Regional, watershed and local correlates of blue crab and bivalve abundances in subestuaries of Chesapeake Bay, USA

Ryan S. King*, Anson H. Hines, F. Doug Craige, Sarah Grap

Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, MD 21037, USA

Abstract

Blue crabs (*Callinectes sapidus*) and deposit- and suspension-feeding bivalves (*Macoma balthica* and *M. mitchelli*) play important roles in the food web of Chesapeake Bay and may serve as indicators of ecological health, particularly in small subestuaries where conditions may be strongly linked to watershed and local factors. We sampled 19 subestuaries of Chesapeake Bay to test hypothesized relationships of blue crabs and bivalves with salinity (a regional indicator), watershed- and local-scale land use, and local habitat and water quality. We divided the subestuaries into five land-use categories: forested, developed, agricultural, mixed agricultural and mixed-developed. We measured water quality, sediment class, physical habitat and adjacent land use/land cover at each of six stations within each subestuary. Fyke nets were employed to estimate blue crab abundance and size-structure, while cores were used to estimate bivalve densities and biomass. Classification and regression tree (CART) analysis indicated that 51% of the variance in blue crab abundance was explained by salinity, watershed land use and shoreline marsh habitat. Crab abundance was greatest at salinities >16 ppt, but in lower salinities crabs were most abundant along marsh shorelines in forested and mixed land-use watersheds. Juvenile crabs <85 mm were more strongly associated with shoreline marshes, particularly in subestuaries with forested and mixed land-use watersheds. *Macoma* spp. were similarly associated with shoreline marshes but mainly in muddy bottoms at moderate-to-high salinities; however the best CART model only explained 25% of variance in bivalve abundance. These results were consistent with our predictions that shoreline wetlands and watershed land use may have important effects on these taxa along the estuarine salinity gradient, and are consistent with hypotheses based on previous descriptive and experimental research linking blue crabs and deposit-feeding bivalves to habitats rich in allochthonous detritus.
© 2005 Elsevier B.V. All rights reserved.

Keywords: *Callinectes sapidus*; Ecological indicators; Estuaries; *Macoma* spp.; Watershed land use; Wetlands

* Corresponding author. Present address: Center for Reservoir and Aquatic Systems Research, Department of Biology, Baylor University, Waco, TX 76798, USA. Tel.: +1 254 710 2150; fax: +1 254 710 2969.

E-mail addresses: kingry@si.edu, Ryan_S_King@baylor.edu (R.S. King).

1. Introduction

The distribution of biota in estuaries is influenced by both natural and anthropogenic factors. Accordingly, scientists and managers are increasingly inter-

ested in developing biotic indicators of ecosystem health in estuaries (e.g., Rakocinski et al., 1997; Smith et al., 2001; Paul et al., 2001). A common approach to ecological assessment in estuaries is the use of community-level attributes that can reliably distinguish between a population of sites classified a priori as "reference" or "impaired". These approaches typically have relied on taxonomic information from macrobenthic species assemblages to develop multimetric indexes of biological integrity (e.g., B-IBI; Weisberg et al., 1997). While effective for identifying sites with degraded benthic communities, these indexes do not directly measure condition of many other important components of an estuarine ecosystem (e.g., productivity, food-web stability; Suter, 2001). Moreover, index development, particularly in the mid-Atlantic region of the USA, has focused primarily on the mainstem of large estuaries or their major tributaries. Little work has been done in nearshore areas of smaller subestuaries, which are highly productive and critical habitats for a variety of important estuarine taxa (e.g., Hines et al., 1990; Everett and Ruiz, 1993; Ruiz et al., 1993).

Numerous socioeconomic and ecological attributes make blue crabs (Callinectes sapidus Rathbun) potentially ideal indicators of environmental conditions in estuarine ecosystems. Blue crabs are distributed throughout Chesapeake Bay and other estuaries of the East and Gulf coasts of North America and disperse across a wide range of salinities following settlement in the polyhaline zone (Van Engel, 1958; Millikin and Williams, 1984). Blue crabs support the most important commercial fishery in mid-Atlantic estuaries (Rugolo et al., 1998). As the dominant benthic predator and as prey for some larger predators, they also play a critical role in energy transfer in estuaries (Baird and Ulanowicz, 1989). Blue crabs feed intensively on benthic infauna, particularly bivalves (e.g., Laughlin, 1982; Mansour, 1992; Ebersole and Kennedy, 1995), suggesting that the spatial distribution of blue crabs might be tied to natural and anthropogenic factors that affect the distribution and abundance of bivalve prey (Seitz and Lipcius, 2001; Seitz et al., 2003a). In addition, blue crabs may be sensitive to anthropogenic shoreline modifications because natural nearshore habitats such as woody debris and marsh creeks are important for both juveniles and molting crabs as refugia from predation

(Hines et al., 1987a,b; Everett and Ruiz, 1993; Dittel et al., 1995; Hines and Ruiz, 1995; Ryer et al., 1997). Finally, blue crabs are sensitive to hypoxia (e.g., Pihl et al., 1991, 1992; Seitz et al., 2003b); thus, their distribution may be directly influenced by cultural eutrophication commonly associated with developed and agricultural land use in watersheds.

Deposit- and suspension-feeding tellinid bivalves (Macoma balthica L. and M. mitchelli Dall) are also ecologically significant taxa that may be useful indicators of estuarine condition. Tellinid bivalves play dominant functional roles in many marine infaunal communities. Similar to blue crabs, these bivalves are widely distributed across a wide range of salinities of the mesohaline to polyhaline zones in Chesapeake Bay (Boesch, 1972, 1973; Mountford et al., 1977; Virnstein, 1977; Hines and Comtois, 1985; Hines et al., 1989). Importantly, they represent a significant proportion of infaunal biomass and are a key energy link between inputs of allochthonous detritus and higher trophic levels (Hines and Comtois, 1985; Baird and Ulanowicz, 1989; Hines et al., 1989; Seitz et al., 2003a). Macoma spp. are found in greatest abundance in muddy sediments with high concentrations of organic carbon (Seitz and Lipcius, 2001), suggesting that adjacent shoreline habitat (e.g., marshes) may be an important factor in their distribution. M. balthica is also sensitive to anthropogenic stressors (e.g., Weisberg et al., 1997; Llansó et al., 2002), suggesting that local and watershed land use (e.g., extent of development or agriculture) may also affect its distribution.

We hypothesize that species such as blue crabs and Macoma spp. may serve as indicators of estuarine conditions because they are functionally important in the estuarine food web and have documented trophic and habitat interactions that provide a mechanistic explanation for their patterns of distribution and abundance. Because they are distributed widely across estuaries, however, we predict that these patterns of abundance will be correlated with variables at differing spatial scales. To test these hypotheses, we established a sampling design across multiple subestuaries that allowed us to sample crab and bivalve abundance and a suite of variables that are commonly correlated with organism abundance. We analyzed patterns in these data to test for predicted correlations based on functional relationships and for correlations

not predicted by our hypothesized relationships. Given the well-known spatial and temporal variability of estuarine systems, a challenge of our approach derives from applying analyses of predictions of both correlation and non-correlation across widely dispersed systems.

Specifically in this paper, we explore regional (salinity), watershed (e.g., land use) and local (e.g., land use, water quality, habitat) correlates of abundances of blue crabs and bivalves in subestuaries of Chesapeake Bay, USA. We hypothesized that blue crab and bivalve abundances would be greatest in (1) subestuaries with the highest salinities, as *Macoma* spp. are adapted to intermediate-to-high salinities (e.g., Boesch, 1973; Mountford et al., 1977; Virnstein, 1977; but see Ysebaert et al., 2002) and these areas are closer to sources of recruitment for blue crabs; (2) subestuaries with forested watersheds, as these areas have the lowest degree of watershed-scale human disturbances; and (3) nearshore areas adjacent to marsh habitats, as these areas are a key source of allochthonous detritus for *Macoma* spp. and thus should result in greater abundance of prey for blue crabs. Although results from previous local-scale field experiments and observational studies provide a basis for these hypotheses, few investigations have explored these relationships at a regional spatial scale—a scale in which controlled experimental manipulations are impossible. Thus, our goals were to evaluate the generality of these hypotheses and to explore the utility of bivalves and blue crabs as indicators of estuarine condition across a large geographical extent.

2. Methods

2.1. Study area and selection of subestuaries

This study was conducted in 19 subestuaries of Chesapeake Bay, the largest estuary in the USA (Fig. 1). This subset was selected from an initial population of over 60 subestuaries based on a suite of criteria: a defined stream network in the watershed (3rd-to-5th order, Straehler system), a defined subestuary, shoreline marshes and proportional estimates of land-cover/land-use classes within watersheds (see next section). Presence of a stream network was important because we expected hydrologic connectivity between land in

the catchment and subestuaries to be an important determinant of water quality and biological integrity. Watersheds were required to have defined subestuaries to maximize our ability to detect linkages to upstream watershed condition. We required subestuaries to have shoreline marshes because we hypothesized that these habitats were important to estuarine organisms.

Watershed boundaries were used within a geographic information system (GIS) to estimate proportions of land cover/land use based on classes resolved in the National Land Cover Database (NLCD, 30-m raster coverage). Watersheds were classified into one of five land-use categories based on the predominant distributions of land-use proportions in the Chesapeake Bay region: (1) forested (≥60% forest+forested wetland cover and <15% development), (2) developed (≥50% commercial+residential cover either in whole watershed or concentrated in the lower portion of watershed adjacent to subestuary), (3) agricultural (≥50% rowcrop+pasture/field cover), (4) mixed-developed (≥15% and <50% developed cover) and (5) mixed-agricultural (≥20% and <50% agricultural cover, and <60% forest cover). Very few watersheds had an even mix of forested, developed and agricultural cover; rather, land cover tended to span a gradient from forested-to-developed or forested-to-agricultural. Thus, "mixed" categories were representative of intermediate levels of development and agriculture relative to watersheds with the greatest amount of remaining forest cover.

Land-use patterns along Chesapeake Bay are spatially contagious. Developed land is primarily located in the upper bay on the western shore and in a very localized area of the lower bay. Agriculture, while widely distributed overall, is most intensive on the eastern shore of the bay in Maryland. Remaining forested areas are located primarily in the middle and southern bay on the western shore. Thus, given these spatial patterns, it was not feasible to select watersheds so that each land-use class was randomly distributed along the north-to-south salinity gradient in the bay. We recognized this as a problem and a limitation of this and any other study on effects of watershed land use on estuaries in this region. However, to minimize this problem to the extent possible, we chose subestuaries that resulted in the greatest spatial distribution of land-use classes across
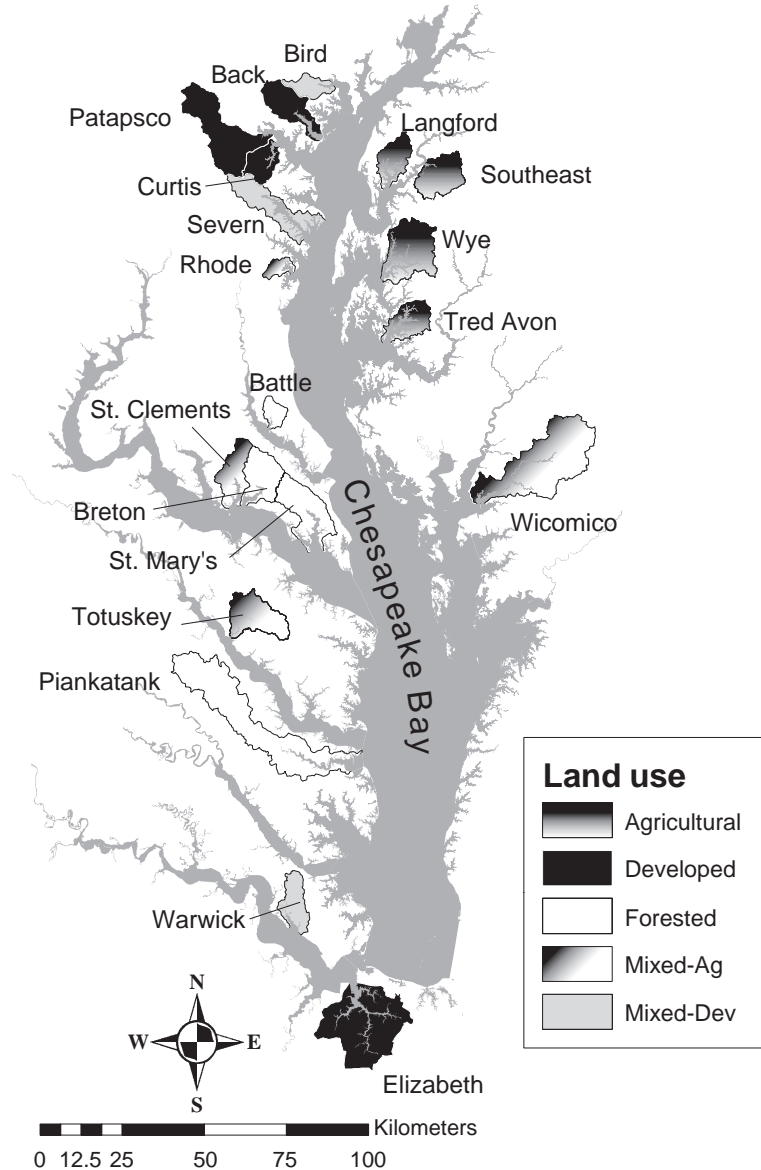

Rhode River stations. These results indicated that sampling of six stations was the most efficient level of effort to characterize blue crab and bivalve abundance for comparisons at the subestuary scale. It was deemed impractical to sample more than six stations when the primary goal was to maximize the extent of sampling at a broad spatial scale. Moreover, we planned to test for local-scale relationships; thus, individual sampling stations, rather than averages among stations within subestuaries, were used as observations.

Sampling stations were located using a stratified-random approach. Because many subestuaries differed markedly in the types and relative amounts shoreline land cover, we used the proportion of shoreline land cover within subestuaries used as a weighting factor for stratification. For example, a subestuary with 60% wetland, 20% forest, 15% developed and 5% agriculture would have resulted in selection of 4 wetland, 1 forested, 1 developed and 0 agricultural stations. To calculate the weights, we summarized areal proportions of land cover within 30 m of the subestuary shoreline. We chose this distance because it was the same width as the pixel resolution in the land-cover dataset and represented the land cover that was most closely associated with the land–water interface. We also focused on the upper reaches of each subestuary (upper quarter to half, depending upon size and morphology of subestuary) to maximize our ability to detect linkages to upstream watershed condition, which otherwise may have been swamped by the influence of the bay if stations were located farther down the subestuary (Han, 1974; Gallegos et al., 1992). Once land-cover strata were identified and weights were calculated, individual stations were located adjacent to appropriate land-cover classes using a random subset of shoreline segments.

The geographical position of stations was determined within the GIS and field navigation was accomplished using a global positioning system (GPS). On occasion, stations were not suitable for sampling due to a variety of factors, such as differences between observed shoreline land cover and that predicted by the NLCD. In these cases, alternative stations identified prior to sampling were used.

In the field, we characterized shoreline land use, bank condition and habitat at each station (Table 1). Shoreline land use was defined the land cover within 30 m of the shoreline in width. When emergent

Table 1
Description of the variables used as predictors of blue crab and bivalve abundance

Variable	Type	Values
Land-use class, watershed	C	Forested, developed, agriculture, mixed-developed, mixed-agriculture
Shoreline land-use/ land-cover[a]	N	0–100%
Forest buffer	N	0–100%
Marsh buffer	N	0–100%
Marsh size	O	0 (none), 1 (>0 and <0.5 ha), 2 (0.5–5 ha), 3 (>5 ha)
Marsh creeks	C	present/absent
Woody debris	O	0 (none), 1 (present), 2 (abundant)
Bottom slope	O	1 (low), 2 (moderate), 3 (high)
SAV abundance	O	0 (absent), 2 (rare), 3 (sparse), 4 (moderate), 5 (dense)
Riprap or bulkhead	N	0–100%
Recreational structures	N	0–9
Water depth[b]	N	0.4–3.9 m
Dissolved oxygen, bottom[b]	N	0.11–15.85 mg/l
Water temperature, bottom[b]	N	26.9–32.1 °C
Salinity, bottom[b]	N	0.3–23.8 ppt
Sediment class[b]	C	mud, muddy sand, sand, coarse sand, peat

The type of variable is denoted by N=numerical, O=ordinal or C=categorical.

[a] Forest, pasture/field, rowcrop, total agriculture (pasture/field+rowcrop), residential, commercial, total developed (residential+commercial) and marsh. Each land-use/land-cover class was treated as a separate explanatory variable.

[b] Estimated within each station at the two locations used for collecting *Macoma* spp. samples. Values represented an average of two measurements/station.

wetland (hereafter, marsh) and forested land-cover classes were <10 m in width, they were defined as buffers. We visually estimated the percentage of each 100-m station occupied by land-use classes and shoreline buffer classes. Habitat assessment included estimates of marsh size (ha), which were obtained in the field for small marshes or via the NLCD for large wetlands. Marsh size estimates were converted to ordinal size classes (Table 1) because marshes varied markedly in size and, in some cases, were contiguous along a very large portion (>1000 m) of the subestuary shoreline; thus, the absolute size of large marshes was difficult to express in a meaningful manner relative to a 100-m sampling station. The number of marsh creeks along each 100-m station

boundary also was measured as an indicator of marsh-subestuary connectivity. Very few stations had >1 marsh creek; thus, this variable was expressed as presence or absence or marsh creeks.

Characterization of nearshore underwater habitat included the enumeration of woody debris snags as a potential indicator of refugia for molting and juvenile blue crabs (Everett and Ruiz, 1993; Ryer et al., 1997). Because woody debris was often difficult to see in turbid water and was relatively amorphous (i.e., difficult to count as discrete units), we converted counts to ordinal abundance classes (Table 1). Submerged aquatic vegetation (SAV) relative abundance was documented using a combination of visual surveys and benthic grabs. Nearshore bottom slope, an ordinal variable expected to potentially influence blue crab distributions (Ruiz et al., 1993) and provide habitat for bivalves (Table 1), was estimated using multiple water-depth measurements along a transect moving away from shore to a distance of approximately 50 m. Percentage of shoreline as riprap or bulkhead and the number and type of recreational structures (docks, piers, boat ramp, boat house) within each station were also estimated as indicators of habitat alteration.

Water depth (m) and surface and bottom water temperature, salinity and dissolved oxygen (DO) were measured approximately 50 m from shore at two locations within the boundaries of the 100-m shoreline segment. Sediment samples were collected using a Petite Ponar grab and each was classified into one of five types based on grain size and abundance of coarse particulate organic matter: (1) mud, (2) muddy sand, (3) sand, (4) coarse sand/gravel and (5) peat (Table 1).

Abundance and size structure of blue crabs were estimated using fyke nets. A pair of nets (0.9×1.2 m frame, 3-m wings, one 5-mm and 20-mm mesh net) was set at each station. Nets were set lead-to-lead (15.2 m combined length), parallel to shore along a depth contour of 0.4–0.8 m, depending upon tides. Distance from shore was ranged from 10–50 m, depending upon steepness of the bottom slope. Nets were deployed for 24 h at each station and retrieved. All crabs were enumerated, measured (carapace width, mm) and released. A total of 114 stations were sampled from the 19 subestuaries (6 stations/subestuary).

We estimated density and biomass of bivalves using core samplers (10-cm diameter). Four cores were collected at each station. Cores were collected to a minimum depth of 30 cm, corresponding to the maximum burrowing depth of *Macoma* spp. (Hines and Comtois, 1985). Cores were washed using a 2-mm sieve and composited to form a single sample for each station. A total of 109 stations were sampled for bivalves from the 19 subestuaries (five stations were not sampled due to impenetrable substrates). All live *Macoma* spp. were enumerated and shell length (SL, anterior to posterior) was measured with calipers accurate to 0.1 mm. Biomass (AFDW) was estimated using a length-mass regression equation developed for each species (S. Grap, unpublished data). All sampling occurred from 1 July to 3 September 2002, a widely used index period for ecological assessment in Chesapeake Bay (e.g., Weisberg et al., 1997). The sequence in which watersheds were sampled was determined randomly.

2.3. Data analysis

Density (no./m^2) and biomass (mg AFDW/m^2) were estimated for each *Macoma* species (*M. balthica* and *M. mitchelli*) and for all *Macoma* spp. at each station. Abundance of juvenile (<85 mm CW) and total blue crabs was expressed as the number of crabs per station based on pooling both counts made from the pair of fyke nets.

Preliminary examination of the *Macoma* spp. and blue crab data revealed relationships to many predictor variables that were strongly nonlinear, heteroscedastic and often involved higher-order interactions—all common properties of complex ecological data. These properties are particularly common when explanatory variables are spatially hierarchical (Urban, 1987). Additionally, we had a combination of numerical, ordinal and categorical predictors that were not well suited for traditional statistical approaches. Thus, to identify the best correlates of blue crab and bivalve abundance, we used classification and regression tree (CART) analysis, an approach ideally suited for complex ecological data with hierarchical structure (Breiman et al., 1984; De' Ath and Fabricius, 2000).

CART explains variation of a single response variable using one or more predictor variables. Response variables can either be categorical (classification tree) or numerical (regression tree). Explan-

atory variables can be numerical, ordinal and categorical. CART works by recursively partitioning data into two mutually exclusive groups by selecting a predictor variable that best explains variation in the response variable. The process is repeated until the tree can no longer be grown based on a set of stopping rules and cross-validation of the model. The goal is to explain as much variation (r^2) in the response variable as possible while minimizing the size of the tree. This is analogous to incorporating explanatory variables into multiple regression. However, CART has been shown to have numerous advantages over linear regression approaches, including (1) making very few assumptions about the properties of the data, (2) the detection of change in both the mean and variance of response variables and (3) superior ability to reveal higher-order interactions (De' Ath and Fabricius, 2000; Olden and Jackson, 2002).

We built a separate CART model for each abundance variable for *Macoma* spp. and blue crabs. Our models were regression trees because the response variables were numerical. Observations were individual stations because stations reflected local-scale conditions and each was characterized by a unique set of explanatory measurements. For models that identified watershed land-use class as predictor, we reran the model with individual watersheds as a class variable (n=19 classes, 6 observations/class) to evaluate whether the apparent land-use effect was driven by observations within just one or two watersheds within a land-use class. In addition to the environmental explanatory variables, we included *Macoma* spp. variables as predictors in the blue crab models, and vice-versa.

Prior to analysis, CART requires that the user define a minimum number of observations permitted within the "leaves" (terminal groups nested within "branches of the tree") and the branches of the tree. We required that terminal groups and branches have no fewer than 10 and 20 observations, respectively (except for models that incorporated individual watersheds as predictors for diagnosing the validity of a watershed land-use effect (terminal group minimum size=6 observations), and for blue crabs <85 mm (7 observations) (see Results for explanation).

We cross-validated each CART model to determine the most appropriate size of the tree (i.e., number of explanatory variables included in the model) and whether the tree could be used to explain variation in data not used to build the model (De' Ath and Fabricius, 2000). Cross-validation was conducted by randomly partitioning the data into 10 groups of equal or similar size and creating a cross-validation regression tree with only nine of the 10 groups. This cross-validation tree was subsequently used to predict response-variable data from each of the stations remaining in the tenth group. The process is repeated 10 times so that each of the 10 groups of sites was used as the cross-validation group once. For each response variable, we evaluated the contribution of each predictor and retained predictors that resulted in an overall improvement in the model r^2 using the average of the 10 cross-validations. Greater detail on CART and its application to ecological data can be found in De' Ath and Fabricius (2000) and Urban (2002). CART analyses were conducted using the RPART library in S-Plus 2000 (Insightful Corp., Seattle, WA, USA).

3. Results

3.1. Blue crabs

Blue crabs were collected from every subestuary and were present at 101 of 114 stations. Juvenile crabs <85 mm were collected at 60 of 114 stations. Juvenile and total crab abundance averaged 4.9 and 15.9 crabs per station, respectively.

Variation in juvenile blue crab abundance was best explained by local shoreline marsh habitat, watershed land use and salinity (Fig. 2). Juvenile crabs were most abundant at stations adjacent to virtually 100% shoreline marsh cover (r^2=19%). However, abundance at pure-marsh stations was also dependent upon watershed land use, as the seven pure-marsh stations located in highly developed or agricultural watersheds had no juvenile crabs compared to >17 per station in forested or mixed watersheds (r^2=17%). We included watershed land-use class in the model even though it resulted in fewer than 10 observations/group because cross-validation indicated it explained an important proportion of variation. Moreover, these seven developed and agricultural stations were located in six different subestuaries, suggesting
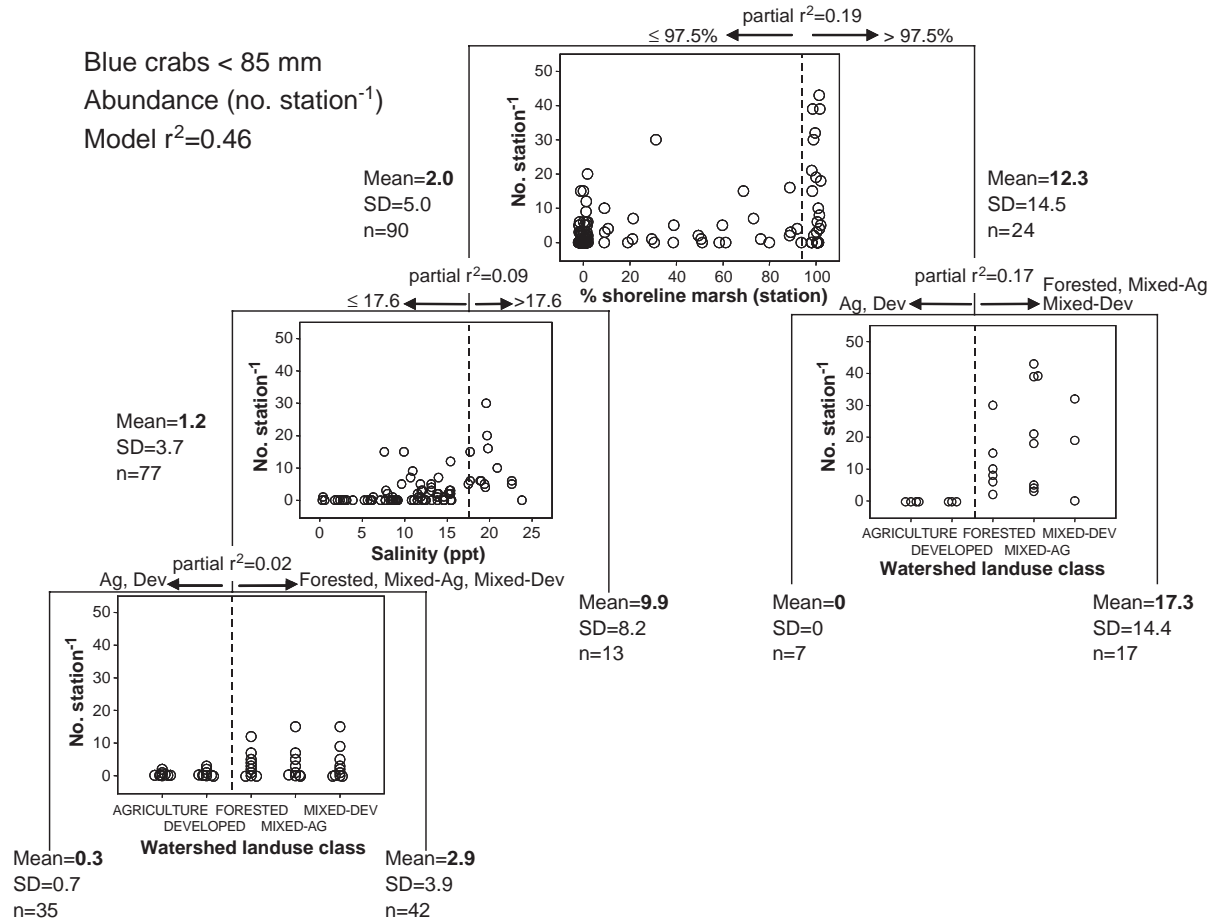
Fig. 2. Results from CART analysis of juvenile blue crabs <85 mm (no. station^{-1}). Scatterplots illustrate the response of juvenile blue crab abundance at each level of the tree. The vertical dotted line in each plot identifies the value of the predictor (x) that best explained variation in juvenile blue crabs. Threshold values of predictors are shown to the left and right of each split above each scatterplot. Variance explained (r^2) for predictors is shown next to each split. Means, standard deviations (S.D.) and number of stations (n) summarize properties of the data to the left and right of every split in the data.

the effect was not specific to multiple stations in just one watershed of each class. Along shorelines not covered completely by marshes, juvenile crabs were most abundant at salinities >17.6 ppt (r^2=9%). However, variation in the 77 observations with salinities <17.6 ppt was further explained by watershed land use, with virtually no crabs at the 35 stations located in developed and agricultural watersheds but at least five non-zero observations in each of the forested and mixed watershed classes. Although this relationship was weak (r^2=2%), cross-validation indicated that this variable

should be retained in the model. The complete tree explained a total of 46% of the variation in juvenile blue crab abundance.

Variation in total blue crab abundance was best explained by salinity, watershed land-use classes and shoreline marshes (r^2=51%, Fig. 3). Crabs were most abundant at salinities >16.3 ppt (r^2=24%), but this only represented 18 stations from three subestuaries in the lower bay. Below 16.3 ppt, crabs were more abundant in forested or mixed land-use watersheds than in subestuaries with highly developed or agricultural watersheds (r^2=16%). Within forested
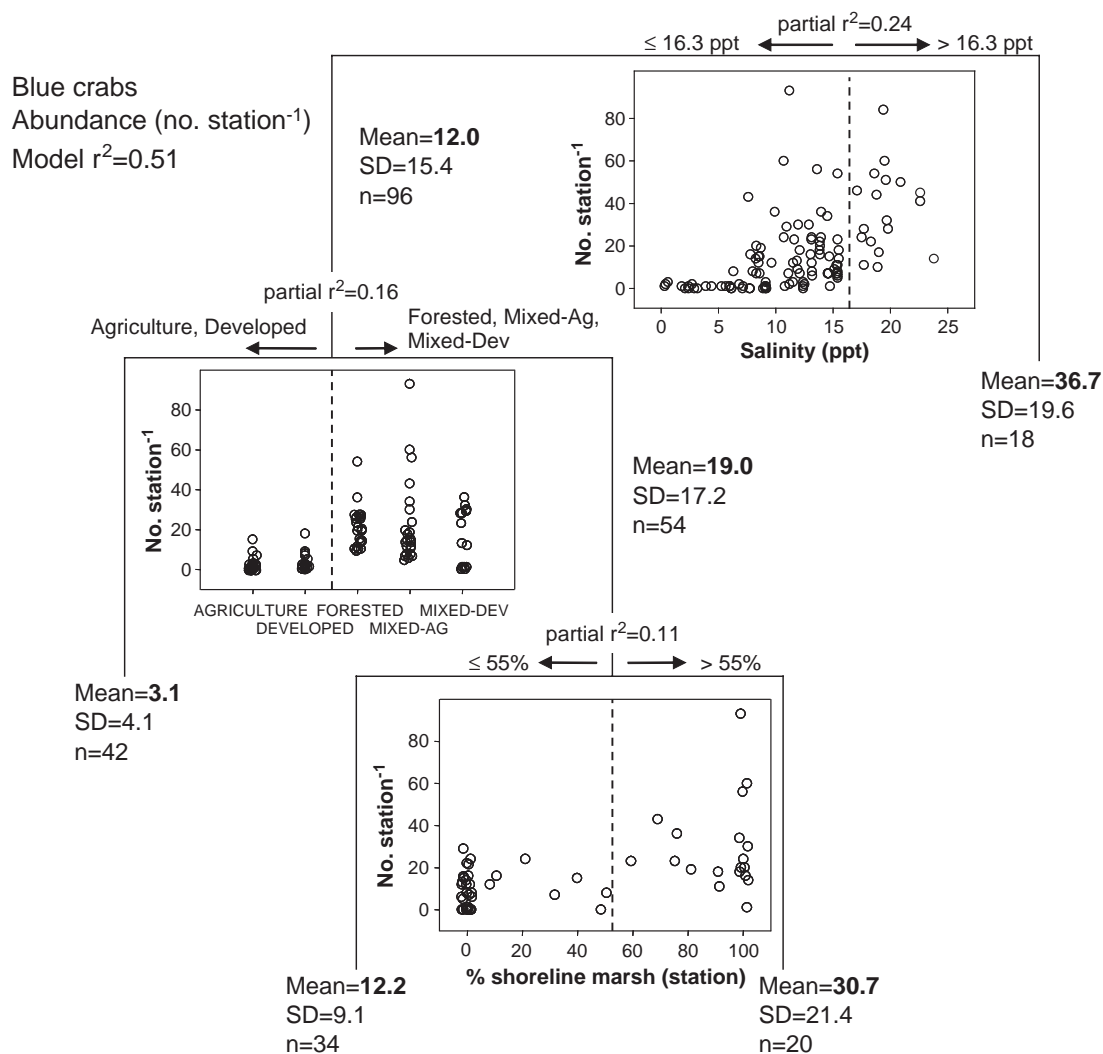
Blue crabs
Abundance (no. station^{-1})
Model r^2=0.51

Fig. 3. Results from CART analysis of total blue crab abundance (no. station^{-1}). See Fig. 2 for details.

and mixed watersheds, shoreline marshes accounted for an additional 11% of the variation, with a mean of nearly 31 crabs at stations with at least 55% shoreline marsh habitat but only 12.2 crabs at stations with predominantly other types of shoreline land use or land cover.

3.2. Bivalves

M. balthica and *M. mitchelli* were present at 65 and 61 of the 109 stations, respectively, and both

species were present at 78 stations. Densities of *M. balthica* and *M. mitchelli* averaged 132 m^{-2} and 49 m^{-2} per station, respectively, whereas biomass averaged 4980 mg/m^2 and 280 mg/m^2, respectively.

Results of CART analysis of total *Macoma* spp. density and biomass indicated that salinity was the primary factor correlated with overall bivalve distribution in subestuaries of Chesapeake Bay (Fig. 4). Stations with the highest density and biomass of *Macoma* spp. were typically associated with salinities >8.4 ppt, although this split only explained
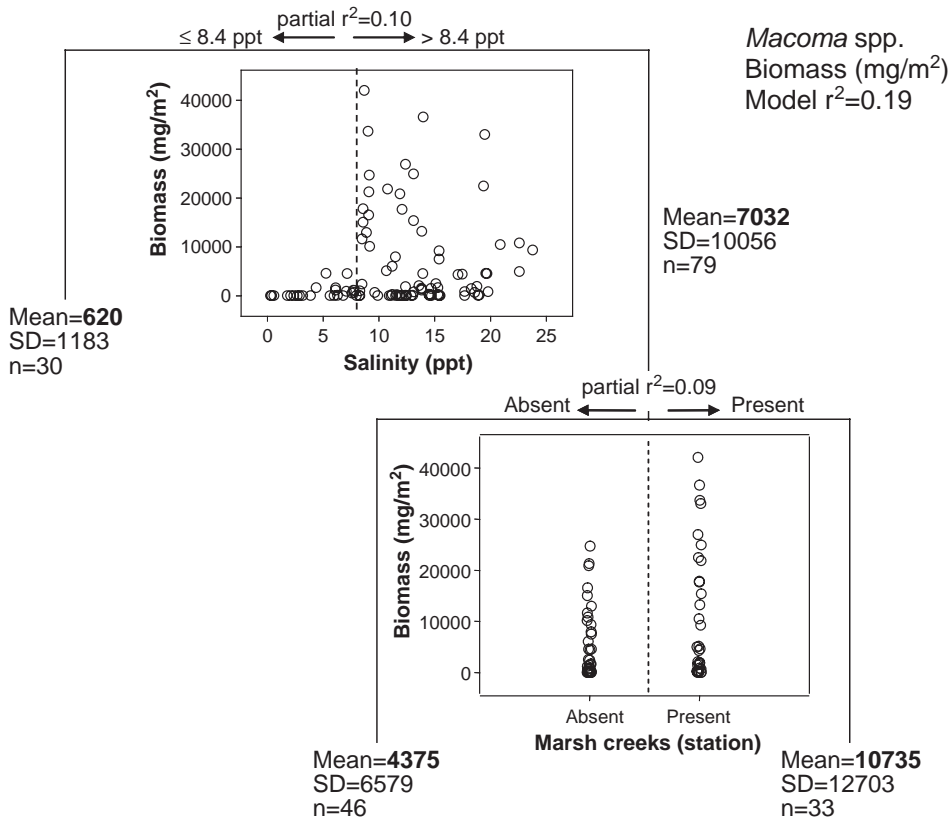
Fig. 4. Results from CART analysis of *Macoma* spp. biomass (AFDW, mg m^{-2} station^{-1}). See Fig. 2 for details.

10% of the total variation. However, above 8.4 ppt, stations with marsh shoreline habitat and at least one marsh creek tended to have the highest *Macoma* spp. biomass-presence of marsh creeks explained an additional 9% of the variation (total model r^2=19%, Fig. 4). For *Macoma* spp. density, salinity was the only variable retained in the model because results from cross-validation indicated that no other explanatory variable sufficiently improved the model to warrant its inclusion.

Results from CART analyses on each of the individual *Macoma* species suggested patterns similar to that of the *Macoma* spp. analysis. Because *M. balthica* dominated the overall *Macoma* spp. biomass, it resulted in a tree identical to the *Macoma* spp. model. However, salinity, sediment class and shoreline marshes best explained variation in *M. balthica* density (model r^2=25%, Fig. 5). Densities were highest stations with at least 35% of the

shoreline in marsh habitat (r^2=11%), but also in mud or muddy sand sediments (r^2=11%) and at salinities >8.3 ppt (r^2=7%). Although these relationships were relatively weak, cross-validation indicated that these models were not over-fit and likely represented real patterns in the data.

Density and biomass of *M. mitchelli* were not well explained by salinity, habitat or other water quality variables. Watershed land-use class provided the best but weak explanation of its variation, with stations located in subestuaries with forested watersheds having higher densities and biomass than the other four watershed classes (r^2=11%). However, most of this explained variation was attributed to high abundances in one of the forested watersheds (Piankatank), which was confirmed after including each forested watershed as classes in the model. Thus, variation in the distribution of *M. mitchelli* was watershed-specific
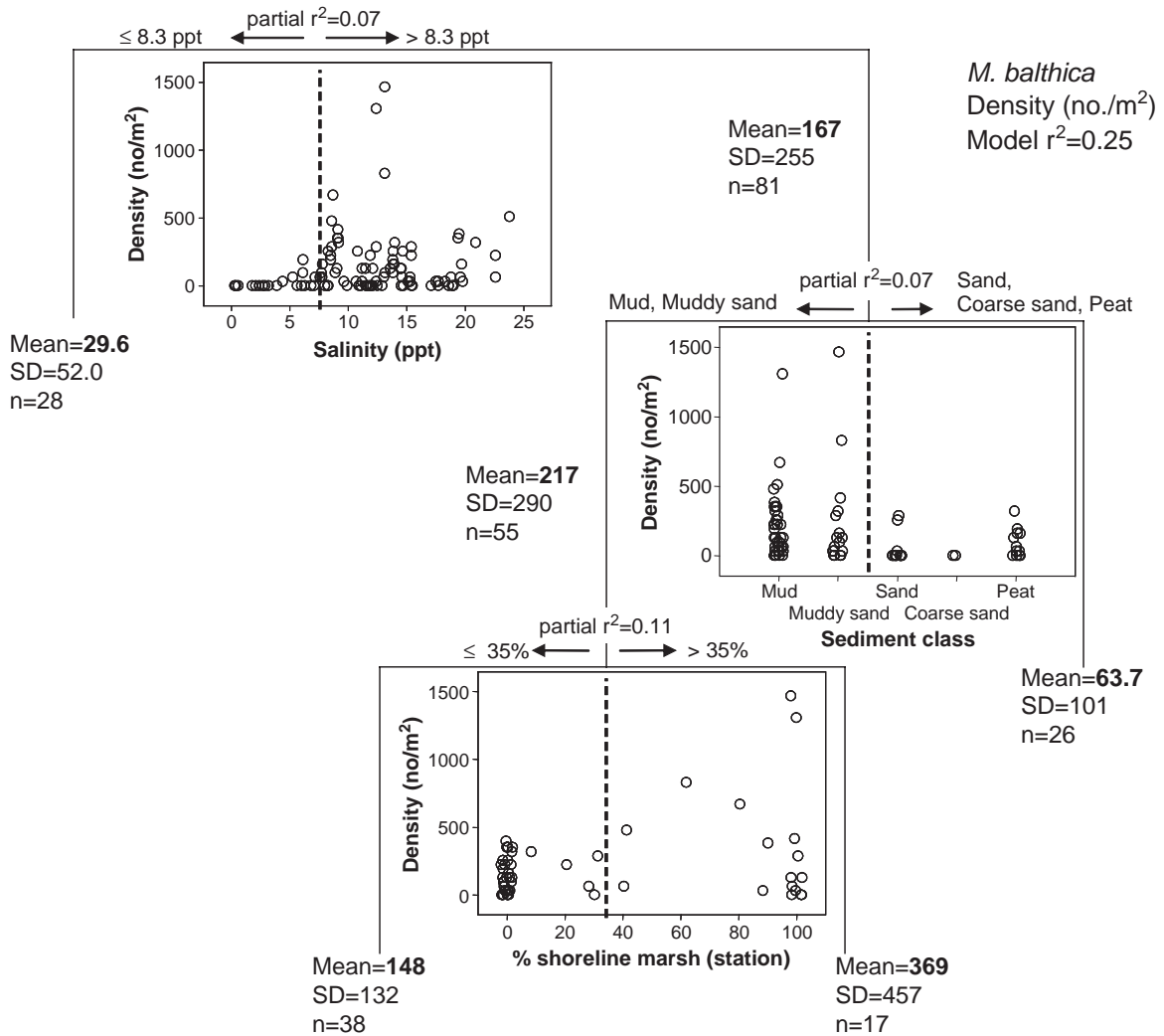
Fig. 5. Results from CART analysis of *Macoma balthica* density (no. m^{-2} station^{-1}). See Fig. 2 for details.

and not predictable using any of the explanatory variables considered.

4. Discussion

Results from the CART analyses were generally consistent with our hypotheses about primary factors influencing the distribution of blue crabs and tellinid bivalves in Chesapeake Bay. First, we expected that the distribution of both taxa would be correlated with salinity. Blue crabs were in greatest abundance in southern Chesapeake Bay subestuaries where salinity was >16 ppt, likely due to the close proximity of these sites to the primary source of blue crab reproduction and recruitment in the lower bay (Van Engel, 1958; Olmi et al., 1990). However, at intermediate-to-low salinities, blue crabs were most often associated with shoreline marshes in forested and mixed land-use watersheds. Greater abundance of crabs along marshes was consistent with the hypothesis that marshes were important sources of organic carbon for deposit-feeding bivalve prey (Seitz and Lipcius, 2001; Seitz et al., 2003a). Shoreline marshes were

particularly influential to juvenile crabs <85 mm, which may have also benefited from the refugia afforded by this structurally complex habitat (Van Montfrans et al., 1991; Ryer et al., 1997). Thus, our results reinforce the importance of coastal marshes to estuarine food webs.

Watershed land use was also an important correlate of blue crab abundance. We found relatively few crabs at stations located in subestuaries with predominantly developed and agricultural land use. A number of causal or possibly spurious factors may have been responsible for this observed pattern. Although there is relatively little direct evidence of linkages between watershed land use and estuarine condition (e.g., Hartwell et al., 1997; Dauer et al., 2000), it is well established that large proportions of development and agriculture in watersheds are likely to degrade the physical, chemical and biological integrity of the freshwater stream network that ultimately discharges into a subestuary (e.g., Roth et al., 1996; Paul and Meyer, 2001). High loads of nutrients, sediments and toxic substances associated with these land-use practices may have consequently degraded nearshore habitat and water quality in the subestuaries we sampled.

Hypoxia resulting from anthropogenic pollution, in particular, is a watershed-scale factor that may have reduced blue crab abundance. Blue crabs are moderately sensitive to episodic hypoxia and cannot tolerate even relatively short periods of low dissolved oxygen (DO<2 mg O_2 l^{-1}) (Seitz et al., 2003b), such that they typically shift their distribution away from areas of reduced DO levels (Pihl et al., 1991; Eby and Crowder, 2002; Bell et al., 2003). Moreover, food resources also diminish in areas with low DO (Diaz and Rosenberg, 1995). We observed DO<2 mg O_2 l^{-1} at >20% of the stations located in developed watersheds compared to zero observations of DO<2 mg O_2 l^{-1}in forested watersheds. We also observed a much higher incidence of supersaturation and vertical stratification of DO in developed watersheds. Although DO was not one of the explanatory variables selected in the CART models, our midday DO measurements may not have adequately characterized DO levels at the watershed scale, in deeper habitats farther from shore or at night when community respiration rapidly depletes DO concentrations (Novotny and Olem, 1994). In general, our data

suggest that watershed land use may be a surrogate indicator of one or many anthropogenic stressors to blue crabs at a subestuary scale.

Developed and agricultural land use also may have been an indicator of factors not related to degraded water or habitat quality. For example, commercial and recreational crabbing pressure may have been greater in these more populated areas and thus could have selectively reduced crab abundance. However, considering that watershed land use was more strongly correlated with the density of juvenile crabs <85 mm, a size class not legally targeted by crabbers, than the density of adult crabs, it seems unlikely that crabbing intensity accounted for much of this variation. In addition, many of the historic concentrations of the Chesapeake blue crab fishery are in rural areas rather than near development, and intensive fishing with commercial crab pots is prohibited in Maryland tributaries of Chesapeake Bay (but is allowed in Virginia tributaries) (Rugolo et al., 1998). Nevertheless, harvesting undoubtedly influences the spatial distribution and abundance of blue crabs and may have been an important source of unexplained variation among regions, subestuaries and stations in our study.

Spatial factors may have confounded the apparent correlation between watershed land use and blue crab abundance. Most of the subestuaries with highly developed and with agricultural watersheds are located in the northwestern and central-eastern shore of the bay, respectively, resulting in a high degree of spatial contagion in watershed land use among subestuaries (Fig. 1). Natural spatial variation related to factors such as dispersal distances for recruiting crabs may have been responsible for at least part of this observed pattern. Thus, while our results do suggest watershed land use to be a correlate of blue crab abundance, we suggest that conclusions regarding the causes of these correlations be made with caution.

Two of the best predictors of blue crab abundance (shoreline marshes and salinity) were also correlates of bivalve distributions in our CART models. *Macoma* spp. are adapted for intermediate-to-high salinities (Boesch, 1972, 1973; Mountford et al., 1977; Virnstein, 1977; Hines and Comtois, 1985; Hines et al., 1987a,b, 1990); thus, we anticipated they would be less abundant in subestuaries located in the

low-mesohaline zone of Chesapeake Bay, or at stations within the headwater regions of certain subestuaries that were oligohaline. Indeed, *Macoma* spp. had lower densities and biomass at salinities <8 ppt. This was particularly true for *M. balthica*, which constituted most of the total *Macoma* spp. biomass. In addition to a dependence on salinity, which was primarily indicative of the regional-scale north-to-south salinity gradient in Chesapeake Bay, CART also identified some key local-scale indicators of *Macoma* spp. At salinities >8 ppt, sediment class and marsh variables were important correlates of *Macoma* spp. distributions. *Macoma* spp. biomass was greatest at stations adjacent to marshes with at least one marsh creek. Marsh creeks likely are conduits for detritus and may result in greater amounts of sedimentary carbon, a key source of food for facultative deposit-feeding *Macoma* spp. (Seitz and Lipcius, 2001; Seitz et al., 2003a). The apparent linkage between *M. balthica* density and shoreline marshes with mud or muddy sand substrate (sediment classes that typically have relatively high concentrations of organic carbon; e.g., Seitz and Lipcius, 2001), further illustrated the potential connection between local-scale shoreline habitat and benthic condition in estuaries.

We hypothesized that similar factors would influence blue crabs and bivalves because of established predator–prey linkages between these taxa (e.g., Lipcius and Hines, 1986; Hines et al., 1990; Eggleston et al., 1992; Seitz et al., 2001, 2003a). Furthermore, given this linkage, we hypothesized that their distribution would be positively correlated. However, abundance of *Macoma* spp. was not an important predictor of blue crabs, or vice-versa (maximum r^2=4%). This conflicts with patterns documented by Seitz and Lipcius (2001) and Seitz et al. (2003a), who found higher densities of blue crabs in habitats supporting high *M. balthica* densities in two subestuaries of Chesapeake Bay. However, our data were collected across a more diverse array of locations and environmental conditions than their study. Moreover, our data were collected during a two-month period when *Macoma* spp. densities may have been temporally reduced by crab predation. Predation, in fact, may explain why we observed only relatively weak relationships between explanatory variables and *Macoma* spp. in our CART models. Crabs may have locally exploited bivalve populations and diminished

the apparent signal between local conditions and *Macoma* spp. abundance by the seasonal point of our sampling (Hines et al., 1990). Moreover, food-web theory predicts a weak coupling between adjoining trophic levels but a much stronger linkage between levels separated by one level (Carpenter et al., 1985; Micheli, 1999). Although speculative, it is possible that blue crabs were more closely linked to shoreline marshes than *Macoma* spp. because blue crabs were one trophic level removed from producers of allochthonous detritus that fueled deposit-feeding benthic prey. However, additional temporal data would be needed to adequately address this hypothesis.

Clearly, an important limitation of our study was the lack of temporal replication. Seasonal and interannual variability strongly influence the relative abundance of blue crabs and bivalves and, perhaps even more importantly, environmental factors such as water quality. Thus, temporal variation may have affected our estimates of environmental conditions, taxa abundances and the relative strength of relationships observed in our study. However, few, if any, investigators have tested for similar relationships using intensive temporal sampling at the same level of spatial effort employed in this study. Rather, we structured our hypotheses around the results of previous work that was based on spatially limited (e.g., within-subestuary scales) but temporally intensive experiments and observational studies. Despite the temporal limitations of our data, we were able to identify linkages between these estuarine taxa and regional, watershed and local factors expected to be important based on this existing body of spatially limited research. Thus, our results likely reflect generalized responses across a broad spatial scale, but may not adequately reflect the strength of relationships or the precise numerical values of the regional, watershed and local variables that apparently affected distributions of these two taxa.

In addition to our positive predictions about correlates of blue crab and bivalve abundance, we note that a broad array of factors we measured were not important correlates in our CART analysis. These non-significant variables are often related to abundance of many similar species, but did not have clear mechanistic relationships to our target species. From an assessment perspective, identification of key correlates of estuarine indicator taxa is potentially of

great value because it is often impractical for many local, state or federal agencies to monitor dynamic populations of such taxa across large spatial scales. Our study demonstrated that abundances of blue crabs and bivalves were highly variable, yet locations with the greatest abundances of both taxa were predictably associated with shoreline marshes (or correlates of marshes such as sediment classes) in areas of intermediate-to-high salinities, while blue crabs were also most abundant in watersheds with relatively high forest cover. Establishing linkages between indicator taxa and easily measured variables, such as watershed land use and shoreline marshes, provides a both a basis for conservation of natural habitat and a framework for monitoring potentially degraded subestuarine ecosystems. In sum, our analysis across a wide array of complex systems indicates that knowledge of functional relationships between estuarine taxa and key environmental factors can help in the selection of useful indicators.

Acknowledgements

References

Baird, D., Ulanowicz, R., 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. Ecol. Monogr. 59, 329–364.

Bell, G.W., Eggleston, D.B., Wolcott, T.G., 2003. Behavioral responses of free-ranging blue crabs to episodic hypoxia: I. Movement. Mar. Ecol. Prog. Ser. 259, 215–225.

Boesch, D.F., 1972. Species diversity of marine macrobenthos in the Virginia area. Chesap. Sci. 12, 206–211.

Boesch, D.F., 1973. Classification and community structure of macrobenthos in the Hampton Roads area, Virginia. Mar. Biol. 21, 226–244.

Breiman, L., Friedman, J.H., Olshen, R.A., Stone, C.J., 1984. Classification and Regression Trees. Wadsworth and Brooks/Cole, Monterey, CA.

Cao, Y., Williams, D.D., Larsen, D.P., 2002. Comparisons of ecological communities: the problems of sample representativeness. Ecol. Monogr. 72, 41–56.

Carpenter, S.R., Kitchell, J.F., Hodgson, J.R., 1985. Cascading trophic interactions and lake productivity. Bioscience 35, 634–639.

Dauer, D.M., Weisberg, S.B., Ranasinghe, J.A., 2000. Relationships between benthic community condition, water quality, sediment quality, nutrient loads, and land use patterns in Chesapeake Bay. Estuaries 23, 80–96.

De' Ath, G., Fabricius, K.E., 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81, 3178–3192.

Diaz, R.J., Rosenberg, R., 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioral responses of benthic macrofauna. Oceanogr. Mar. Biol. Annu. Rev. 33, 245–303.

Dittel, A.I., Hines, A.H., Ruiz, G.M., Ruffin, K.K., 1995. Effects of shallow water refuge on behavior and density-dependent mortality of juvenile blue crabs in Chesapeake Bay. Bull. Mar. Sci. 57, 902–916.

Ebersole, E.L., Kennedy, V.S., 1995. Prey preferences of blue crabs *Callinectes sapidus* feeding on three bivalve species. Mar. Ecol. Prog. Ser. 118, 167–177.

Eby, L.A., Crowder, L.B., 2002. Hypoxia-based habitat compression in the Neuse River Estuary: context-dependent shifts in behavioral avoidance thresholds. Can. J. Fish. Aquat. Sci. 59, 952–965.

Eggleston, D.B., Lipcius, R.N., Hines, A.H., 1992. Density-dependent predation by blue crabs upon infaunal clams with contrasting distribution and abundance patterns. Mar. Ecol. Prog. Ser. 85, 55–68.

Everett, R.A., Ruiz, G.M., 1993. Coarse woody debris as a refuge from predation in aquatic communities. An experimental test. Oecologia 93, 475–486.

Gallegos, C.L., Jordan, T.E., Correll, D.L., 1992. Event-scale response of phytoplankton to watershed inputs in a subestuary: timing, magnitude, and location of blooms. Limnol. Oceanogr. 37, 813–828.

Han, G.C., 1974. Salt balance and exchange in the Rhode River, a tributary embayment to the Chesapeake Bay. Ph.D. dissertation, The Johns Hopkins University, 189 pp.

Hartwell, S.I., Dawson, C.E., Durell, E.Q., Alden, R.W., Adolphson, P.C., Wright, D.A., Coelho, G.M., Magee, J.A., Ailstock, S., Norman, M., 1997. Correlation of measures of ambient toxicity and fish community diversity in Chesapeake Bay, USA, tributaries-urbanizing watersheds. Environ. Toxicol. Chem. 16, 2556–2567.

Hines, A.H., Comtois, K.L., 1985. Vertical distribution of estuarine infauna in sediments in a subestuary of central Chesapeake Bay. Estuaries 8, 251–261.

Hines, A.H., Ruiz, G.M., 1995. Temporal variation in juvenile blue crab mortality: nearshore shallows and cannibalism in Chesapeake Bay. Bull. Mar. Sci. 57, 884–901.

Hines, A.H., Lipcius, R.N., Haddon, A.M., 1987. Population dynamics and habitat partitioning by size, sex, and molt stage of blue crabs *Callinectes sapidus* in a subestuary of central Chesapeake Bay. Mar. Ecol. Prog. Ser. 36, 55–64.

Hines, A.H., Haddon, P.J., Miklas, J.J., Wiechert, L.A., Haddon, A.M., 1987. Estuarine invertebrates and fish: sampling design and constraints for long-term measurements of population dynamics. ASTM STP vol. 940. American Society for Testing and Materials, Philadelphia, pp. l40–l64.

Hines, A.H., Posey, M.H., Haddon, P.J., 1989. Effects of adult suspension- and deposit-feeding bivalves on recruitment of estuarine infauna. Veliger 32, 109–119.

Hines, A.H., Haddon, A.M, Wiechert, L.A., 1990. Guild structure and foraging impact of blue crabs and epibenthic fish in a subestuary of Chesapeake Bay. Mar. Ecol. Prog. Ser. 67, 105–126.

Laughlin, R.A., 1982. Feeding habits of the blue crab, *Callinectes sapidus* Rathbun, in the Apalachicola estuary. Florida. Bull. Mar. Sci. 32, 807–822.

Lipcius, R.N., Hines, A.H., 1986. Variable functional responses of a marine predator in dissimilar homogeneous microhabitats. Ecology 67, 1361–1371.

Llansó, R.J., Scott, L.C., Hyland, J.L, Dauer, D.M., Russell, D.E., Kutz, F.W., 2002. An estuarine benthic index of biotic integrity for the mid-Atlantic region of the United States: II. Index development. Estuaries 25, 1231–1242.

Mansour, R.A., 1992, Foraging ecology of the blue crab in lower Chesapeake Bay. Ph.D. dissertation, College of William and Mary, Williamsburg, VA. 297 pp.

Micheli, F., 1999. Eutrophication, fisheries, and consumer-resource dynamics in marine-pelagic systems. Science 285, 1396–1398.

Millikin, M.R., Williams, A.B., 1984. Synopsis of biological data on the blue crab, *Callinectes sapidus* Rathbun. FAO Fisheries Synopsis 138. NOAA Tech. Rep. NMFS1, 43 pp.

Mountford, N.K., Holland, A.F., Mihursky, J.A., 1977. Identification and description off macrobenthic communities in the Calvert Cliffs region of the Chesapeake Bay. Chesap. Sci. 18, 360–369.

Novotny, V., Olem, H., 1994. Water Quality: Prevention, Identification, and Management of Diffuse Pollution. Van Nostrand Reinhold, New York.

Olden, J.D., Jackson, D.A., 2002. A comparison of statistical approaches for modelling fish species distributions. Freshw. Biol. 47, 1976–1995.

Olmi III, E.J., Montfrans, J., van Lipcius, R.N., Orth, R.J., Sadler, P.W., 1990. Variation in planktonic availability and settlement of blue crab megalopae in the York River, Virginia. Bull. Mar. Sci. 46, 230–243.

Paul, M.J., Meyer, J.L., 2001. Streams in the urban landscape. Ann. Rev. Ecolog. Syst. 32, 333–365.

Paul, J.F., Scott, K.J., Campbell, D.E., Gentile, J.H., Strobel, C.S., Valente, R.M., Weisberg, S.B., Holland, A.F., Ranasinghe, J.A., 2001. Developing and applying a benthic index of estuarine condition for the Virginian Biogeographic Province. Ecol. Ind. 1, 83–99.

Pihl, L., Baden, S.P., Diaz, R.J., 1991. Effects of periodic hypoxia on distribution of demersal fish and crustaceans. Mar. Biol. 108, 349–360.

Pihl, L., Baden, S.P., Diaz, R.J., Schaffner, L.C., 1992. Hypoxia-induced structural changes in the diet of bottom-feeding fish and Crustacea. Mar. Biol. 112, 349–361.

Rakocinski, C.F., Brown, S.S., Gaston, G.R., Heard, R.W., Walker, W.W., Summers, J.K., 1997. Macrobenthic responses to natural and contaminant related gradients in northern Gulf of Mexico estuaries. Ecol. Appl. 7, 1278–1298.

Roth, N.E., Allan, J.D., Erickson, D.L., 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landsc. Ecol. 11, 141–156.

Rugolo, L.J., Knotts, K.S., Lange, A.M., Crecco, V.A., 1998. Stock assessment of Chesapeake Bay blue crab (*Callinectes sapidus* Rathbun). J. Shellfish Res. 17, 493–517.

Ruiz, G.M., Hines, A.H., Posey, M.H., 1993. Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. Mar. Ecol. Prog. Ser. 99, 1–16.

Ryer, C.H., van Montfrans, J., Moody, K.E., 1997. Cannibalism, refugia, and the molting blue crab. Mar. Ecol. Prog. Ser. 147, 77–85.

Seitz, R.D., Lipcius, R.N., 2001. Variation in top-down and bottom up control of marine bivalves at differing spatial scales. ICES J. Mar. Sci. 58, 689–699.

Seitz, R.D., Lipcius, R.N., Hines, A.H., Eggleston, D.B., 2001. Density-dependent predation, habitat variation, and the persistence of marine bivalve prey. Ecology 82, 2435–2451.

Seitz, R.D., Lipcius, R.N., Stockhausen, W.T., Delano, K.A., Seebo, M.A., Gerdes, P.D., 2003a. Potential bottom-up control of blue crab distribution at various spatial scales. Bull. Mar. Sci. 257, 179–188.

Seitz, R.D., Marshall Jr., L.S., Hines, A.H., Clark, K.L., 2003b. Effects of hypoxia on predator–prey dynamics of the blue crab *Callinectes sapidus* and the Baltic clam *Macoma balthica* in Chesapeake Bay. Mar. Ecol. Prog. Ser. 257, 179–188.

Smith, R.W., Bergen, M., Weisberg, S.B., Cadien, D., Dalkey, A., Montagne, D., Stull, J.K., Verlarde, R.G., 2001. Benthic response index for assessing infaunal communities on the southern California mainland shelf. Ecol. Appl. 11, 1073–1087.

Suter, G.W., 2001. Applicability of indicator monitoring to ecological risk assessment. Ecol. Ind. 1, 101–112.

Urban, D.L., 1987. Landscape ecology: a hierarchical perspective can help scientists understand spatial patterns. Bioscience 37, 119–127.

Urban, D.L., 2002. Classification and regression trees. In: McCune, B., Grace, J.B. (Eds.), Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon, USA, pp. 222–232.

Van Engel, W.A., 1958. The blue crab and its fishery in the Chesapeake Bay: Part I. Reproduction, early development, growth, and migration. Commer. Fish. Rev. 20, 6–17.

Van Montfrans, J., Ryer, C.H., Orth, J.J., 1991. Population dynamics of blue crabs *Callinectes sapidus* Rathbun in a lower Chesapeake Bay tidal marsh creek. J. Exp. Mar. Biol. Ecol. 153, 1–14.

Virnstein, R.W., 1977. The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. Ecology 58, 1199–1217.

Weisberg, S.B., Ranasinghe, J.A., Dauer, D.M., Schaffner, L.C., Diaz, R.J., Frithsen, J.B., 1997. An estuarine benthic index of biotic integrity (B-IBI) for Chesapeake Bay. Estuaries 20, 149–158.

Ysebaert, T., Meire, P., Herman, P.M.J., Verbeek, H., 2002. Macrobenthic species response surfaces along estuarine gradients: prediction by logistic regression. Mar. Ecol. Prog. Ser. 225, 79–95.