.4192	1.10	0.3518
RIVERxSTATIONxMONTH	6	5.5957	5.1%	0.9326	2.44	0.0279
ERROR	147	56.0990	51.6%	0.3816		

Table 25. (a) Two-way analysis of variance for Station and Month within each level of River, and the dependent variable, log-transformed polychaete density in 1989.

RIVER	SOURCE OF VARIATION	DF	SS	MS	F	P <
JAMES	STATION	1	13.0260	13.0260	41.79	0.0001
	MONTH	3	6.6948	2.2316	7.16	0.0004
	STATIONXMONTH	3	1.1344	0.3781	1.21	0.3148
	ERROR	49	15.2728	0.3118		
YORK	STATION	1	9.8206	9.8206	26.12	0.0001
	MONTH	3	3.8797	1.2932	3.44	0.0233
	STATIONXMONTH	3	1.8991	0.6330	1.68	0.1818
	ERROR	52	19.5480	0.3759		
RAPP	STATION	1	0.0799	0.0799	0.17	0.6795
	MONTH	3	1.6799	0.5599	1.21	0.3165
	STATIONXMONTH	3	3.8198	1.2733	2.75	0.0532
	ERROR	46	21.2783	0.4626		

(b) Ryan's Q results for months in the James and York. Means sharing the same line are not significantly different.

James:	SEPTEMBER	AUGUST	JUNE	JULY
	0.52	0.94	1.25	1.36
	———	———		
		———	———	———

York:	JUNE	JULY	SEPTEMBER	AUGUST
	1.33	1.49	1.75	1.97
	———	———	———	
		———	———	———

occurred in July and August (Table 26a). Stations differed in July in the York and in July and August in the James (Table 26b(i)): abundance was greatest downriver. River differences occurred at downriver and upriver (Table 26b(ii)) sites in both months. Polychaetes were more abundant in the York than Rappahannock at downriver stations in July and August (Table 26d) with intermediate densities in the James. No consistent patterns occurred at upriver stations in these months (Table 26d).

Analysis of River and Month within each level of Station indicated significant river differences, but no seasonal or interaction effects at downriver stations (Table 27a). Polychaetes were most abundant in the York river (Table 27c). The River X Month interaction was significant for upriver stations (Table 27a). River differences occurred in July, August and September (Table 27b(i)). Polychaetes were most abundant in the Rappahannock in July (Table 27d) and in the York and Rappahannock in August and September (Table 27d). Seasonal variation in abundance occurred in all rivers (Table 27b(ii)). Although no clear seasonal patterns were detectable in the York (Table 27e), polychaete densities were greater in early and mid-summer than Fall in the James and Rappahannock (Table 27e), respectively.

In the analysis of crustacean abundance (Fig. 21) for Station and Month within each level of River, there were significant differences between stations in the York and James (Table 29a), but no seasonal effects in either river (Table 29a): abundance was generally greater in the lower York and upper James. A significant Station X Month interaction effect occurred in the Rappahannock (Table 29a), requiring examination within levels of the main effects. Monthly differences in crustacean abundance occurred in the upper Rappahannock (Table 29b(ii)): lowest densities occurred in July (i.e., no crustaceans collected, Table 29c). Significant station differences occurred in June and August (Table 29b(i)): highest densities occurred upriver.

Table 26. (a) Two-way analysis of variance for River and Station within each level of Month, and the dependent variable, log-transformed polychaete density in 1989.

MONTH	SOURCE OF VARIATION	DF	SS	MS	F	P<
JUNE	RIVER	2	0.5096	0.2548	0.55	0.5834
	STATION	1	5.4097	5.4097	11.60	0.0016
	RIVERXSTATION	2	2.3581	1.1791	2.53	0.0931
	ERROR	38	17.7161	0.4662		
JULY	RIVER	2	0.2470	0.1235	0.28	0.7573
	STATION	1	2.0518	2.0518	4.65	0.0372
	RIVERXSTATION	2	5.8790	2.9400	6.66	0.0032
	ERROR	39	17.2009	0.4410		
AUG	RIVER	2	8.4053	4.2027	14.98	0.0001
	STATION	1	2.0672	2.0672	7.37	0.0097
	RIVERXSTATION	2	6.7064	3.3532	11.96	0.0001
	ERROR	40	11.2192	0.2805		
SEPT	RIVER	2	9.7182	4.8591	14.63	0.0001
	STATION	1	6.3773	6.3773	19.20	0.0001
	RIVERXSTATION	2	0.1208	0.0604	0.18	0.8346
	ERROR	30	9.9628	0.3321		

Table 26 (cont).

(b) Lower-level (i.e, one-way) analysis of variance for (i) Station within each level of River, and (ii) River within each level of Station in July and August.

(i)

MONTH	RIVER	SOURCE OF VARIATION	DF	SS	MS	F	P <
JULY	JAMES	STATION	1	2.0363	2.0363	5.21	0.0386
		ERROR	14	5.4748	0.3911		
	YORK	STATION	1	4.2839	4.2839	7.94	0.0137
		ERROR	14	7.5577	0.5398		
	RAPP	STATION	1	1.6106	1.6106	4.25	0.0637
		ERROR	11	4.1684	0.3790		
AUG	JAMES	STATION	1	7.6979	7.6979	45.84	0.0001
		ERROR	13	2.1831	0.1679		
	YORK	STATION	1	0.3396	0.3396	2.19	0.1612
		ERROR	14	2.1729	0.1552		
	RAPP	STATION	1	0.7361	0.7361	1.39	0.2588
		ERROR	13	6.8633	0.5279		

(ii)

MONTH	STATION	SOURCE OF VARIATION	DF	SS	MS	F	P <
JULY	DOWNRIVER	RIVER	2	2.6376	1.3188	3.74	0.0438
		ERROR	18	6.3487	0.3527		
	UPRIVER	RIVER	2	3.6067	1.8033	3.49	0.0492
		ERROR	21	10.8522	0.5168		
AUG	DOWNRIVER	RIVER	2	3.8575	1.9288	6.42	0.0070
		ERROR	20	6.0101	0.3005		
	UPRIVER	RIVER	2	11.4250	5.7125	21.93	0.0001
		ERROR	20	5.2092	0.2605		

Table 26 (cont).

(c) Ryan's Q results for rivers in September. Means sharing the same line are not significantly different. * $P < 0.05$

JAMES		RAPPAHANNOCK		YORK
0.52		1.08		1.75
———	*	———	*	———

(d) Ryan's Q results for rivers within each level of station in July and August. Means sharing the same line are not significantly different. * $P < 0.05$

Downriver, July:

RAPPAHANNOCK	JAMES	YORK
1.09	1.72	2.01
———	———	
	———	———

Upriver, July:

YORK	JAMES		RAPPAHANNOCK
0.98	1.00		1.81
———	———	*	———

Downriver, August:

RAPPAHANNOCK	JAMES	YORK
1.10	1.61	2.12
———	———	
	———	———

Upriver, August:

JAMES		RAPPAHANNOCK	YORK
0.17		1.54	1.82
———	*	———	———

Table 27. (a) Two-way analysis of variance for River and Month within each level of Station, and the dependent variable, log-transformed polychaete density in 1989.

STATION	SOURCE OF VARIATION	DF	SS	MS	F	P <
DOWNRIVER	RIVER	2	7.0643	3.5322	11.29	0.0001
	MONTH	3	0.4895	0.1632	0.52	0.6688
	RIVERXMONTH	6	4.1539	0.6923	2.21	0.0517
	ERROR	70	21.8980	0.3128		
UPRIVER	RIVER	2	12.1189	6.0595	13.64	0.0001
	MONTH	3	3.8816	1.2939	2.91	0.0396
	RIVERXMONTH	6	10.5827	1.7638	3.97	0.0016
	ERROR	77	34.2010	0.4442		

(b) Lower-level (i.e., one-way) analysis of variance for (i) River within each level of Month, and (ii) Month within each level of River, upriver.

(i)

MONTH	SOURCE OF VARIATION	DF	SS	MS	F	P <
JUNE	RIVER	2	2.4197	1.2099	1.97	0.1666
	ERROR	19	11.6559	0.6135		
JULY	RIVER	2	3.6067	1.8033	3.49	0.0492
	ERROR	21	10.8522	0.5168		
AUGUST	RIVER	2	11.4250	5.7125	21.93	0.0001
	ERROR	20	5.2092	0.2605		
SEPTEMBER	RIVER	2	5.6333	2.8167	7.39	0.0049
	ERROR	17	6.4837	0.3814		

Table 27 (cont).

(ii)

RIVER	SOURCE OF VARIATION	DF	SS	MS	F	P <
JAMES	MONTH	3	5.1807	1.7269	4.00	0.0192
	ERROR	24	10.3623	0.4318		
YORK	MONTH	3	5.5424	1.8475	3.29	0.0370
	ERROR	25	14.0293	0.5612		
RAPP	MONTH	3	3.7413	1.2471	3.56	0.0267
	ERROR	28	9.8094	0.3503		

(c) Ryan's Q results for rivers, downriver, and months pooled. Means sharing the same line are not significantly different. * P < 0.05

RAPPAHANNOCK	JAMES		YORK
1.34	1.50		2.02
________	________	*	________

(d) Ryan's Q results for rivers, upriver in July, August and September. Means with the same letter are not significantly different. * P < 0.05

July:	YORK	JAMES		RAPPAHANNOCK
	0.98	1.00		1.81
	________	________	*	________
August:	JAMES		RAPPAHANNOCK	YORK
	0.17		1.54	1.82
	________	*	________	________
September:	JAMES		RAPPAHANNOCK	YORK
	0.00		0.87	1.35
	________	*	________	________

Table 27 (cont).

(e) Ryan's Q results for months upriver in the York, Rappahannock and James rivers. Means sharing the same line are not significantly different.

York:	JUNE	JULY	SEPTEMBER	AUGUST
	0.68	0.98	1.35	1.82
	———	———	———	
		———	———	———
Rappahannock:	SEPTEMBER	JUNE	AUGUST	JULY
	0.87	1.45	1.54	1.81
	———	———	———	
		———	———	———
James:	SEPTEMBER	AUGUST	JUNE	JULY
	0.00	0.17	0.87	1.00
	———	———		
		———	———	———

Table 28. Three-way analysis of variance with river, station and month as factors, and the dependent variable, log-transformed crustacean density, for each set of eight benthic grabs per station in 1989. In cases of n=0, the mean for benthic densities which grouped similarly in cluster analysis was substituted to insure a minimum sample size of two within all treatment combinations.

SOURCE OF VARIATION	DF	SS	PERCENTAGE OF VARIATION	MS	F	P<
RIVER	2	0.0542	0.04%	0.0271	0.06	0.9380
STATION	1	3.4679	3.0%	3.4679	8.19	0.0048
MONTH	3	2.5118	2.2%	0.8373	1.98	0.1201
RIVERxSTATION	2	28.3339	24.6%	14.1670	33.44	0.0001
RIVERxMONTH	6	7.7793	6.8%	1.2966	3.06	0.0075
STATIONxMONTH	3	1.1529	1.0%	0.3843	0.91	0.4393
RIVERxSTATIONxMONTH	6	9.5854	8.3%	1.5976	3.77	0.0016
ERROR	147	62.2824	54.1%	0.4237		

Table 29. (a) Two-way analysis of variance for Station and Month within each level of River, and the dependent variable, log-transformed crustacean density in 1989.

RIVER	SOURCE OF VARIATION	DF	SS	MS	F	P <
JAMES	STATION	1	8.9333	8.9333	19.25	0.0001
	MONTH	3	0.5160	0.1720	0.37	0.7745
	STATIONXMONTH	3	3.5567	1.1856	2.55	0.0660
	ERROR	49	22.7408	0.4641		
YORK	STATION	1	9.8979	9.8979	20.41	0.0001
	MONTH	3	0.5659	0.1886	0.39	0.7614
	STATIONXMONTH	3	1.4011	0.4670	0.96	0.4173
	ERROR	52	25.2219	0.4850		
RAPP	STATION	1	12.9706	12.9706	41.67	0.0001
	MONTH	3	9.2092	3.0697	9.86	0.0001
	STATIONXMONTH	3	5.7806	1.9269	6.19	0.0013
	ERROR	46	14.3196	0.3113		

(b) Lower-level (i.e., one-way) analysis of variance for (i) Station within each level of Month and (ii) Month within each level of Station in the Rappahannock river.

(i)

MONTH	SOURCE OF VARIATION	DF	SS	MS	F	P <
JUNE	STATION	1	13.0646	13.0646	271.33	0.0001
	ERROR	14	0.6741	0.0481		
JULY	STATION	no crustaceans collected				
	ERROR					
AUG	STATION	1	3.7148	3.7148	5.80	0.0315
	ERROR	13	8.3204	0.6400		
SEPT	STATION	1	2.6199	2.6199	3.94	0.0825
	ERROR	8	5.3251			

Table 29 (cont).

(ii)

STATION	SOURCE OF VARIATION	DF	SS	MS	F	P <
DOWNRIVER	MONTH	3	0.5742	0.1914	1.64	0.2162
	ERROR	18	2.1054	0.1170		
UPRIVER	MONTH	3	14.4155	4.8052	11.02	0.0001
	ERROR	28	12.2142	0.4362		

(c) Ryan's Q results for months at R30. Means sharing the same line are not significantly different. * P < 0.05

JULY	SEPTEMBER	AUGUST	JUNE
0.00	1.28	1.34	1.81
——— *	—————	—————	—————

Significant interaction effects occurred in the analysis of River and Station within each level of Month (Table 30a). Station differences occurred in June in the York and Rappahannock (Table 30b(i)): densities were highest downriver in the York but upriver in the Rappahannock. River differences occurred at both downriver and upriver (Table 30b(ii)) stations in June. Crustaceans were most abundant downriver in the York but least abundant upriver in the York (Table 30c) in June. In July, station differences occurred in the James (Table 30b(i)): crustaceans were most abundant upriver. Rivers differed at both downriver and upriver (Table 30b(ii)) stations. Crustaceans were most abundant downriver in the York (Table 30c) but upriver in the James (Table 30c). Similarly to June, station differences occurred in August in the York and Rappahannock (Table 30b(i)): abundance was greatest downriver in the York but upriver in the Rappahannock. Rivers differed at downriver sites (Table 30b(ii)): greatest densities occurred in the York (Table 30c). In September, station differences occurred only in the York (Table 30b(i)): abundance was greater downriver. River differences occurred downriver but not upriver (Table 30b(ii)): more crustaceans occurred in the York than Rappahannock (no crustaceans collected) and the order of river abundance, from greatest to least was: York, James, Rappahannock (Table 30c).

When analyzing River and Month within each level of Station, there were significant river differences downriver (Table 31a): greatest densities occurred in the York (Table 31c). The River X Month interaction was significant (Table 31a) for upriver stations. River differences occurred in June and July (Table 31b(i)): crustaceans were more abundant in the Rappahannock and James in June, and in the James in July (Table 31d). Months differed upriver in the Rappahannock (Table 31b(ii)), with no crustaceans collected in July (Table 31e) and equally high densities in June, August and September.

In summary, as in 1988, bivalves were more abundant at upriver stations, and were generally most abundant in the Rappahannock river.

Table 30. (a) Two-way analysis of variance for River and Station within each level of Month, and the dependent variable, log-transformed crustacean density in 1989.

MONTH	SOURCE OF VARIATION	DF	SS	MS	F	P<
JUNE	RIVER	2	0.7473	0.3737	1.15	0.3264
	STATION	1	2.6673	2.6673	8.23	0.0067
	RIVERXSTATION	2	17.2227	8.6114	26.58	0.0001
	ERROR	38	12.3111	0.3240		
JULY	RIVER	2	4.8449	2.4225	7.13	0.0023
	STATION	1	1.9609	1.9609	5.77	0.0212
	RIVERXSTATION	2	7.4712	3.7356	10.99	0.0002
	ERROR	39	13.2581	0.3399		
AUG	RIVER	2	0.6939	0.3470	0.64	0.5341
	STATION	1	0.4698	0.4698	0.86	0.3585
	RIVERXSTATION	2	7.7274	386372	7.10	0.0023
	ERROR	40	21.7816	0.5445		
SEPT	RIVER	2	1.2228	0.6114	1.23	0.3071
	STATION	1	0.0267	0.0267	0.05	0.8186
	RIVERXSTATION	2	5.3385	2.6693	5.36	0.0102
	ERROR	30	14.9315	0.4977		

Table 30 (cont).

(b) Lower-level (i.e, one-way) analysis of variance for (i) Station within each level of River, and (ii) River within each level of Station in June, July, August and September.

(i)

MONTH	RIVER	SOURCE OF VARIATION	DF	SS	MS	F	P <
JUNE	JAMES	STATION	1	1.8903	1.8903	2.72	0.1274
		ERROR	11	7.6463	0.6951		
	YORK	STATION	1	4.9352	4.9352	16.08	0.0015
		ERROR	13	3.9907	0.3070		
	RAPP	STATION	1	13.0646	13.0646	271.33	0.0001
		ERROR	14	0.6741	0.0481		
JULY	JAMES	STATION	1	8.9865	8.9865	40.15	0.0001
		ERROR	14	3.1337	0.2238		
	YORK	STATION	1	0.4456	0.4456	0.62	0.4456
		ERROR	14	10.1245	0.7232		
	RAPP	STATION	no crustaceans collected				
		ERROR					
AUG	JAMES	STATION	1	1.2730	1.2730	2.43	0.1429
		ERROR	13	6.8049	0.5235		
	YORK	STATION	1	3.2095	3.2095	6.75	0.0211
		ERROR	14	6.6562	0.4754		
	RAPP	STATION	1	3.7148	3.7148	5.80	0.0315
		ERROR	13	8.3204	0.6400		

Table 30 (cont).

MONTH	RIVER	SOURCE OF VARIATION	DF	SS	MS	F	P <
SEPT	JAMES	STATION	1	0.0586	0.0586	0.13	0.7303
		ERROR	11	5.1560	0.4687		
	YORK	STATION	1	2.6866	2.6866	6.64	0.0257
		ERROR	11	4.4505	0.4046		
	RAPP	STATION	1	2.6199	2.6199	3.94	0.0825
		ERROR	8	5.3251	0.6656		

(ii)

MONTH	STATION	SOURCE OF VARIATION	DF	SS	MS	F	P <
JUNE	DOWNRIVER	RIVER	2	5.3529	2.6764	7.83	0.0033
		ERROR	19	6.4911	0.3416		
	UPRIVER	RIVER	2	12.5008	6.2504	20.40	0.0001
		ERROR	19	5.8201	0.3063		
JULY	DOWNRIVER	RIVER	2	3.6777	1.8389	5.35	0.0150
		ERROR	18	6.1816	0.3434		
	UPRIVER	RIVER	2	9.2480	4.6240	13.72	0.0002
		ERROR	21	7.0766	0.3370		
AUG	DOWNRIVER	RIVER	2	4.0063	2.0032	4.57	0.0232
		ERROR	20	8.7617	0.4381		
	UPRIVER	RIVER	2	4.3533	2.1767	3.34	0.0559
		ERROR	20	13.0199	0.6510		
SEPT	DOWNRIVER	RIVER	2	3.6954	1.8477	4.79	0.0276
		ERROR	13	5.0119	0.3855		
	UPRIVER	RIVER	2	2.8865	1.4432	2.47	0.1141
		ERROR	17	9.9196	0.5835		

Table 30 (cont).

(c) Ryan's Q results for rivers in downriver and upriver in June and July, and downriver in August and September. Means sharing the same line are not significantly different. * P < 0.05

June

Downriver:

RAPPAHANNOCK	JAMES		YORK
0.00	0.45	*	1.15
———	———		———

Upriver:

YORK		JAMES	RAPPAHANNOCK
0.00	*	1.22	1.81
———		———	———

July

Downriver:

RAPPAHANNOCK	JAMES		YORK
0.00	0.00	*	0.86
———	———		———

Upriver:

RAPPAHANNOCK	YORK		JAMES
0.00	0.53	*	1.50
———	———		———

Downriver

August:

JAMES	RAPPAHANNOCK		YORK
0.30	0.35	*	1.20
———	———		———

September:

RAPPAHANNOCK	JAMES	YORK
0.00	0.52	1.32
———	———	
	———	———

Table 31. (a) Two-way analysis of variance for River and Month within each level of Station, and the dependent variable, log-transformed crustacean density in 1989.

STATION	SOURCE OF VARIATION	DF	SS	MS	F	P <
DOWNRIVER	RIVER	2	16.2898	8.1449	21.56	0.0001
	MONTH	3	1.8895	0.6298	1.67	0.1820
	RIVERXMONTH	6	0.7444	0.1241	0.33	0.9199
	ERROR	70	26.4462	0.3778		
UPRIVER	RIVER	2	12.1628	6.0814	13.07	0.0001
	MONTH	3	1.4951	0.4984	1.07	0.3665
	RIVERXMONTH	6	16.9005	2.8168	6.05	0.0001
	ERROR	77	35.8362	0.4654		

(b) Lower-level (i.e., one-way) analysis of variance for (i) River within each level of Month, and (ii) Month within each level of River, upriver.

(i)

MONTH	SOURCE OF VARIATION	DF	SS	MS	F	P <
JUNE	RIVER	2	12.5008	6.2504	20.40	0.0001
	ERROR	19	5.8201	0.3063		
JULY	RIVER	2	9.2480	4.6240	13.72	0.0002
	ERROR	21	7.0766	0.3370		
AUGUST	RIVER	2	4.3533	2.1767	3.34	0.0559
	ERROR	20	13.0199	0.6510		
SEPTEMBER	RIVER	2	2.8865	1.4433	2.47	0.1141
	ERROR	17	9.9196	0.5835		

Table 31 (cont).

(ii)

RIVER	SOURCE OF VARIATION	DF	SS	MS	F	P <
JAMES	MONTH	3	2.8733	0.9578	1.48	0.2444
	ERROR	24	15.5033	0.6460		
YORK	MONTH	3	1.1067	0.3689	1.14	0.3537
	ERROR	25	8.1187	0.3247		
RAPP	MONTH	3	14.4155	4.8052	11.02	0.0001
	ERROR	28	12.2142	0.4362		

(c) Ryan's Q results for rivers, downriver, months pooled. Means sharing the same line are not significantly different. * P < 0.05

RAPPAHANNOCK	JAMES		YORK
0.11	0.30		1.13
————	————	*	————

(d) Ryan's Q results for rivers, upriver in June and July. Means sharing the same line are not significantly different. * P < 0.05

June:

YORK		JAMES	RAPPAHANNOCK
0.00		1.22	1.81
————	*	————	————

July:

RAPPAHANNOCK	YORK		JAMES
0.00	0.53		1.50
————	————	*	————

(e) Ryan's Q results for months upriver in the Rappahannock. Means sharing the same line are not significantly different. * P < 0.05

JULY		SEPTEMBER	AUGUST	JUNE
0.00		1.28	1.34	1.81
————	*	————	————	————

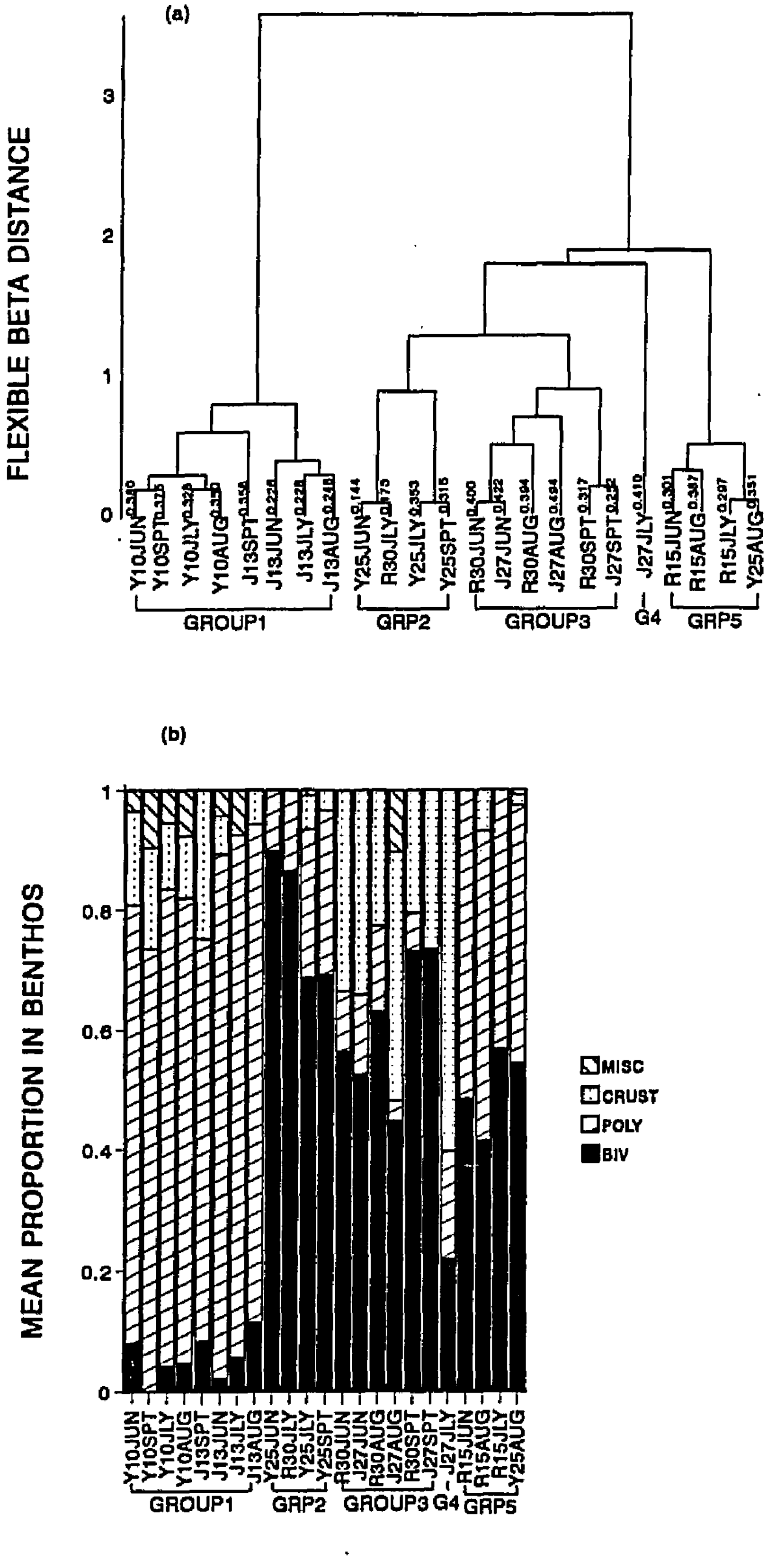
There were no distinct seasonal trends in bivalve abundance. Polychaetes were again most abundant downriver, but with lower proportions in the Rappahannock. However, seasonal and river-specific patterns were not as marked in 1989. For example, although polychaetes were often most abundant in the York, river-dominance varied, depending on station location and month. Polychaetes were generally most abundant in the summer (i.e., June & July). However, seasonal variation in abundance depended on river or station, and the Summer/Fall pattern of abundance was often not apparent. There were no consistent seasonal or river-specific trends in crustacean abundance. Crustaceans were most abundant downriver in the York and upriver in the James and Rappahannock. River-dominance depended on station location and month.

Benthic Similarity.-- Benthic abundance data clustered into five groups separable primarily by the proportions of bivalves and polychaetes, and secondarily by crustaceans (Fig. 22a). Group 1 consisted of downriver stations, Y10 and J13. Polychaetes dominated the benthos (0.67-0.87), whereas the proportions of bivalves were low (0.0-0.11, Fig. 22b). Bivalves dominated the benthos (0.68-0.89, Fig. 22b) of group 2 upriver stations (i.e, Y25 and R30), which also had the lowest benthic diversity (Fig. 22a). Group 3 included the upriver stations R30 and J27 (Fig. 22a), which were diverse and consisted of relatively high proportions of crustaceans (0.21-0.41), lower proportions of polychaetes (0.03-0.14), and moderate to high proportions of bivalves (0.44-0.73, Fig. 22b). This was the only group in which insects occurred (Fig. 22b). Group 4 was the upriver station J27 in July where crustaceans dominated, and bivalves and polychaetes occurred in moderate proportions (Fig. 22b). Group 5 was the downriver station, R15 from June through August, and the upriver station, Y25 in August (Fig. 22a). This group contained almost equal proportions of bivalves (0.41-0.57) and polychaetes (0.43-0.52), but very few crustaceans or miscellaneous species (Fig. 22b).

To clarify station differences, months were pooled. As above,

Figure 22. (a) Cluster diagram representing benthic similarity in 1989 for station (Y10, J13, R15, Y25, R30, J27) and month (June, July, August, September) combinations. The Shannon-Weiner diversity index is given at the root of each branch.

(b) Benthic composition illustrated as proportion in the benthos for the station-month combinations described in (a). Animals predominating the benthos were bivalves, polychaetes and crustaceans. Rare benthic organisms were pooled into a miscellaneous category (i.e., ophiuroids, fish, gastropods, tunicates, anemones, sponges, bryozoans, insects).


(a)
FLEXIBLE BETA DISTANCE
3
2
1
0
Y10JUN 0.380
Y10SPT 0.325
Y10JLY 0.328
Y10AUG 0.350
J13SPT 0.558
J13JUN 0.226
J13JLY 0.228
J13AUG 0.248
Y25JUN 0.144
R30JLY 0.375
Y25JLY 0.353
Y25SPT 0.315
R30JUN 0.400
J27JUN 0.422
R30AUG 0.394
J27AUG 0.494
R30SPT 0.317
J27SPT 0.252
J27JLY 0.410
R15JUN 0.301
R15AUG 0.387
R15JLY 0.297
Y25AUG 0.351
GROUP1
GRP2
GROUP3
G4
GRP5
(b)
MEAN PROPORTION IN BENTHOS
1
0.8
0.6
0.4
0.2
0
Y10JUN
Y10SPT
Y10JLY
Y10AUG
J13SPT
J13JUN
J13JLY
J13AUG
Y25JUN
R30JLY
Y25JLY
Y25SPT
R30JUN
J27JUN
R30AUG
J27AUG
R30SPT
J27SPT
J27JLY
R15JUN
R15AUG
R15JLY
Y25AUG
GROUP1
GRP2
GROUP3
G4
GRP5
▧ MISC
▤ CRUST
□ POLY
■ BIV

downriver stations (Y10 and J13) grouped together (group 1) while R15 clustered with the three upriver stations (group 2; Fig. 23a). Group 1 contained the greatest proportions of polychaetes, gastropods, and miscellaneous species (Fig. 23b). Group 2 contained the greatest proportions of bivalves and crustaceans (Fig. 23b). Benthic diversity was lowest at J13 (group 1) and highest at J27 (group 2, Fig. 23a). Contrary to 1988, in 1989 there were no obvious seasonal patterns (Fig. 24).

In summary, polychaetes, bivalves and crustaceans dominated the benthos in 1989 (Fig. 21). Bivalves dominated the benthos of upriver stations, while polychaetes were dominant downriver, except in the lower Rappahannock where bivalve and polychaete densities and proportions were nearly equal (Figs. 21 & 23b). Proportionally more crustaceans occurred in the upper James (Fig. 23b). There were no consistent seasonal trends in benthic abundance (Fig. 24), although abundance analyses sometimes indicated greater polychaete densities in Summer (Fig. 21). As in 1988, bivalves were generally most abundant in the Rappahannock while polychaete densities were generally highest in the York (Fig. 21).

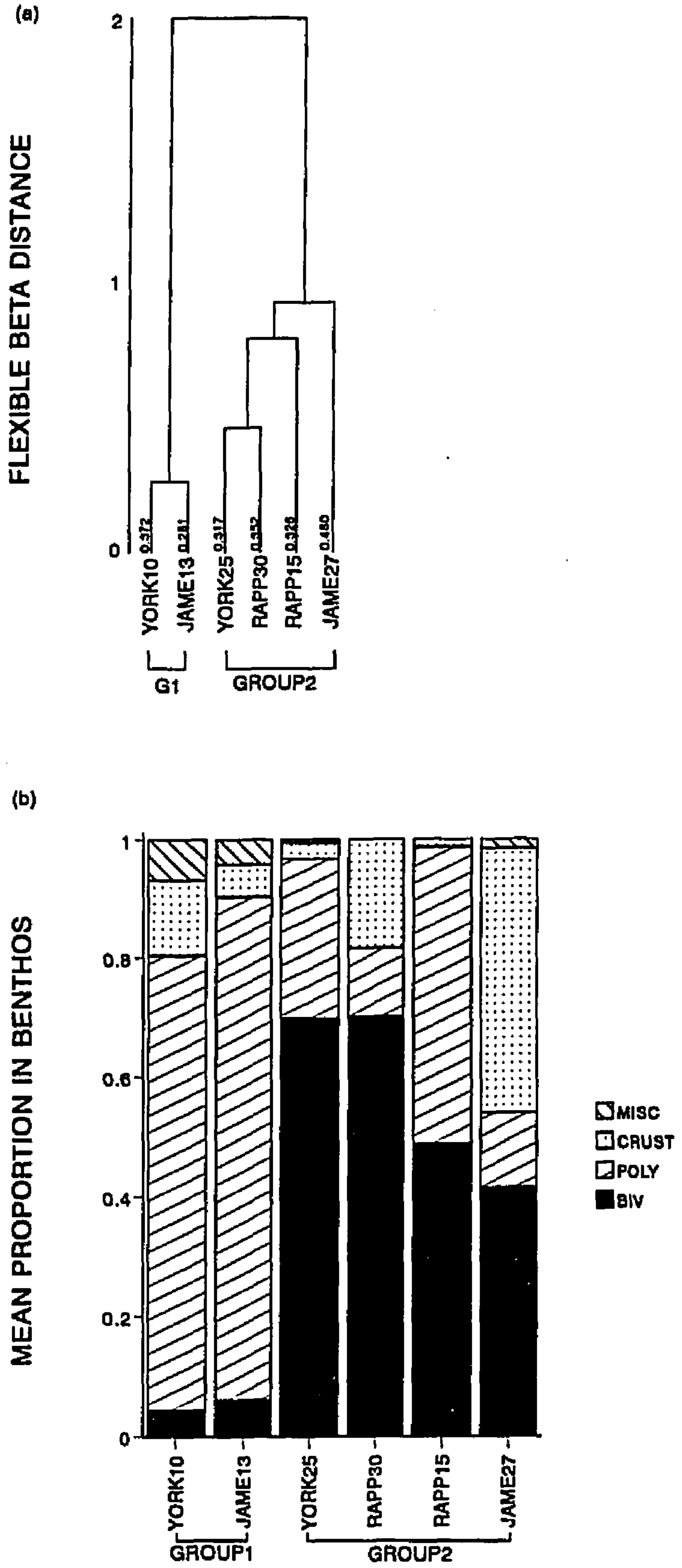
Dietary Overlap and Selection

1988

The results of dietary and benthic analyses indicated dominance by three prey categories - bivalves, polychaetes and small crustaceans. Therefore, although α was calculated for all benthic categories, the results are presented only for the dominant prey types to illustrate trends in diet selection.

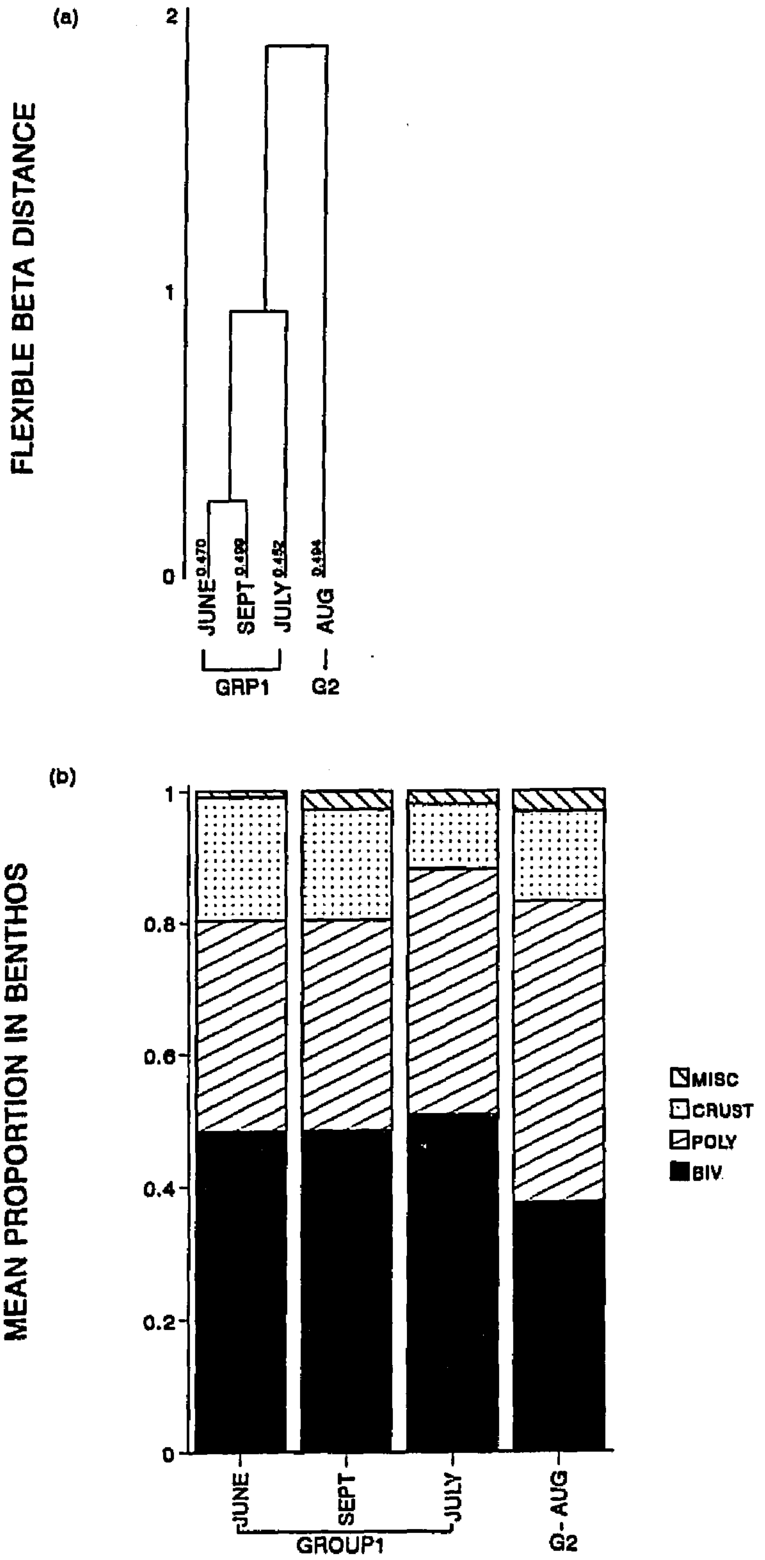
All crabs consumed bivalves in proportions significantly greater than their abundance in the benthos, and the magnitude of α generally increased with crab size (Table 32a,b). Crabs generally consumed polychaetes in significantly lower proportions than their abundance in the benthos (Tables 32a-c). However, juveniles and small adults

Figure 23. (a) Cluster diagram representing benthic similarity in 1989 among the six stations sampled. Months were pooled. The Shannon-Weiner diversity index is given at the root of each branch. (b) Benthic composition illustrated as proportion in the benthos for the stations described in (a). Animals predominating the benthos were bivalves, polychaetes and crustaceans. Rare benthic organisms were pooled into a miscellaneous category (i.e., gastropods, ophiuroids, fish, tunicates, anemones, sponges, bryozoans, insects).



(a)
FLEXIBLE BETA DISTANCE
2
1
0
YORK10 0.372
JAME13 0.281
YORK25 0.317
RAPP30 0.352
RAPP15 0.328
JAME27 0.480
G1
GROUP2
(b)
MEAN PROPORTION IN BENTHOS
1
0.8
0.6
0.4
0.2
0
YORK10
JAME13
YORK25
RAPP30
RAPP15
JAME27
GROUP1
GROUP2
MISC
CRUST
POLY
BIV

Figure 24. (a) Cluster diagram representing benthic similarity in 1989 among the four months sampled. Rivers and stations were pooled. The Shannon-Weiner diversity index is given at the root of each branch. (b) Benthic composition illustrated as proportion in the benthos for the months described in (a). Animals predominating the benthos were bivalves, polychaetes and crustaceans. Rare benthic organisms were pooled into a miscellaneous category (i.e., gastropods, ophiuroids, fish, tunicates, anemones, sponges, bryozoans, insects).


(a)
FLEXIBLE BETA DISTANCE
2
1
0
JUNE 0.470
SEPT 0.499
JULY 0.452
AUG 0.494
GRP1
G2
(b)
MEAN PROPORTION IN BENTHOS
1
0.8
0.6
0.4
0.2
0
MISC
CRUST
POLY
BIV
JUNE
SEPT
JULY
G- AUG
GROUP1
G2

selected polychaetes in July, while juveniles exhibited neutral selection in September (Table 32a) and in the Rappahannock (Table 32b). Small crustaceans, other than crabs, were either consumed in proportion to their availability in the benthos or avoided (Table 32a-c). There were no consistent upriver/downriver differences in prey selection (Table 32c), although the general pattern of bivalve selection and polychaete and crustacean avoidance were evident at all stations.

A seasonal trend occurred with generally higher α indices for bivalve prey in the Fall (i.e., September & October, Table 32a). Polychaetes were selected only in July, corresponding to the period of lowest bivalve selection (Table 32a). There were no seasonal trends in crustacean consumption (Table 32a).

Although bivalves were selected in all rivers (Table 32b), the magnitude of α varied such that values were generally highest in the York, followed by the James then Rappahannock. Crustaceans and polychaetes were generally avoided, with overall highest indices in the Rappahannock followed by the James then York (Table 32b).

In order to determine dietary overlap between different size classes, the data were collapsed across river, station and month. Pairwise dietary overlap was generally high between all size classes (Table 34). However, the lowest overlap occurred between juveniles (60-99 mm CW) and large adults (> 134 mm CW; Table 34): adults consumed proportionally more bivalves, crabs and fish, while juveniles consumed more polychaetes and miscellaneous prey (Fig. 9).

1989

As in 1988, electivity indices are presented only for the dominant dietary and benthic components - bivalves, polychaetes and crustaceans (Table 33). Although crabs generally selected bivalves for consumption, strongest selection occurred by larger juveniles and adults, again indicating a trend of increasing consumption with crab size (Tables 33a,b). The smallest juveniles (i.e., < 60 mm CW) selected crustaceans in June and July (Table 33a) and in the James and Rappahannock rivers

Table 32. Diet selection (i.e., α) of blue crabs calculated for dominant benthic and dietary components in 1988. * $P < 0.05$ ** $P < 0.01$ *** $P < 0.005$ **** $P < 0.00005$ NS $P > 0.05$

(a) Electivity by Month and Size Class (mm CW), stations and rivers pooled.

	PREY TYPE					
	BIVALVE		CRUSTACEAN		POLYCHAETE	
MONTH	X (± S.E.)	t	X (± S.E.)	t	X (± S.E.)	t
JULY (1/n=0.200)						
60-99	0.57(0.04)	8.30****	0.13(0.03)	-2.55*	0.31(0.04)	2.91***
100-134	0.60(0.03)	11.54****	0.14(0.03)	-2.34*	0.26(0.03)	2.03*
> 134	0.83(0.03)	20.29****	0.03(0.02)	-9.92****	0.136(0.03)	-2.38*
AUGUST (1/n=0.167)						
60-99	0.72(0.07)	7.84****	0.22(0.06)	0.80NS	0.04(0.01)	-9.26****
100-134	0.77(0.04)	16.60****	0.17(0.03)	0.24NS	0.04(0.01)	-15.02****
> 134	0.86(0.03)	26.70****	0.10(0.02)	-2.77**	0.03(0.01)	-16.35****
SEPTEMBER (1/n=0.167)						
60-99	0.74(0.13)	4.35***	0.18(0.13)	0.10NS	0.08(0.07)	-1.27NS
100-134	0.84(0.08)	8.81****	0.08(0.06)	-1.48NS	0.029(0.02)	-5.66****
> 134	0.96(0.01)	55.70****	0.00(0.00)		0.04(0.01)	-9.06****
OCTOBER (1/n=0.167)						
60-99	0.96(0.02)	33.09****	0.00(0.00)		0.04(0.02)	-5.21***
100-134	0.91(0.05)	14.63****	0.07(0.05)	-1.83NS	0.02(0.02)	-9.09****
> 134	0.80(0.09)	6.97****	0.09(0.07)	-1.18NS	0.04(0.03)	-3.87***

Table 32 (cont).

(b) Electivity by River and Size Class, months and stations pooled.

	PREY TYPE					
	BIVALVE		CRUSTACEAN		POLYCHAETE	
RIVER	X (± S.E.)	t	X (± S.E.)	t	X (± S.E.)	t
JAMES (1/n=0.167)						
60-99	0.61(0.05)	8.27****	0.08(0.03)	-3.46***	0.06(0.01)	-6.94****
100-134	0.79(0.04)	15.13****	0.10(0.04)	-1.77NS	0.06(0.02)	-5.08****
> 134	0.86(0.22)	18.06****	0.08(0.04)	-2.32*	0.04(0.01)	-8.71****
YORK (1/n=0.167)						
60-99	0.95(0.03)	28.85****	0.01(0.01)	-22.93****	0.02(0.02)	-9.09****
100-134	0.90(0.03)	23.49****	0.04(0.02)	-6.19****	0.02(0.01)	-14.96****
> 134	0.98(0.01)	103.98****	0.00(0.00)		0.01(0.004)	-33.13****
RAPPAHANNOCK (1/n=0.200)						
60-99	0.61(0.05)	8.92****	0.17(0.04)	-0.72NS	0.19(0.04)	-0.12NS
100-134	0.66(0.03)	13.65****	0.23(0.03)	1.04NS	0.11(0.02)	-5.26****
> 134	0.83(0.03)	22.61****	0.11(0.03)	-3.53***	0.05(0.01)	-12.55****

Table 32 (cont).

(c) Electivity by Station, months and sizes pooled.

	PREY TYPE					
	BIVALVE		CRUSTACEAN		POLYCHAETE	
STATION	X (± S.E.)	t	X (± S.E.)	t	X (± S.E.)	t
J13 (1/n=0.167)	0.67(0.12)	4.33***	0.00(0.00)		0.00(0.00)	
J27 (1/n=0.333)	0.63(0.04)	7.70****	0.13(0.03)	-7.90****	0.24(0.04)	-2.61**
Y10 (1/n=0.167)	0.88(0.10)	7.26***	0.00(0.00)		0.00(0.00)	
Y25 (1/n=0.250)	0.92(0.02)	38.02****	0.027(0.01)	-15.95****	0.05(0.01)	-17.08****
R15 (1/n=0.250)	0.71(0.07)	6.87****	--		0.22(0.06)	-0.53NS
R30 (1/n=0.250)	0.68(0.02)	19.40****	0.18(0.02)	-3.74***	0.14(0.01)	-7.65****

(Table 33b), but exhibited neutral selection in August and September (Table 33a) and in the York (Table 33b). Larger juveniles (i.e., 60-99 mm CW) selected crustaceans in July (Table 33a). In contrast, crabs > 134 mm CW always avoided crustaceans (except large adults in the York which exhibited random selection; Table 33a,b). Crabs 100-134 mm CW exhibited variable responses (i.e., avoidance or consumption in proportion to their abundance in the benthos) to crustacean prey, depending on month or river (Table 33a,b). Polychaetes were generally avoided by the largest crabs (i.e., ≥ 100 mm CW, Table 33a,b). However, juveniles exhibited neutral selection (i.e., all rivers and months, Table 33a,b), avoidance (i.e., James and Rappahannock rivers, Table 35b), or preference (i.e., York River, Table 33b). As in 1988, there were no consistent upriver/downriver patterns in prey selection (Table 33c). Bivalves were generally always a preferred prey, while crustaceans and polychaetes were either avoided or consumed in proportion to their abundance in the benthos (Table 33c).

Although bivalves were preferred in all months (Table 33a), the overall magnitude of α was higher in June and September. Crustaceans were significantly preferred by the smallest juveniles (i.e., < 60 mm CW) in Summer (i.e., June and July), but were consumed in proportion to their abundance in the benthos in Fall (i.e., August and September, Table 33a). There were no seasonal trends in polychaete consumption.

River differences occurred such that bivalves were preferred in the James and York, while selection in the Rappahannock varied with size class (Table 33b). Crustaceans were preferred by small juveniles in the James and Rappahannock, but were consumed in proportion to their abundance in the benthos in the York (Table 33b). There were no general patterns in electivity for polychaetes (Table 33b).

Pairwise dietary overlap (Table 34) was lowest between small juveniles (i.e., < 60 mm CW) and large adults (i.e., > 134 mm CW): juveniles consumed crustaceans and polychaetes, while large individuals ate bivalves and crabs (Figs. 12 & 14) Greatest overlap occurred between 1988 year class juveniles/small adults and large adults (i.e.,100-134 & > 134 mm CW, Table 34).

Predator-Prey Abundance Patterns and Relationships

Residual analyses indicated no serious violations of model assumptions or model misspecification after log-transformation of the data. The following regression equations are depicted for log (X + 1)-transformed data and represent best fit models after stepwise regression with backwards elimination. Large juvenile and adult blue crab abundance (i.e., > 80 mm CW; Y_1) was positively and significantly correlated with mean bivalve density (i.e., X_2; $t=2.91$, $P < 0.004$; Fig. 25a) and small juvenile (i.e, X_1; ≤ 80 mm CW; $t=3.92$, $P < 0.0005$; Fig. 25b) abundance, but independent of station (i.e., S; $t=-1.83$, $P < 0.071$) and year (i.e., Y; $t=1.93$, $P < 0.056$). The model explained 43.3 % (ANOVA; $F=19.14$, $df=4,91$, $P < 0.0005$) of the total variation in crab abundance and was:

$$Y_1 = 0.435 + 0.332X_1 + 0.264X_2 - 0.244S + 0.187Y$$

Large juvenile and adult crab abundance (i.e., Y_1) was independent of the abundance of new juvenile recruits (Fig. 25c), and the best fit model did not include X_1. The analysis indicated a significant and positive relationship between the abundance of crabs > 80 mm CW and bivalve density (i.e., X_2; $t=2.74$, $P < 0.007$), no relationship with polychaete density (i.e., X_3; $t=-1.31$, $P < 0.194$), and a negative relationship with station (i.e., S; $t=-2.52$ $P < 0.013$). The model explained 35.3 % of the variation in crab abundance (ANOVA; $F=18.25$, $df=3,92$, $P < 0.0005$), and was:

$$Y_1 = 1.04 + 0.265X_2 - 0.0943X_3 - 0.362S$$

The abundance of juveniles ≤ 80 mm CW (i.e., Y_1) was significantly and positively correlated with large crab abundance (i.e., X_1; $t=4.01$, $P < 0.0005$), negatively correlated with station (i.e., S; $t=-2.44$, $P < 0.017$), year (i.e., Y; $t=-4.11$, $P < 0.0005$), and mean crustacean density (i.e.X_4; $t=-2.13$, $P < 0.036$), and independent of mean clam density (i.e., X_2; $t=-1.23$, $P < 0.222$). The equation explained

Table 33. Diet selection (i.e., α) of blue crabs calculated for dominant benthic and dietary components in 1989. * P < 0.05 ** P < 0.01 *** P < 0.005 **** P < 0.00005 NS P > 0.05

(a) Electivity by Month and Size Class (mm CW), stations and rivers pooled.

	PREY TYPE					
	BIVALVE		CRUSTACEAN		POLYCHAETE	
MONTH	X (± S.E.)	t	X (± S.E.)	t	X (± S.E.)	t
JUNE (1/n=0.167)						
< 60	0.46(0.09)	3.00**	0.39(0.09)	2.35*	0.09(0.04)	-1.80NS
60-99	0.75(0.06)	9.46****	0.08(0.03)	-2.70*	0.07(0.03)	-2.97NS
100-134	0.82(0.05)	13.74****	0.09(0.04)	-1.96NS	0.05(0.02)	-5.48****
> 134	0.91(0.03)	23.27****	0.05(0.03)	-4.25***	0.03(0.01)	-11.94****
JULY (1/n=0.167)						
< 60	0.25(0.08)	1.04NS	0.51(0.09)	3.98***	0.15(0.06)	-0.28NS
60-99	0.46(0.05)	5.83****	0.35(0.05)	3.88***	0.12(0.03)	-1.49NS
100-134	0.66(0.04)	11.62****	0.15(0.03)	-0.47NS	0.14(0.02)	-0.95NS
> 134	0.86(0.04)	17.65****	0.04(0.03)	-4.78***	0.09(0.04)	-1.94NS
AUGUST (1/n=0.167)						
< 60	0.45(0.08)	3.62***	0.25(0.07)	1.16NS	0.30(0.07)	1.86NS
60-99	0.45(0.08)	3.74***	0.03(0.02)	-6.85****	0.14(0.05)	-0.54NS
100-134	0.72(0.07)	8.55****	0.03(0.02)	-8.44****	0.13(0.05)	-0.72NS
> 134	0.93(0.04)	20.78****	0.04(0.04)	-3.56***	0.03(0.01)	-9.67****
SEPTEMBER (1/n=0.167)						
< 60	0.41(0.06)	4.01***	0.28(0.06)	1.93NS	0.24(0.05)	1.40NS
60-99	0.62(0.23)	1.97NS	0.00(0.00)		0.38(0.23)	0.91NS
100-134	0.99(0.002)	385.44****	0.00(0.00)		0.002(0.002)	-76.47****
> 134	0.92(0.04)	19.67****	0.05(0.03)	-3.53***	0.034(0.021)	-6.47****

Table 33 (cont)

(b) Electivity by River and Size Class, months and stations pooled.

	PREY TYPE					
	BIVALVE		CRUSTACEAN		POLYCHAETE	
RIVER	X (± S.E.)	t	X (± S.E.)	t	X (± S.E.)	t
JAMES (1/n=0.143)						
< 60	0.38(0.06)	3.80***	0.37(0.06)	3.68***	0.09(0.04)	-1.06NS
60-99	0.59(0.07)	6.43****	0.12(0.04)	-0.65NS	0.06(0.03)	-2.48*
100-134	0.92(0.03)	27.76****	0.03(0.01)	-8.25****	0.02(0.01)	-17.01****
> 134	0.98(0.01)	100.08****	0.003(0.003)	-45.14****	0.01(0.01)	-16.30****
YORK (1/n=0.167)						
< 60	0.55(0.06)	6.49****	0.13(0.04)	-0.93NS	0.30(0.05)	2.49*
60-99	0.49(0.07)	4.51***	0.05(0.02)	-5.24****	0.11(0.05)	-1.15NS
100-134	0.58(0.08)	5.26****	0.07(0.04)	-2.48*	0.14(0.05)	-0.47NS
> 134	0.88(0.06)	12.39****	0.11(0.06)	-0.94NS	0.01(0.01)	-31.40****
RAPPAHANNOCK (1/n=0.333)						
< 60	0.17(0.06)	-2.78**	0.61(0.08)	3.59***	0.22(0.06)	-1.87NS
60-99	0.48(0.05)	2.94***	0.27(0.04)	-1.60NS	0.25(0.04)	-2.01*
100-134	0.62(0.04)	6.58****	0.14(0.03)	-6.51****	0.25(0.03)	-2.51*
> 134	0.82(0.03)	14.44****	0.04(0.02)	-18.64****	0.14(0.03)	-6.57****

Table 33 (cont).

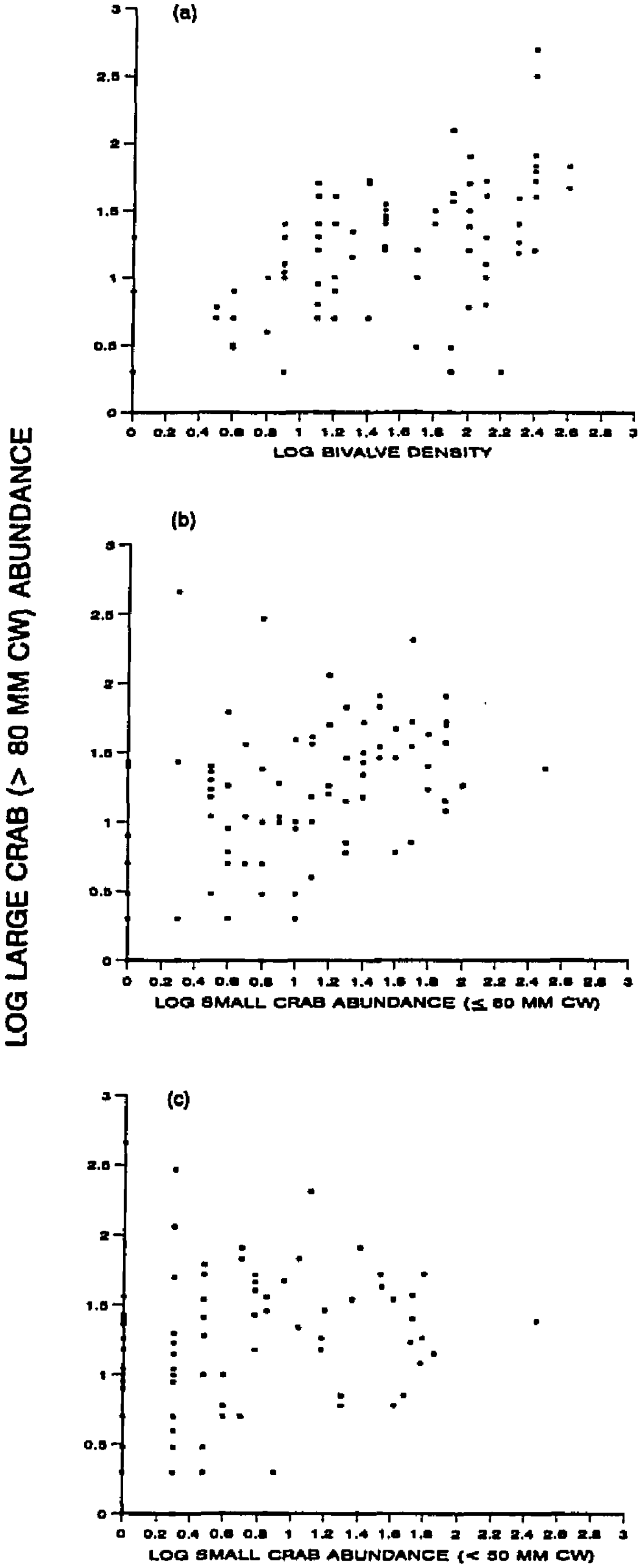
(c) Electivity by Station, months and sizes pooled.

	PREY TYPE					
	BIVALVE		CRUSTACEAN		POLYCHAETE	
STATION	X (± S.E.)	t	X (± S.E.)	t	X (± S.E.)	t
J13 (1/n=0.167)	0.28(0.09)	1.12NS	0.08(0.05)	-1.72NS	0.17(0.08)	-0.01NS
J27 (1/n=0.250)	0.73(0.03)	15.18****	0.17(0.03)	-3.09***	0.06(0.02)	-11.78****
Y10 (1/n=0.167)	0.51(0.06)	5.37****	0.04(0.02)	-6.30****	0.22(0.06)	0.91NS
Y25 (1/n=0.250)	0.61(0.04)	8.57****	0.17(0.04)	-2.16*	0.22(0.03)	-0.92NS
R15 (1/n=0.333)	0.79(0.09)	5.05***	0.19(0.09)	-1.47NS	0.01(0.01)	-41.97****
R30 (1/n=0.333)	0.51(0.03)	6.08****	0.19(0.02)	-5.75****	0.29(0.02)	-1.70NS

Table 34. Pairwise proportional dietary overlap for blue crab size classes collected in 1988 and 1989. Rivers, stations and months were pooled.

SIZE	60-99		100-134		> 134	
CLASS (MM)	1988	1989	1988	1989	1988	1989
< 60	-	0.671	-	0.579	-	0.506
60-99	-	-	0.897	0.843	0.799	0.762
100-134	-	-	-	-	0.895	0.914

Figure 25. Relationship between (a) large juvenile and adult blue crab (> 80 mm CW) abundance and mean bivalve density, (b) large juvenile and adult blue crab and smaller juvenile (≤ 80 mm CW) abundance, and (c) large juvenile and adult blue crab abundance and new juvenile recruit (< 50 mm CW) abundance. Data are log(X+1)-transformed.


LOG LARGE CRAB (> 80 MM CW) ABUNDANCE
(a)
0
0.5
1
1.5
2
2.5
3
0 0.2 0.4 0.6 0.8 1 1.2 1.4 1.6 1.8 2 2.2 2.4 2.6 2.8 3
LOG BIVALVE DENSITY
(b)
0
0.5
1
1.5
2
2.5
3
0 0.2 0.4 0.6 0.8 1 1.2 1.4 1.6 1.8 2 2.2 2.4 2.6 2.8 3
LOG SMALL CRAB ABUNDANCE (≤ 80 MM CW)
(c)
0
0.5
1
1.5
2
2.5
3
0 0.2 0.4 0.6 0.8 1 1.2 1.4 1.6 1.8 2 2.2 2.4 2.6 2.8 3
LOG SMALL CRAB ABUNDANCE (< 50 MM CW)

35.0 % (ANOVA; $F=11.22$, $df=5,90$, $P < 0.0005$) of the variation in juvenile abundance, and was:

$$Y_i = 1.19 + 0.436X_1 - 0.130X_2 - 0.164X_4 - 0.363S - 0.456Y$$

The abundance of new juvenile recruits (i.e., Y_i = < 50 mm CW crabs) was negatively correlated with station (i.e., S; $t=-4.57$, $P < 0.0005$) and year (i.e., Y; $t=-3.09$, $P < 0.003$), but independent of bivalve density (i.e., X_2; $t=-1.39$, $P < 0.169$). The regression equation explained 25.4 % of the variation in new recruit abundance, and was:

$$Y_i = 1.33 - 0.148X_2 - 0.678S - 0.336Y$$

In summary, adult and large juvenile blue crab abundance was positively correlated to the density of a key infaunal prey (i.e., bivalves) and the abundance of smaller conspecifics. New recruits were most abundant upriver and in 1989, but distributional patterns were unrelated to the abundance of either conspecifics or major benthic infaunal prey (i.e., bivalves, crustaceans, or polychaetes).

DISCUSSION

The key findings of this investigation were: (1) Blue crab diets were separable on the basis of proportional consumption of dominant dietary components - bivalves, crabs and polychaetes. Small crustaceans constituted a significant proportion of the diet of new juvenile recruits (< 60 mm CW) in 1989. (2) Bivalves were preferred prey, regardless of crab size, station, river or season. (3) Spatial (i.e., upriver v downriver) and size-related differences in diet occurred in both years. (4) There was marked spatial variation in the abundance and distribution of both blue crabs and dominant benthic infauna (i.e., bivalves and polychaetes): crabs and bivalves were most abundant upriver, while polychaetes were more abundant downriver. (5) Blue crab diet, abundance and distributional patterns were strongly correlated with the abundance of their preferred prey, suggesting the occurrence of an aggregative response in this system. (6) Cannibalism was common, occurring most frequently in areas of low alternative preferred prey abundance and during periods of peak juvenile recruitment into the three subestuaries. Furthermore, the abundance of large crabs was positively correlated with that of smaller conspecifics.

Diet Selection

Ontogenetic changes in diet selection were suggested by the differentially high consumption of small crustaceans and polychaetes by juvenile blue crabs, the decline in bivalve consumption and cannibalism with decreasing crab size, and the low index of dietary overlap between juveniles and adults. In 1989, the index of dietary overlap between new juvenile recruits and large adults (i.e., < 60 mm & > 134 mm CW) was as low as that between fish species constituting the guild of epibenthic predators in upper Chesapeake Bay (Hines et al. 1990). These results suggest the occurrence of at least two distinct trophic groups in lower

Chesapeake Bay. Laughlin (1982) similarly concluded that ontogenetic variability in diet selection occurred for blue crabs in Apalachicola Bay, Florida such that three distinct trophic groups could be distinguished. Although bivalves were the dominant dietary component of all size classes, the percent composition or inclusion of other prey types varied with crab size. He suggested that allometric constraints in feeding apparatus as well as differing locomotory and sensory capabilities could account for these dietary differences (Laughlin 1982). Size-related differences in diet selection have been documented for other crab species, and may be related to ontogenetic changes in the functional morphology of the feeding apparatus (Ropes 1968, 1988, Paul 1981, Stevens et al. 1982, Perez & Bellwood 1988, Stoner & Buchanan 1990).

Spatial variability in diet selection occurred such that crabs collected downriver consumed a greater variety of prey types, while upriver crabs predominantly ate bivalves. Although polychaetes were most abundant downriver, high benthic densities were not reflected in the diets of crabs which preferentially consumed bivalves and either avoided or consumed polychaetes in proportion to their availability in the benthos. Thus, in areas of relatively lower bivalve densities, blue crabs expanded their diets to include locally abundant fauna. This result is consistent with other studies suggesting that blue crabs are dietary opportunists whose feeding habits reflect prey availability (Darnell 1959, Tagatz 1968, Odum & Heald 1972, Laughlin 1982, Alexander 1986, Ryer 1987, Hines & Wolcott 1990, Hines et al. 1990, Stoner & Buchanan 1990).

River-specific prey density and predator dietary patterns, although sometimes inconsistent, were characterized by general trends. For example, bivalves were often most abundant in the benthos, and occurred in greatest proportions in the diets of crabs in the Rappahannock river. However, river dominance varied with month, station and year.

There were no obvious seasonal patterns in diet selection in either year. These results probably reflect the weak (1988) or nonexistent (1989) seasonal trend in abundance of preferred bivalve prey. Prey availability can be a function of prey density, burial depth or specific morphological features of prey (Blundon & Kennedy 1982a,b, Arnold 1984, Lipcius & Hines 1986, West & Williams 1986, Hines et al. 1990, Sponaugle & Lawton 1990). In this investigation, the dominant dietary and benthic component (i.e., Macoma balthica) did not exhibit marked differences in size throughout the sampling period (Appendix 5). These size classes are generally available and vulnerable to predation by larger blue crabs (Blundon & Kennedy 1982a,b).

The Aggregative Response

Predator aggregation in high density patches can provide a partial prey refuge in low density patches (Hassell 1978), thus stabilizing predator-prey systems (Hassell & May 1974). In this investigation, blue crabs congregated upriver in areas of highest bivalve (i.e., Macoma balthica) abundance. Regression analysis indicated a positive correlation between the abundance of large crabs (> 80 mm CW) and mean bivalve density, while electivity analysis indicated that bivalves were preferred prey. Blue crabs can have marked effects on the population dynamics of Macoma balthica (Hines et al. 1990, Eggleston et al. 1992). Field evidence indicates a rapid decline in clam densities in summer in association with intense blue crab predation (Hines et al. 1990). However, Macoma find at least partial refuge from blue crabs through greater burial depth (Blundon & Kennedy 1982b) and low population densities (Eggleston et al. 1992).

Aggregative responses have been described for various marine vertebrates and invertebrates (Hill 1979, Decho & Fleeger 1988, Fairweather 1988, Friedland et al. 1989, Piatt et al. 1989), and is measured either by counts of predator numbers or as time spent per unit area of differing prey densities (Hassell & May 1974). Ultrasonic telemetry has provided information on movement and foraging activity of blue crabs in the Rhode River subestuary, Maryland (Wolcott & Hines 1988, 1989, Hines & Wolcott 1990, Hines et al. in prep). Investigations indicate changes in movement patterns (i.e., from rapid directional movement to slow meandering) associated with encountering high density prey patches. Crabs forage selectively on clams at high densities but opportunistically on other prey (Hines & Wolcott 1990). Thus, the combined results of this and other investigations (Wolcott & Hines 1988, 1989, Hines & Wolcott 1990, Hines et al., in prep) indicate that blue crabs commonly aggregate in areas of high prey abundance, selectively consume bivalves, and expand their diets in areas of low bivalve (i.e.. preferred prey) density.

Hassell & May (1974) describe two behavioral models of predator searching behavior which allow predictions about the predator's response to prey density. In the first model, the predator exhibits changes in turning behavior after encountering prey, such that its movement becomes one of "tight" turning. A random walk or other prefeeding pattern of movement is resumed if no further prey are encountered. This behavior appears to be typical of blue crabs (Wolcott & Hines 1988, 1989, Hines & Wolcott 1990, Hines et al. in prep), and results in a sigmoid, (i.e., density-dependent), potentially stabilizing aggregative response curve (Hassell & May 1974). The second model suggests a threshold time for encountering prey and also generally produces a sigmoid aggregative response (Hassell & May 1974). The existence of a threshold time has not been documented for blue crabs. Departure from prey patches is probably related to agonistic interactions (i.e., interference) between searching crabs (Hines, pers. comm., R.N. Lipcius & K. Moody unpub. data). The combination of aggregation and interference can stabilize the blue crab-bivalve predator-prey system by providing partial refuges for prey in low density patches, and by promoting emigration from patches which have been heavily exploited (Hassell 1978).

An alternative explanation for the abundance and distributional patterns of blue crabs in this study is avoidance of adverse abiotic (i.e., hypoxic or anoxic) conditions which commonly occur downriver in the three subestuaries investigated (Seliger et al. 1985, Kuo & Neilson 1987, Kuo et al. 1991). Pihl et al. (1991) observed emigration of mantis shrimp, blue crabs, and demersal fish from hypoxic areas in the lower York River. However, the fish and blue crabs returned to these sites as conditions improved (Pihl et al. 1991). The response of benthic infauna depends on the severity (i.e., length of time and dissolved oxygen level) of the hypoxic event: intense hypoxia or anoxia (< 1 mg/l & < 0.2 mg/l O_2, respectively) can result in defaunation while moderate events result in decreased burial depth and surface exposure (Holland 1985, Holland et al. 1977, 1987, Diaz et al. 1992, Rosenberg et al. 1991, Pihl et al. 1992). Thus, brief hypoxic events can enhance foraging of epibenthic predators by increasing prey availability (Diaz & Schaffner 1990, Pihl et al. 1992, Diaz et al. 1992). In this investigation, hypoxia (< 2 mg/l O_2, Diaz et al. 1992) occurred downriver in the Rappahannock (i.e., R15) in September, 1989 (Appendix 2), and was characterized by the absence of all benthic prey (Fig. 21) and a sample size of 9 blue crabs. Near-hypoxic conditions occurred at R15 in July and August, 1988 (Appendix 1) and June, 1989 (Appendix 2). However, bivalves were collected in both months in 1988 (Fig. 17), while bivalves and polychaetes were abundant in June, 1989 (Fig. 21). Blue crabs were also collected during these months in both years (i.e., 90 and 28 crabs in July and August, 1988, respectively, and 11 in June, 1989). Subsequent sampling indicated high densities of polychaetes in September, 1988 (Fig. 17; 31 blue crabs) and moderate densities of bivalves and polychaetes in July 1989 (Fig. 21; 5 blue crabs). Although blue crabs emigrate from hypoxic areas, the results of this investigation indicate generally lower abundances downriver in all rivers regardless of oxygen concentration. These results in conjunction with diet and prey preference analyses suggest that crabs were aggregating upriver in response to abundance and distributional patterns of their preferred prey (i.e., bivalves).

Cannibalism

Spatial, seasonal, annual and size-related differences in the frequency of cannibalism were documented in this investigation: (1) large crabs (i.e., > 134 mm CW) cannibalized most frequently, (2) cannibalism occurred least frequently in the Rappahannock river where densities of preferred alternative prey (i.e., Macoma balthica) were generally highest, (3) frequency of occurrence was highest during the months of new juvenile recruitment into the subestuaries and in 1989 corresponding to the relatively greater abundance of juveniles in that year. Evidence that density-dependent rates of cannibalism may regulate blue crab populations includes: density-dependent autotomy and cannibalism of tethered juvenile blue crabs (Smith 1990, 1991a,b), increased occurrence of crabs in blue crab stomachs in late summer when alternative (bivalve) prey availability and densities are reduced (Hines et al. 1990), the highly developed and complex intraspecific agonistic behaviors of blue crabs (Jachowski 1974), the significant effect of previous year-classes on the stock-recruitment relationship for blue crabs in Chesapeake Bay (Lipcius & Van Engel 1990), and increased cannibalism when juvenile recruitment is higher (this study). Cannibalism may be an efficient mechanism of population control in age/size-structured populations (Fox 1975, Polis 1981, 1988). Furthermore, prey profitability analyses indicate that crustaceans are energetically more valuable than bivalve prey (Thayer et al. 1973, Hill 1979), and in one investigation non-portunid crabs were the principal prey of large (> 100 mm CW) blue crabs (Fitz & Wiegert 1991).

The magnitude of intraspecific predation required to substantially affect the blue crab population in Chesapeake Bay is unknown. Investigations in other systems indicate that cannibalism can be a major mortality factor, perhaps eliminating entire cohorts and resulting in fluctuations in recruitment and skewed age or size distributions (Fox 1975, Polis 1981). Blue crabs exhibit large fluctuations in abundance due to a variety of biotic and abiotic factors (Van Engel 1987, Hines et al. 1987, Lipcius & Van Engel 1990). Van Engel (1987) estimated total mortality from the egg to adult stage ranging from 0.999973 to 0.999996, with fisheries mortality accounting for an additional 0.0000031 to 0.0000251 and removal rates by other sources ranging from 0.0000024 to 0.000001. The hard crab fishery removes crabs ≥ 127 mm CW, the dominant cannibals in the Chesapeake Bay system. Despite the intensive fishery, we documented the highest frequency of occurrence of cannibalism of any investigation thus far. Hines et al. (1990) found that blue crabs constituted 3-12 % (by volume) of the diet of large conspecifics in upper Chesapeake Bay, while the highest frequency of occurrence (i.e., 11 %) was recorded by Laughlin (1982) for large blue crabs (> 60 mm CW) in the Apalachicola estuary, Florida. In contrast, Peery's (1989) laboratory investigations indicated cannibalism rates of 2-85 %, depending on relative sizes of predator and prey. Lipcius and Van Engel (1990) found a significant and dome-shaped stock-recruitment relationship for blue crabs in Chesapeake Bay. This "overcompensatory" model (i.e., Ricker model) is appropriate where adults cannibalize prerecruits, or when intraspecific competition for critical resources occurs between adults and progeny (Fogarty et al. 1991). Furthermore, the highest variance in recruitment occurs at intermediate levels of spawning stock size; recruitment variance increases with population fecundity and variance in mortality, but decreases with increasing mortality (Fogarty et al. 1991). Similarly, several investigators have suggested that density-dependent, inter-age mechanisms (i.e., cannibalism, competition for food) could be responsible for the cyclic abundance patterns of the commercially exploited Dungeness crab (Cancer magister) (Botsford & Wickham 1978 and others cited therein, Stevens et al. 1982). In contrast, McKelvey et al. (1980) concluded that cannibalism of juveniles by adults was unimportant in the generation of the 9-year cycle. However, evidence that small (i.e., 15-60 mm CW) Dungeness crabs are the primary cannibals (i.e., frequency of occurrence: 24.9 %) suggests the need to re-evaluate the model (Stevens et al. 1982).

Cannibalism and intraguild predation may be responsible for fluctuations in recruitment of the Cape anchovy (Engraulis capensis), and cycles in the abundance of commercially important clupeoids in the Benguela system, South Africa (Szeinfeld 1991). Leonardsson (1991) commonly observed cannibalism by the isopod, Saduria entomon, in the laboratory. However, gut contents investigations of field collected Saduria indicated a very low incidence of conspecifics in the diets of large isopods: small conspecifics occurred in only 3.3 % of the guts of larger isopods, and only in one locality. Nevertheless, he concluded that cannibalism could be a critical factor affecting the size structure and spatial distribution of this species (Leonardsson 1991).

In contrast, we observed conspecifics in 39.4 % of the guts of large blue crabs in 1989, and throughout the distributional range investigated. Furthermore, cannibalism occurred even when bivalves were abundant and available (Blundon & Kennedy 1982b) in the benthos (Appendix 5). In laboratory prey size selection experiments, Ap Rheinallt (1986) observed relatively higher predation of larger juvenile Carcinus maenas by Liocarcinus puber. Larger shore crabs were more active resulting in greater encounter rates between predator and prey, and were grasped and retained more easily than small prey (Ap Rheinallt 1986). Similarly, in Chesapeake Bay, relatively high encounter rates with small conspecifics during periods of juvenile recruitment may explain the consumption of conspecifics when alternative bivalve prey are abundant and available in the benthos. Cannibalism between disparate size classes is most common in nature (Polis 1981, 1988), and can provide direct and immediate nutritional benefits (Polis 1988). Polis (1988) suggests that interference competition (i.e., cannibalism) that supplies immediate net energy gains to the individual are likely to evolve regardless of population structure (i.e., spatially structured v open populations).

Predator-Prey Dynamics in Soft-Bottom Communities

Predation may be the most important biotic factor determining the organization of marine communities (Connell 1975). The role of predation in structuring marine rocky intertidal communities is well-established: either a single keystone predator or strong interactors within a guild of predators (Paine 1966, 1980, 1992) enhance species diversity and abundance patterns by negatively affecting the actions of a dominant competitor. The importance of functional groups (Menge et al. 1986b) or guilds of predators in regulating community structure in environmentally less severe habitats of low temperate and tropical rocky intertidal zones has also been established (Menge 1983, Menge et al. 1986a,b). These studies suggest the absence of a single keystone species, and the importance of complex interactions between predator species, prey species and abundance, recruitment dynamics and environmental stress (Menge 1983, Menge et al. 1986a,b, Menge & Sutherland 1987, Menge & Olson 1990, Paine 1980, 1992).

Blue crabs are known to have major impacts on prey abundance and distribution in estuarine systems (Virnstein 1977, 1979, Holland et al. 1980, West & Williams 1986, Kneib 1982, Woodin 1981, Lin 1989, Martin et al. 1989, Sponaugle & Lawton 1990, Hines et al. 1990). Bivalves are a dominant dietary component, and mortality rates vary with habitat type (i.e., sediment), density and species (Lipcius & Hines 1986, Hines et al. 1990, Eggleston et al. 1992). Furthermore, predator density can have profound effects on the magnitude of predation intensity, potentially affecting the dynamics of both blue crab and bivalve prey (i.e., *Macoma balthica*) populations in Chesapeake Bay (Mansour & Lipcius 1991). The combined evidence (Virnstein 1977, 1979, Holland et al. 1980, Hines et al. 1990) suggests that blue crabs are strong interactors (sensu Paine 1980, 1992) within the guild of epibenthic predators in Chesapeake Bay. A species is a strong interactor if its absence results in pronounced changes in community structure (Paine 1980). The effect depends on predator food preference, distributional and abundance patterns, and whether the prey is the competitive dominant in the community (Paine 1980, 1992). Our results indicate that blue crabs prefer bivalve prey (i.e., Macoma balthica), and aggregate in areas of highest bivalve densities. Although a dominant competitor has not been identified for the Chesapeake Bay system, field investigations indicate that bivalves (i.e., Macoma balthica, Mya arenaria) may regulate community composition through direct and indirect effects on recruitment (Hines et al. 1989). Hines et al. (1989) observed a decline in total macroinfuanal abundance with increasing clam density, but results for component species were variable (i.e., positive or negative) depending on clam density, clam species and year. Thus, blue crabs conform to Paine's (1980, 1992) criteria for "strong" interactors in several respects including: (1) their marked preferences for specific prey, (2) declines in macroinfaunal abundance which are directly related to blue crab predation such that, in their absence, pronounced changes in community structure occur (predator exclusion studies: Virnstein 1977, 1979, Holland et al. 1980, Hines et al. 1990), and (3) abundance and distributional patterns which are positively correlated with those of preferred prey. However, Paine's (1980, 1992) definition unequivocally requires modification of the actions of a competitive dominant. In Chesapeake Bay, no study has identified a single species whose actions result in the formation of a "monoculture" (sensu Paine 1992).

In summary, blue crab predation may be the most important biotic factor determining bivalve distribution and abundance patterns in Chesapeake Bay. Density-dependent functional, aggregative and interference responses promote prey persistence despite intense seasonal blue crab predation such that: (1) foraging rates decline at low bivalve densities (i.e., functional response: Lipcius & Hines 1986, Mansour & Lipcius 1991, Eggleston et al. 1992), (2) aggregation in high prey density patches provides refuge for bivalves at low densities, and (3) aggregation results in interference (i.e., cannibalism or agonistic interactions: Mansour & Lipcius 1991, Hines, pers. comm.) which promotes predator emigration. Finally, the occurrence of distinct trophic groups suggests that blue crabs may differentially affect infaunal components. For example, polychaetes and small crustaceans (i.e., amphipods, isopods) are most vulnerable to juvenile blue crab predation, while bivalves and conspecifics are subject to intense predation by large juveniles and adults. Thus, food web models should incorporate trophic stages (Peters 1977, Laughlin 1982, Stoner & Buchanan 1990, Polis 1991), since, as this study has shown, differences in diet between juveniles and adults can be as great as those between some species (Hines 1982, Hines et al. 1990).

Appendix 1. Bottom temperature, salinity, dissolved oxygen and tow depth recorded for each river-station-month combination in 1988.

RIVER	STATION	MONTH	BOTTOM TEMP(°C)	BOTTOM SALINITY(ppt)	BOTTOM DO(mg/l)	DEPTH(m) (TOW 1/TOW 2)*
JAMES	J13	JUNE	11.5	22.1	7.3	11.1
		JULY	26.0	18.0	6.0	12.4
		AUG	28.0	19.0	5.5	11.5
		SEPT	23.0	19.5	6.5	11.2
		OCT	20.0	20.0	8.5	13.6
	J27	JUNE	26.0	8.0	--	10.6
		JULY	25.0	7.0	3.4	7.4
		AUG	30.5	6.0	5.4	8.7
		SEPT	24.0	9.5	6.0	8.4
		OCT	20.0	13.0	8.2	6.5
YORK	Y10	JUNE	16.5	15.8	4.3	7.1
		JULY	24.9	19.0	4.5	7.6
		AUG	--	--	--	8.7
		SEPT	23.0	20.5	6.0	7.8
		OCT	--	--	--	7.6
	Y25	JUNE	19.0	12.5	4.8	8.1
		JULY	26.0	15.0	4.2	8.1
		AUG	30.0	16.0	4.8	8.1
		SEPT	23.5	23.5	6.0	7.8
		OCT	21.0	18.0	7.5	7.6
RAPP	R15	JUNE	17.2	--	3.4	17.4
		JULY	24.5	17.0	2.6	15.8
		AUG	27.5	16.0	2.4	15.2
		SEPT	24.5	18.0	3.0	13.1
		OCT	14.0	16.0	8.5	15.8
	R30	JUNE	20.9	11.0	4.0	6.2
		JULY	26.0	9.0	4.0	6.2
		AUG	29.0	13.0	4.1	--
		SEPT	23.5	13.0	6.0	6.1
		OCT	12.5	13.0	8.2	6.1

* Tow depths were similar unless indicated otherwise.

Appendix 2. Bottom temperature, salinity, dissolved oxygen and tow depth recorded for each river-station-month combination in 1989.

RIVER	STATION	MONTH	BOTTOM TEMP(°C)	BOTTOM SALINITY(ppt)	BOTTOM DO(mg/l)	DEPTH(m) (TOW 1/TOW 2)*
JAMES	J13	JUNE	23.0	18.0	4.6	13.1/13.7
		JULY	26.5	20.5	3.6	12.2/12.8
		AUG	--	--	--	12.2/11.6
		SEPT	24.6	21.0	5.6	13.4/13.1
		OCT	19.0	16.0	6.4	13.1
	J27	JUNE	26.0	2.0	5.0	7.5/7.3
		JULY	29.5	1.0	4.6	8.2/7.6
		AUG	--	--	--	8.2
		SEPT	25.6	6.3	6.3	8.5
		OCT	19.0	3.5	7.2	8.8
YORK	Y10	JUNE	25.0	19.0	6.0	7.9
		JULY	27.0	18.0	3.0	8.5/8.2
		AUG	25.5	16.7	5.0	8.5/10.1
		SEPT	25.3	19.8	--	8.2/9.8
		OCT	19.0	17.0	6.3	8.2/8.8
	Y25	JUNE	26.0	10.0	6.0	8.5
		JULY	29.5	10.5	3.6	7.9
		AUG	26.0	13.3	5.4	8.5
		SEPT	--	--	--	9.1/9.8
		OCT	19.5	12.5	5.8	8.5
RAPP	R15	JUNE	24.0	15.0	2.3	14.6/14.9
		JULY	27.0	13.0	3.0	14.9
		AUG	25.5	7.5	3.4	14.3
		SEPT	25.1	15.6	0.6	15.2/14.3
		OCT	19.3	15.0	6.4	14.6
	R30	JUNE	25.5	6.0	5.2	5.2/7.0
		JULY	26.0	6.0	4.0	5.5
		AUG	25.6	5.5	6.1	5.2
		SEPT	26.2	10.0	4.9	5.5/6.7
		OCT	20.0	7.0	6.2	5.5

* Tow depths were similar unless indicated otherwise.

Appendix 3. Food items occurring in the guts of blue crabs collected in 1988 and 1989. * indicates occurrence only in 1989 samples.

Category	Identifiable Fragments
Hydroid	hydrocaulus, stolon, polyps
Bivalve	umboes, shell fragments, whole spat
Mya arenaria	
Macoma sp.	
Mulinia lateralis	
Mussels	
Anadara sp.	
Crassostrea virginica	
Other	
Gastropods	
Mitrella lunata	shell fragments, apex, columella, inner whorls
Cephalaspidea	
Pyramidellidae	
Other	
Crabs	
Callinectes sapidus	carapace fragments, claws, paddle fins, distal portion of walking legs
Xanthidae	
Majidae	
Polychaetes	
Nereis sp.	mandibles, setae, tube fragments, whole but digested specimens
Glycera	
Pectinaria	
Insects	
Choronomidae	antennae, carapace fragments, head pieces, legs, mandibles
Other	
Other Crustacea	carapace and/or shell fragments, whole animals, appendages
Amphipoda	
Cirripedia	
Isopoda	
Other	
Fish	otoliths, scales, eyes, bones with attached flesh
*Ophiuroidea	body fragments
Plants	Fragments

Appendix 4. Animals collected through benthic sampling in 1988 and 1989.

- Polychaeta
  - Goniadidae
    - *Glycinde solitaria*
  - Onuphidae
    - *Diopatra cuprea*
  - Pectinariidae
  - Glyceridae
  - Spionidae
  - Maldanidae
  - Ampharetidae
  - Hesionidae
  - Nereidae
  - Orbiniidae
  - Amphinomidae
  - Terebellidae
    - *Loimia medusa*
  - Capitellidae

- Phoronidea
  - *Phoronis* sp.

- Nemertinea

- Bivalvia
  - *Macoma mitchilli*
  - *Macoma balthica*
  - *Macoma tenta*
  - *Mulinia lateralis*
  - *Tagelus* sp.
  - *Ensis directus*
  - *Anadara* sp.
  - Pholadidae
  - Other

- Crustacea
  - Crangonidae
    - *Crangon septemspinosa*
  - Amphipoda
    - Gammaridae
    - Caprellidae
  - Ogyridae
    - *Ogyrides limicola*
  - Xanthidae
  - Isopoda
  - Portunidae
    - *Callinectes sapidus*

- Ophiuroidea

Appendix 4 (cont).

- Gastropoda
  - *Mitrella lunata*
  - Cephalaspidea
  - Pyramidellidae
  - Other

- Insecta
  - Chironomidae (larvae)

- Teleostomi
  - *Anchoa mitchelli*
  - *Trinectes maculatus*
  - *Leiostomus xanthurus*

- Anthozoa
  - Actiniaria

- Ascidiacea

- Porifera

- Bryozoa

Appendix 5. Mean size (± standard deviation) measured as shell length in mm for the dominant bivalve species collected in the benthos upriver from July - October, 1988 and June - September, 1989.

STATION	SPECIES	MONTH	SIZE (MM SL)	
			1988	1989
J27	*Macoma balthica*	June	-	15.1 (6.4)
		July	15.9 (1.3)	11.8 (6.2)
		August	15.8 (4.1)	17.8 (6.7)
		September	13.1 (2.1)	12.4 (8.9)
		October	16.6 (1.5)	-
	Macoma mitchilli	June	-	12.9 (2.4)
		July	12.5 (2.4)	9.5 (2.3)
		August	12.1 (2.1)	14.4 (1.8)
		September	9.8 (3.4)	13.8 (1.1)
		October	-	-
Y25	*Macoma balthica*	June	-	15.3 (2.1)
		July	12.5 (1.9)	15.0 (2.4)
		August	9.5 (9.2)	15.7 (1.6)
		September	-	16.2 (1.6)
		October	7.0 (7.4)	-
	Macoma mitchilli	June	-	13.0
		July	-	17.0
		August	-	11.5 (4.9)
		September	10.0	10.9 (1.5)
		October	10.8 (2.4)	-
R30	*Macoma balthica*	June	-	11.2 (4.9)
		July	11.8 (4.2)	11.7 (4.0)
		August	12.9 (3.5)	12.5 (2.0)
		September	12.3 (2.7)	13.9 (4.1)
		October	14.7 (4.5)	-
	Macoma mitchilli	June	-	14.0 (2.8)
		July	13.0	13.7 (1.5)
		August	11.0	9.4 (2.8)
		September	4.4 (0.9)	9.9 (2.4)
		October	6.8 (2.4)	-

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CHAPTER 2

DENSITY-DEPENDENT FORAGING AND MUTUAL INTERFERENCE IN BLUE CRABS PREYING UPON INFAUNAL CLAMS

ABSTRACT

Predator-prey dynamics between the blue crab *Callinectes sapidus* and an infaunal soft-shelled clam, *Macoma balthica*, were examined in laboratory experiments to assess the joint effects of varying predator and prey densities upon predator foraging rates and prey survival. A full-factorial experimental design involved 2 prey densities (4 and 16 clams m^{-2}) and 3 predator densities (1, 2 and 4 crabs m^{-2}) with 6 trials per treatment combination. Blue crabs exhibited density-dependent foraging under all conditions: proportionally more clams were consumed at the higher clam density. Furthermore, at the higher crab densities mutual interference was evident in the incidence of wounds and deaths to crabs resulting from cannibalism or intraspecific aggression. Thus, the combined impact of varying crab and clam densities resulted in (1) the maintenance of a density-dependent refuge from blue crab predation for large infaunal clams, irrespective of crab density, and (2) intraspecific aggression resulting in injury and mortality of blue crabs at high crab densities. The collective results indicate that both predator and prey densities must be examined experimentally for their joint impact upon predator-prey dynamics in marine systems.

DENSITY-DEPENDENT FORAGING AND INTERFERENCE IN BLUE CRABS

INTRODUCTION

In marine systems, predation regulates community structure and varies in intensity in many rocky and soft-sediment marine benthic habitats (Connell 1975, Peterson 1979a, Paine 1980, Menge et al. 1986a,b, Hall et al. 1990). Predator-prey interactions in marine soft-bottom communities are particularly complex because they are dominated by guilds of generalist predators capable of switching among diverse prey (Hines et al. 1990), and because there are few communities with competitively dominant prey capable of monopolizing resources (Peterson 1979a, Dayton 1984). Menge (1983) defined key components of predation intensity, which are fundamentally based on the effectiveness and the abundance of individual predators (i.e., functional and aggregative responses). Though a quantitative focus on these basic components and their joint effects is required to understand marine benthic predator-prey dynamics, few, if any, studies have attempted to integrate the influence of functional and aggregative responses.

The functional response describes a short-term behavioral phenomenon where predators increase prey consumption as prey abundance increases (Solomon 1949, Holling 1959). This response may be linear, hyperbolic (inversely density-dependent) or sigmoid (density-dependent), each with specific effects upon predator-prey dynamics (Murdoch 1973). Analyses of functional responses have yielded useful results concerning the regulation of prey populations by predators in marine benthic systems (Boulding & Hay 1984, Katz 1985, Lipcius & Hines 1986, Eggleston 1990a,b, Sponaugle & Lawton 1990).

The numerical response, the relationship between the number of predators and prey abundance, is a function of predator behavior (e.g., aggregative response), fecundity and survivorship patterns (Holling 1959). In the aggregative response predators may regulate prey populations by congregating in areas of high prey density and by leaving those prey patches where the rate of prey capture falls below a threshold (Readshaw 1973). The general aggregative response is sigmoid in form, and tends to stabilize predator-prey systems (Hassell & May 1974). Predator aggregation around high density patches can provide a partial refuge for prey in low density patches (Hassell 1978). Aggregative responses have been described for various marine vertebrates and invertebrates (Hill 1979, Decho & Fleeger 1988, Fairweather 1988, Friedland et al. 1989, Piatt et al. 1989).

Predator aggregation can also enhance the foraging rates of individual predators if they are attracted to prey patches by the foraging of conspecifics, or when mutual attacks are more successful than individual attacks (Hassell & May 1973, 1974, Anger et al. 1977). Conversely, mutual interference resulting from predator aggregation may adversely affect either a predator's searching efficiency or its feeding rate. The general interference response describes the relationship between searching efficiency or attack rate and predator density, and is curvilinear with interference becoming negligible at low predator densities (Hassell 1978). The combination of aggregation and interference may stabilize predator-prey dynamics by providing partial refuges for prey in low density patches, and by promoting dispersal of predators from patches in which prey have been heavily exploited (Hassell 1978).

Blue crabs affect local population densities of their bivalve prey (Virnstein 1977, 1979, Peterson 1979b, Holland et al. 1980, Seed 1980, Blundon & Kennedy 1982a,b, Arnold 1984, Lipcius & Hines 1986, Sponaugle & Lawton 1990) and play a major role in energy transfer within estuaries (Baird & Ulanowicz 1989). However, little is known about the combined role of predator and prey densities in predator-prey interactions, especially the aggregative response and intraspecific competition or interference. The objective of this study was to quantify the combined effect of the functional, aggregative, and interference (i.e., intraspecific competition) responses upon prey and predator survival and predator foraging rates in a marine predator-prey system, specifically that between the blue crab *Callinectes sapidus* Rathbun and the infaunal clam *Macoma balthica* (L.), in Chesapeake Bay.

THE PREDATOR-PREY SYSTEM

The blue crab Callinectes sapidus is a large [males up to 227 mm carapace width (CW)] epibenthic omnivore occurring in various habitats along the Northwest Atlantic Ocean, Gulf of Mexico and Caribbean Sea (Williams 1984). Blue crabs serve as both prey and consumers, and are abundant and actively foraging from late spring through autumn in Chesapeake Bay, USA (Hines et al. 1987, 1990). The diet of Chesapeake Bay blue crabs consists of bivalves (predominantly Macoma balthica), crabs (both blue crabs and xanthids), fish and polychaetes, and to a lesser extent amphipods and isopods (Hines et al. 1990, this study Chapter 1).

The tellinid Macoma balthica is an infaunal, soft-shelled clam commonly occurring in muddy and muddy sand habitats along both sides of the North Atlantic (from the Arctic Sea to Georgia along the western Atlantic) and along the Pacific coast from polar regions to its southern limit in San Francisco Bay (Beukema & Meehan 1985, Martini & Morrison 1987). In Chesapeake Bay, M. balthica is an abundant, deep-burrowing (depth to 40 cm), deposit or suspension feeder, and occurs predominantly in mud substrates of meso-polyhaline regions (Hines & Comtois 1985, Hines et al. 1989, 1990). Two settlement pulses occur: a relatively weak winter pulse and a marked spring pulse peaking in May, ceasing in June, and with populations declining rapidly in July and August primarily in association with intense blue crab predation (Holland et al. 1980, 1987, Blundon & Kennedy 1982b, Holland 1985, Hines et al. 1989, 1990). Large adults find at least partial refuge through greater burial depth (> 10 cm) (Blundon & Kennedy 1982b) and through a low-density refuge (Eggleston et al. 1992), as observed in another soft-shelled infaunal clam, Mya arenaria (Lipcius & Hines 1986). The combined effect of varying predator and prey densities upon the dynamics of this system remains unquantified.

MATERIALS AND METHODS

This study used a full-factorial experimental design with 2 prey densities of 4 and 16 clams m^{-2} (i.e., clams $tank^{-1}$) and 3 predator densities of 1, 2 and 4 crabs m^{-2} (i.e., crabs $tank^{-1}$). Experimental clam densities resemble low to moderate field densities (Hines et al. 1990, Eggleston et al. 1992), while crab densities are similar to moderate and high blue crab densities (> 25 mm CS, 6.9 crabs m^{-2}) in Chesapeake Bay (Orth & Van Montfrans 1987). Controls included both clam densities but without crabs. Experiments were conducted under natural photoperiod from mid-July through mid-October 1989 (mean water temperature ± SE: 22.1 ± 0.3°C).

Six circular tanks 1.13 m in diameter (1 m^2) were filled with fine muddy sand (97.3 % sand, 1.5 % silt, 1.3 % clay) to a depth of 15 cm and unfiltered, ambient York River (Virginia, USA) water to a level 25 cm above the sediment surface. Blue crabs were captured in traps whereas *Macoma balthica* were collected by suction-dredge from local muddy and muddy sand habitats. Male intermolt crabs, 115 to 160 mm CW, were held separately, fed ad libitum with live *M. balthica* and mussels *Geukensia demissa*, and acclimated to laboratory conditions for 1 wk. *M. balthica*, 27 to 39 mm SL (shell length), were held in open-system tanks and also acclimated for 1 wk.

Crabs were matched for size to within 10 % CW. All crabs were exposed to randomly chosen combinations of crab and clam densities to avoid learning specific treatment combinations (Murdoch & Oaten 1975). Crabs were checked daily; any crabs that died overnight, either from unknown causes or cannibalism, were replaced by similarly sized new crabs and treated in the same manner as their predecessors. All sizes of crabs used in this investigation were equally capable of excavating and feeding on the size classes of clams offered (Blundon & Kennedy

1982a,b). All sizes of experimental clams bury to similar depths (Blundon & Kennedy 1982b, Hines & Comtois 1985), and were therefore equally available to crabs. Only crabs that fed during acclimation, and clams that exhibited a healthy siphon-withdrawal reflex were used.

The experimental procedure involved introduction of clams and crabs into tanks during daylight hours (11:00 to 14:00 h). Macoma balthica were randomly buried 10 cm below the sediment surface and allowed 48 h prior to crab introduction to acclimate to experimental conditions and bury to a natural depth (Hines & Comtois 1985). Crabs starved for 48 h were released into the center of each tank at the start of a trial. Trials ended with removal of crabs after 72 h, and determination of clam mortality through counts of survivors and umbos of eaten clams. Between each trial, experimental tank water was replaced with ambient river water, while the sediment was vigorously aerated. Twenty-four hours prior to clam introduction, water inflow was discontinued and sediment aeration reduced.

Six trials were conducted for each combination of crab and clam density with systematic interspersion of each treatment combination (Underwood 1981, Hurlbert 1984). The numbers and proportions of eaten clams were analyzed as a function of clam and crab density in a 2-way fixed-factor analysis of variance (ANOVA). Prior to analyses, the raw numbers were log-transformed, while proportional mortality data were arc-sine square-root transformed to normalize the data and remove heteroscedasticity (Cochran's test; Sokal & Rohlf 1981, Underwood 1981, SPSS Inc. 1988). In 3 instances, 1 trial each of a treatment combination (i.e., 3 of 36 trials) was lost due to system failure. In these cases, the mean of the treatment combination for that trial was substituted to maintain a balanced experimental design, and the error MS df was reduced accordingly before calculating F values (Underwood 1981). Means were back-transformed for graphical presentation.

Variations in proportional mortality with prey density can be used to distinguish density-dependent (i.e., relatively lower proportional mortality at low clam density) from inversely density-dependent (i.e., relatively higher proportional mortality at low clam density) predation (Lipcius & Hines 1986). Usually, 3 to 6 prey densities are required to determine the general shape of a functional response curve, although the type of functional response is detectable only at low to moderate prey densities. However, 2 prey densities permit statistical differentiation among density-independent, inversely density-dependent and density-dependent functional response curves at low to moderate prey densities (Lipcius & Hines 1986). Other investigations (Eggleston et al. 1992) indicated the range of M. balthica densities required to distinguish between functional response curves and described the general shape of the curves for the blue crab-Macoma predator-prey system. Therefore, a subset of clam densities was selected from within this range for this investigation.

Crab mortality resulting from cannibalism and intraspecific aggression was analyzed with Dunnett's multiple comparison procedure, which compares 2 or more proportions to a control proportion (Zar 1984).

RESULTS

There was 100 % survivorship of control clams. Proportional mortality of clams and consumption rates of blue crabs differed significantly by clam density (Fig. 1a,b, Table 1). Blue crabs exhibited density-dependent foraging in all treatments: proportionally more clams were consumed at the high clam density (Fig. 1b). The data for consumption rates and proportional mortality of clams as a function of crab density suggested a decreasing trend (Fig. 1a,b); however, the power to detect a significant crab density effect was low (a posteriori test; Zar 1984; power < 0.20) for both the numbers eaten and proportional mortality. The interaction effect between crab density and clam density was not significant (Table 1).

Consumption rates and proportional mortalities standardized by crab density (number eaten and proportional mortality divided by crab density per treatment; Fig. 1c,d) differed significantly by clam density and crab density (Table 2). Again, crabs exhibited density-dependent foraging, with highest clam mortalities per crab and consumption rates per crab at the higher clam density (Fig. 1c,d). The interaction effect between clam and crab density was not significant in either case (Table 2).

Cannibalism and intraspecific aggression by blue crabs, as indicated by crab deaths, carapace wounds and loss of appendages, occurred in both the 2-crab and 4-crab density treatments at both clam densities. The results of other investigations (Lipcius & Hines 1986, Martin et al. 1989, Eggleston et al. 1992) using similar crab densities and tanks indicate that the crab densities used in this investigation were not likely to result in mortality associated with adverse abiotic conditions. Furthermore, since only hard intermolt crabs were used in each trial and none of these crabs molted during the trials, it is

Figure 1. *Callinectes sapidus* preying on *Macoma balthica*. Mortality of clams as a function of crab and clam density for (A) mean number of clams eaten (± SE), (B) mean proportional clam mortality (± SE), (C) mean number of clams eaten per crab (± SE), (D) mean proportional clam mortality per crab (± SE).

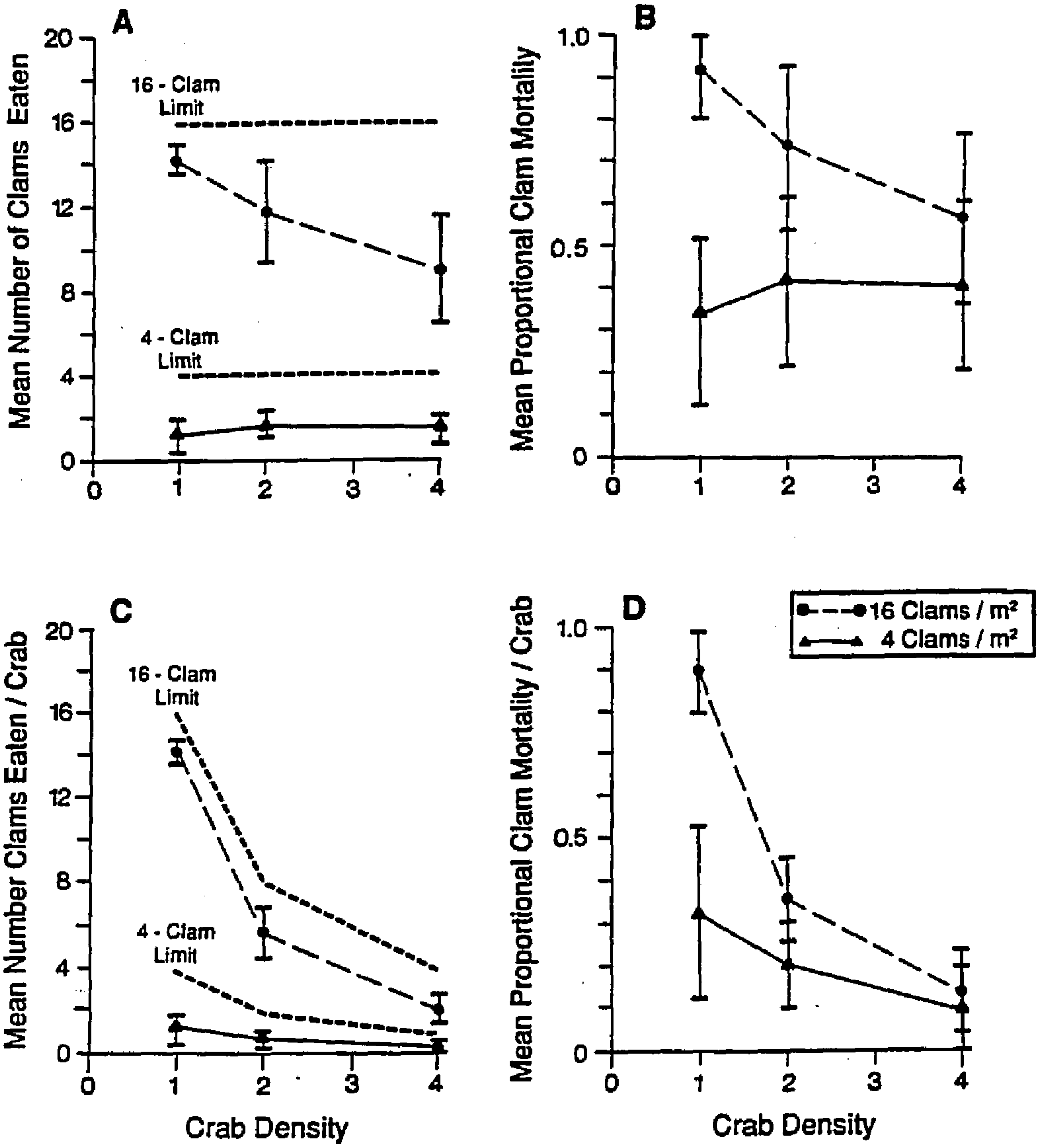
A
B
C
D
Mean Number of Clams Eaten
Mean Proportional Clam Mortality
Mean Number Clams Eaten / Crab
Mean Proportional Clam Mortality / Crab
16 - Clam Limit
4 - Clam Limit
16 Clams / m²
4 Clams / m²
Crab Density
0
4
8
12
16
20
0.5
1.0
1
2
3
4

Table 1. Two-way fixed factor ANOVA of number eaten and proportional clam mortality as a function of clam and crab density. * P < 0.05, **** P < 0.001, NS: P > 0.05

SOURCE OF VARIATION	SS	DF	MS	F
Number Eaten				
Clam density	9.756	1	9.756	22.13****
Crab density	0.314	2	0.157	0.36 NS
Clam X Crab interaction	0.838	2	0.419	0.95 NS
Error	11.905	27	0.441	
Proportional Mortality				
Clam density	2.072	1	2.072	6.20*
Crab density	0.167	2	0.084	0.25 NS
Clam X Crab interaction	0.360	2	0.180	0.54 NS
Error	9.028	27	0.334	

Table 2. Two-way fixed factor ANOVA of consumption rate and proportional clam mortality standardized by crab density (see text) as a function of clam and crab density. * P < 0.05, ** P < 0.01, **** P < 0.001, NS: P > 0.05

SOURCE OF VARIATION	SS	DF	MS	F
Number Eaten Per Crab				
Clam density	8.596	1	8.596	28.87****
Crab density	2.070	2	1.035	3.47*
Clam X Crab interaction	1.136	2	0.568	1.91 NS
Error	8.040	27	0.298	
Proportional Mortality Per Crab				
Clam density	1.060	1	1.060	8.28**
Crab density	2.158	2	1.079	8.43****
Clam X Crab interaction	0.732	2	0.366	2.86 NS
Error	3.453	27	0.128	

unlikely that any crabs were more susceptible to cannibalism than others in the same tank. Thus, it was assumed that death from causes other than cannibalism or intraspecific aggression occurred at the proportional mortality rate observed in the 1-crab treatments (0.083 crabs $tank^{-1}72h^{-1}$; Table 3). This rate was adjusted for the number of crabs in each tank (see Table 3), yielding 4 hypothetical proportional mortalities due to sources other than cannibalism and intraspecific aggression in the 2-crab and 4-crab treatments. The 4 observed proportional mortalities were then compared with these hypothetical proportional mortalities with Dunnett's multiple comparison test (Zar 1984). The resulting tests showed mortality significantly higher than the hypothetical proportions in the 4-crab, 4-clam treatment, which had the lowest ratio of clam:crab abundance, but not in the remaining 3 treatments (Table 3), though these were also greater than zero.

Table 3. Mortalities of crabs as a function of crab and clam density. Hypothetical proportional mortalities were calculated for each treatment combination by multiplying crab density by 0.083 (i.e., the value derived from the 1-crab, 4-clam and 16-clam density treatments, which reflected the proportion dead due to causes other than cannibalism or intraspecific aggression). In 2-crab trials the hypothetical proportional mortality = 0.083 X 2 = 0.166; in 4-crab trials, 0.083 X 4 = 0.332. * P < 0.05, Dunnett's multiple comparison procedure for comparing proportions with a hypothetical proportion (Zar 1984). In this procedure, the observed proportions in the column 'Proportion with a dead crab' were compared with those in the column 'Hypothetical proportional mortality'. The procedure accounts for the number of comparisons. NS: P > 0.05, Dunnett's procedure.

CLAM DENSITY	CRAB DENSITY	TRIALS WITH A DEAD CRAB	TOTAL TRIALS	PROPORTION WITH A DEAD CRAB	HYPOTHETICAL PROPORTIONAL MORTALITY	PROPORTION CANNIBALIZED
4 or 16	1	1	12	0.083	0.083	0.000
4	2	3	6	0.333 NS	0.166	0.167 NS
4	4	3	5	0.600 *	0.332	0.268 *
16	2	4	6	0.333 NS	0.166	0.167 NS
16	4	2	5	0.400 NS	0.332	0.068 NS

DISCUSSION

Blue crabs exhibited density-dependent foraging in all treatment combinations of crab and clam densities. Although the occurrence of a density-dependent functional response was not unexpected given the outcomes of previous studies (i.e., with the soft-shelled infaunal clam *Mya arenaria* in sand, Lipcius & Hines 1986; with *Macoma balthica* in mud and sand Eggleston et al. 1992), the results were novel in that the density-dependent refuge for clams was maintained irrespective of crab density. Thus adult *M. balthica* obtain a refuge from blue crab predation at low densities (i.e. ca 1 to 4 clams per tank), and this refuge appears to be retained even when crab densities are high.

Furthermore, several observations strongly suggest the existence of mutual interference and intraspecific aggression between crabs with increased predator density. First, crab mortality and injury occurred at a significant rate in at least one of the crab density treatments, and may have been statistically non-significant in the other treatments due to low statistical power (ca 0.20). A similar result was observed by Martin et al. (1989) in enclosures of equal area as those used in this experiment, and a density of 2 crabs per enclosure (ca 1 m^2). Second, the frequency with which clam densities in the 16-clam trials remained above the low-density refuge (i.e., 1 to 4 clams per tank), and thereby were not reduced substantially was noted. The data showed an increase in the number of trials remaining above the low-density refuge as crab density increased (i.e., 0 or 5 with 1 crab, 2 of 6 with 2 crabs, and 3 of 5 with 4 crabs), suggesting that mutual interference between crabs further enhanced the low-density refuge. Third, although a single blue crab could consume all experimental clams, the numbers of clams eaten decreased, though not significantly, in the 2-crab and 4-crab treatments.

Other field and laboratory studies also indicate that cannibalism is common in blue crabs (Darnell 1959, Tagatz 1968, Laughlin 1982, Martin et al. 1989, Peery 1989, Hines et al. 1990, this study Chapter 1). In the Apalachicola estuary, Florida, USA, Laughlin (1979) observed an inverse relationship between blue crab recruitment levels and subsequent population abundance, and suggested that high densities of juveniles may stimulate cannibalism and exploitative competition. Blue crabs constituted 11 % of the total diet of large crabs (> 61 mm CW) in that estuary (Laughlin 1982). Cannibalism is an extreme form of interference competition, occurring in a wide variety of vertebrates and invertebrates. It is most frequent during periods of low availability of alternative prey or high predator density, and acts as a density-dependent regulator of population size (Fox 1975, Polis 1981).

In Chesapeake Bay, blue crabs and their prey exhibit seasonal cycles in abundance. The blue crab population is composed of 2 year-classes that are actively foraging in the tributaries of Chesapeake Bay from April through December (Hines et al. 1987, Lipcius & Van Engel 1990). Therefore, the potential for intraspecific agonistic interactions leading to cannibalism is high, especially as alternative prey are depleted later in the season. Further evidence that density-dependent rates of cannibalism may regulate blue crab populations includes: density-dependent autotomy (Smith 1990), increased occurrence of crabs in blue crab stomachs in late summer when alternative (bivalve) prey availability and densities are reduced (Hines et al. 1990, this study Chapter 1), cannibalism of tethered juvenile blue crabs (Smith & Hines 1991), the highly developed and complex intraspecific agonistic behaviors of blue crabs (Jachowski 1974), and the significant effect of previous year-classes on the stock-recruitment relationship for blue crabs in Chesapeake Bay (Lipcius & Van Engel 1990).

The results of this study indicate that the interactive effects of prey density and predator density are also important for clam persistence in prey patches. Furthermore, these results show how the aggregative and interference responses may affect the magnitude of predation intensity. The aggregative and interference responses are strongly interrelated (Hassell 1978): by congregating in patches of high prey density, the probability of interference is enhanced, which then modifies the functional and aggregative responses. Crowley & Martin (1989) derived 2 functional response models of interference, and applied them to data on cannibalistic functional responses of dragonfly larvae. In a distraction model a predator's attention is divided between other predators and the prey, whereas in a preemption model the predator's response to other predators takes precedence over feeding. Both models fit the data well: there was an inverse relationship between feeding rate and predator density, indicating strong interference among these cannibalistic predators (Crowley & Martin 1989). MacLeod & Valiela (1975) found a similar trend of decreasing prey consumption with increasing predator density for nudibranch predators. At the highest predator density, nudibranchs spent more time in small inactive groups rather than actively searching for prey. For blue crabs, it is unclear whether agonistic interactions lead primarily to avoidance responses (as in some starfish; Palumbi & Freed 1988) and hence predator dispersal, or if cannibalism is the relatively more frequent response to low alternative prey availability or high conspecific population density. Behavioral studies are required to quantify the nature of the interactions between blue crabs.

A predator's combined aggregative, functional and interference response must be defined in investigations of predator-prey dynamics and community organization in marine soft-bottom benthic communities. In Chesapeake Bay, the combination of responses allows prey to persist, despite intense predation, by affecting the magnitude of predation in prey patches. Previous work on the blue crab-bivalve (i.e., Macoma balthica and Mya arenaria) predator-prey system in Chesapeake Bay has concentrated on the interactive effects of prey species, prey density and habitat type (e.g., sediment) on clam survivorship (Lipcius & Hines

1986, Hines et al. 1990, Eggleston et al. 1992). The field and laboratory evidence accumulated thus far indicates that predator foraging and prey mortality rates vary significantly across gradients in prey availability, and the physical properties of microhabitats (Blundon & Kennedy 1982a,b, Arnold 1984, Lipcius & Hines 1986, West & Williams 1986, Hines et al. 1990, Sponaugle & Lawton 1990). The results of this study suggest differences in the magnitude of the functional response resulting from predator density, such that prey mortality and predator foraging rates may be reduced within prey patches where predators aggregate. Other studies have shown that interference between predators is important to the outcome of interactions between predators and prey, and determines predator dispersion and prey persistence (Beddington 1975, MacLeod & Valiela 1975, Sih 1981, Eveleigh & Chant 1982, Ens & Goss-Custard 1984, Palumbi & Freed 1988). This study further indicates that predator density and interference may be important in the population dynamics of marine species, by affecting foraging rates and perhaps promoting cannibalism when alternative food resources are limited. Further field investigations are required to quantify these components of predation and determine effects on both predator and prey population dynamics, and community organization in marine systems.

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