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COMMUNITY AND TROPHIC ORGANIZATION OF NEKTON UTILIZING SHALLOW MARSH HABITATS, YORK RIVER, VIRGINIA

STEPHEN M. SMITH,1 JAMES G. HOFF,2 STEVEN P. O'NEIL,3 AND MICHAEL P. WEINSTEIN3

ABSTRACT

Nekton were collected by trawl and Wegener ring at each of two stations within tidal creeks and at adjacent shoal stations in the polyhaline and oligomesohaline zones of the York River estuary, Virginia. Species richness was significantly higher \((P < 0.05)\) in Goalders Creek (oligomesohaline) compared with Blevins Creek (polyhaline) and may reflect the general absence of stenohaline marine “southern” taxa which seasonally occupy the tidal creeks of warm-temperate estuaries. In general, diversity was low in both creeks with dominance mainly shared by two species, *Leiostomus xanthurus* and *Anchoa mitchelli*. *Trinectes maculatus* also was abundant at the Goalders Creek shoal station, about 200 m outside of the creek mouth. A detailed analysis of the distribution of *L. xanthurus* indicated that after recruitment ceased, this species was largely resident in the creeks for several months, only emerging in the fall (October). Furthermore, emigration from Blevins Creek occurred earlier than at the upstream locality. Of the “transient” marine species encountered, *L. xanthurus* seemed to be the most tidal creek dependent. However, this may be due partly to the collection methodology employed.

Diet composition of six dominant species comprising >98% of the total number of individuals collected indicated that all were essentially trophic opportunists feeding on a wide variety of food items. Ontogenetic shifts in diet were also observed for the five most abundant species. Lack of dietary specialization and the consequently large degree of diet overlap in all species may reflect the nonlimiting nature of food abundance in the primary nurseries, however a seasonal change in relative fullness values may indicate periodic food scarcity.

The structural and functional role of shallow estuarine habitats has received increasing attention in the past few years. Although widely recognized as primary nurseries, two of these habitats, marshes and seagrass meadows, have only recently come under scrutiny in the lower Chesapeake Bay. Much of the impetus for these efforts was derived from priorities established by the Chesapeake Bay Program (Environmental Protection Agency 1979). As a result, areas covered with submerged aquatic vegetation (SAV) were investigated between 1977 and 1981. The role of SAV as primary nurseries, especially for blue crabs, *Callinectes sapidus*, was confirmed (Orth4). It was suggested (and, in some cases, demonstrated experimentally) that a principal function of vegetated habitats was that of predation refugium for the early life stages of many species (Heck and Thoman 1981; Lascara 1981; see also Nelson 1979 and Coen et al. 1981). Although sea-grass meadows were contrasted with immediately adjacent unvegetated areas, their value compared with tidal salt marshes was not established.

To place the utilization of SAV and tidal creeks by the immature life stages of dominant species into better perspective, Weinstein and Brooks (1983) undertook a direct comparison of these areas along a contiguous marsh-seagrass ecosystem on the eastern shore of Virginia. Two results of their study were the observations that the dominant finfish in the area — spot, *Leiostomus xanthurus*—was nearly four times more abundant in the tidal creek throughout the study period, and that larger juvenile and adult blue crabs made nearly equal use of both habitats. A further outcome of this study was the obvious need for additional inventories of shallow waters of the lower Chesapeake Bay with regard to the relative value of different habitats to resident species.

For this reason we have extended our program to include a survey of habitat utilization by nekton occupying oligohaline and polyhaline tidal creeks.
of the York River estuary and have included a comparison of the tidal creeks with adjacent shoal areas (about 200 m outside of the tidal creek mouths). Along with data on community composition and structure, we have begun baseline studies of diet composition of dominant species. These aspects of community ecology of York River tidal marshes are reported herein.

STUDY AREA AND METHODS

The York River is one of six major tributaries which enter the Chesapeake Bay along its western shoreline. The narrow estuary covers about 208 km² and extends 46 km from York Marsh Light to West Point, Va. (Fig. 1). The upper portion of the York is characterized by broad, shallow flats and tidal creeks dominated by *Spartina* spp. along the shoreline. Upstream the river channel averages 8-9 m in depth, but broadens downstream and reaches a maximum depth of 18-23 m. The Guinea Marshes (Fig. 1) is a major *Spartina alterniflora*-dominated marsh system located near the estuary mouth. Much of the adjacent shallows in this region is carpeted with dense stands of eelgrass, *Zostera marina*, and widgeon grass, *Ruppia maritima*. Salinities are usually in the polyhaline range.

Two tidal creeks were selected for study. Goal­ders Creek (Fig. 1:location A) was located in the oligohaline-mesohaline zone just below the city of West Point. Blevins Creek (Fig. 1:location B), a part of the Guinea Marsh system, was situated in the polyhaline zone where salinities always exceeded 16%. In each creek, one station was established as far upstream as possible, one near the creek mouth, and one about 200 m offshore. All collections were made monthly on consecutive days (March-October 1983), with sampling initiated as close to daytime high tides as possible. Miller and Dunn (1980) collected a greater proportion of fish with stomachs containing food at this time. Creek bottoms were of the mud-silt type and ranged from 1 to 1.5 m deep.

The primary collecting device utilized in this study was a 4.9 m otter trawl consisting of wings and body of 19 mm mesh and a liner of 6.3 mm mesh. This gear was towed for 2-min intervals at a speed of about 1.0 m/s at each station. In an earlier study at Guinea Marshes, Orth and Heck (1980) demonstrated that six hauls of the trawl were necessary in seagrass habitats to attain asymptotic returns on community information (as judged by several diversity indices). Because of the expectedly lower diversity in the tidal creeks (Weinstein and Brooks 1983), it was determined that four consecutive hauls at each tidal creek station would be sufficient to attain the same level of community information.

Ancillary collections were taken in the tidal creek with a modified Wegener ring (Wegener et al. 1973). The gear was used in depths <1 m, in the vicinity of the trawling stations. The side walls of the ring consisted of 1.5 mm woven netting, with the original design of the gear being changed to include a 305 mm "skirt" and chain attached to the

**FIGURE 1.**—Location of study areas in York River estuary, Va. Three permanent sampling stations were established—near the headwaters, at the mouth, and 200 m offshore of an oligomesohaline (A = Goal­ders Creek) and polyhaline (B = Blevins Creek) tidal creeks.
leadline hoop which helped fill contours along the bottom. Samples were obtained by tossing the ring from shore and then applying rotenone at a 30 ppb concentration within the confines of the net (Weinstein and Brooks 1983). Stricken fishes were then captured with dip net or swept off the bottom.

Fishes were sorted into 20 mm (or less) size classes and up to 20 randomly selected individuals from each class used for trophic analyses. Stomach fullness was recorded as a relative fullness index (RFI) value (Hyslop 1980). Stomach contents were subsequently analyzed using a modified Carr and Adams (1972) sieve fractionation technique. Total dry weights for each sieve fraction were then obtained and proportioned among the prey taxa identified from a five drop subsample taken before drying. On the assumption that particles of equal size have approximately the same weight, this method agglomerates food particles of roughly the same size.

The Carr and Adams technique provided rapid, accurate identification of food items for a large number of stomachs and has been used with success by several investigators (Sheridan 1979; Sheridan and Livingston 1979; Stoner 1980; Livingston 1982). A useful modification employed in this study was the application of a low pressure stream of compressed air delivered through a Pasteur pipette which greatly aided in removing food particles adhering to the finer screens of the sieves.

Numerical classification analysis used here is similar to the procedures employed by Weinstein (1979) and Weinstein and Brooks (1983). Briefly, marsh creek communities and trophic ecology of dominant species were compared by classification methods using "normal" and "inverse" classification (Clifford and Stephenson 1975). The former method groups sites (or predators) by their species (or prey taxon) attributes; while inverse classification (used only for community analysis purposes here) groups species according to their site of occurrence (i.e., the sites become the attributes of the species). Similarity between sites (or predators) was calculated as the complement of the Canberra metric index:

\[ 1/n \sum_{j} \frac{|x_{1j} - x_{2j}|}{(x_{1j} + x_{2j})} \]  

(1)

where \( n \) = number of attributes, and \( x_{1j} \) and \( x_{2j} \) are the values of the \( j \)th attribute for any pair of entities. The merits of the Canberra metric index have been discussed by Clifford and Stephenson (1975).

Separate matrices were constructed for each comparison from untransformed, pooled monthly data and clustered by the unweighted pair, group-average strategy (Clifford and Stephenson 1975). Species occurring at only one station (singletons) were eliminated prior to the community analyses. Combined trawl and Wegener ring data were used separately in these procedures. Dendrograms for site and species dissimilarity (community analyses) were constructed and cross-tabulated in a two-way coincidence table.

All nekton were preserved in 10% buffered Formalin\(^\text{a} \) Standard length (SL, carapace width for blue crabs) was recorded for all taxa. Up to 30 individuals/species were measured from each collection, subsampling for lengths was employed when sorted collections contained more than 30 individuals of a given species. Prior to each collection, temperature and salinity were recorded with an immersion thermometer and a temperature-compensated refractometer.

RESULTS

Abundance and Seasonality

Only two species—spot and the bay anchovy, *Anchoa mitchelli*—comprised >90% of the total number of individuals captured at Blevins Creek and adjacent shoals. Using this same criterion, upstream densities were more equitably distributed with four species in the creek and six on the shoal sharing dominance (Table 1). Blue crabs; white perch, *Morone americana*; and the hogchoker, *Trinectes maculatus*, were in this group in Gaolders Creek, while in late summer and fall the Atlantic croaker, *Micropogonias undulatus*, and the weakfish, *Cynoscion regalis*, were also abundant at the shoal station (Table 1).

Species richness (\( S \)) was also greater in all months in the Gaolders Creek system compared with the polyhaline Blevins Creek (Fig. 2) and was significantly greater for the entire study period (Wilcoxon sign-ranks test; \( P < 0.05 \)). No apparent trend, however, was evident in the number of individuals captured at each locality (Fig. 2), except that peak catches of two dominant species, spot and bay anchovy, were greater in Blevins Creek and resulted in the large disparity in catches in

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\( ^\text{a} \)Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.
May and July. Except for the spike seen in Figure 2, resultant from a large influx of bay anchovy into Blevins Creek in July, combined catches of all other taxa were at a minimum for the summer months (June-August) coincident with peak summer temperatures.

Seasonal abundance of the more common species was typically associated with recruitment of young-of-year individuals into the tidal creeks and adjacent shoals. Young spot dominated in both creeks but were subsequently replaced by postlarval and juvenile bay anchovy (July), and thereafter at Goalders Creek by hogchoker (August), weakfish (August-September), and Atlantic croaker (October). In addition, white catfish, *Ictalurus catus*, and white perch were frequently captured in the Goalders Creek vicinity during early spring when salinities were at their lowest recorded levels. Because of the overall seasonal abundance, it was possible to examine spatial and temporal distributions of spot in greater detail (Fig. 3, Table 2). As expected, spot were more abundant outside of the creeks very early in recruitment; but by June had established a greater degree of residency within the creeks compared with the adjacent shoals. This pattern of large creek to shoal abundance ratios (Fig. 3) continued (with a single exception) until October when spot emerged from Blevins Creek. Note, however, that at the termination of the sampling program, this emigration had not taken place upstream. Similar

### TABLE 1.—Pooled species abundance and percent composition for all trawl collections, York River estuary, Va.

<table>
<thead>
<tr>
<th>Species</th>
<th>Goalders Creek upstream</th>
<th>Goalders Creek downstream</th>
<th>Goalders Creek shoal</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Leiostomus xanthurus</em></td>
<td>709 170.69</td>
<td>1,646 160.09</td>
<td>1,439 150.31</td>
</tr>
<tr>
<td><em>Anchoa mitchilli</em></td>
<td>83 18.26</td>
<td>385 114.05</td>
<td>412 14.40</td>
</tr>
<tr>
<td><em>Callinecetes sapidus</em></td>
<td>69 16.88</td>
<td>373 113.62</td>
<td>310 10.84</td>
</tr>
<tr>
<td><em>Morone americana</em></td>
<td>48 14.79</td>
<td>144 15.26</td>
<td>308 10.77</td>
</tr>
<tr>
<td><em>Alosa aleutensis</em></td>
<td>35 3.49</td>
<td>75 2.74</td>
<td>91 3.18</td>
</tr>
<tr>
<td><em>Morone saxatilis</em></td>
<td>27 2.69</td>
<td>57 2.08</td>
<td>77 2.69</td>
</tr>
<tr>
<td><em>Ictiurus catus</em></td>
<td>25 2.49</td>
<td>17 0.62</td>
<td>59 2.06</td>
</tr>
<tr>
<td><em>Brevoorta tyrannis</em></td>
<td>3 0.30</td>
<td>16 0.58</td>
<td>57 1.99</td>
</tr>
<tr>
<td><em>Pomatomus saltatrix</em></td>
<td>1 0.10</td>
<td>8 0.29</td>
<td>33 1.15</td>
</tr>
<tr>
<td><em>Peprilus a/epidotus</em></td>
<td>1 0.10</td>
<td>3 0.11</td>
<td>28 0.98</td>
</tr>
<tr>
<td><em>Anguilla rostrata</em></td>
<td>1 0.10</td>
<td>1 0.11</td>
<td>13 0.45</td>
</tr>
<tr>
<td><em>Trinectes maculatus</em></td>
<td>1 0.10</td>
<td>3 0.11</td>
<td>12 0.42</td>
</tr>
<tr>
<td>Total</td>
<td>1,003 100.00</td>
<td>2,797 100.00</td>
<td>2,630 100.00</td>
</tr>
</tbody>
</table>

*Species comprising >90% of the total number of individuals.*

### TABLE 2.—Relative abundance of *Leiostomus xanthurus* at tidal creek stations, York River estuary.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Goalders Creek</td>
<td>Upstream</td>
<td>0</td>
<td>1</td>
<td>401</td>
<td>85</td>
<td>51</td>
<td>58</td>
<td>68</td>
</tr>
<tr>
<td></td>
<td>Downstream</td>
<td>0</td>
<td>52</td>
<td>624</td>
<td>318</td>
<td>236</td>
<td>172</td>
<td>93</td>
</tr>
<tr>
<td>Blevins Creek</td>
<td>Upstream</td>
<td>0</td>
<td>19</td>
<td>493</td>
<td>326</td>
<td>262</td>
<td>60</td>
<td>105</td>
</tr>
<tr>
<td></td>
<td>Downstream</td>
<td>0</td>
<td>18</td>
<td>586</td>
<td>337</td>
<td>102</td>
<td>150</td>
<td>221</td>
</tr>
</tbody>
</table>
patterns of earlier downstream emigration were observed during 1976-78 in the Cape Fear estuary, N.C. (Weinstein and Walters 1981; Weinstein pers. obs.), the cause of which remains unexplained. It is evident from Table 2 that spot may have been more restricted in their upstream movement in Goalders Creek where salinities averaged about 2% lower at the upstream station than at the creek mouth. The ratio of upstream to downstream station catch was twice as high at Blevins Creek, supporting this pattern. Other species which seem to prefer a specific portion of the tidal creek to shoal habitat gradient included hogchoker, weakfish, and Atlantic croaker which had creek-to-shoal ratios (over all months) of 0.13, 0.10, and 0.02, respectively. Moreover, these species were far more abundant at upstream sites (Table 1).

Community Composition

A two-way coincidence table, using a similarity value of 0.200 to define clusters (Clifford and Stephenson 1975), was constructed in order to summarize species and site relationships for pooled monthly collections at each station (Table 3). Included in this analysis are samples collected with the Wegener ring, a gear which was expected to be more successful in collecting both cryptic species (e.g., Gobiidae) and shore-zone taxa (e.g., cyprinodonts [Cyprinodontidae] and silverside [Atherinidae]). It should be pointed out, however, that any comparisons between the Wegener ring and trawl samples are qualitative since no attempt was made to compare gear selectivity, efficiency, and area encompassed by a unit effort for each sampling device (Weinstein and Brooks 1983).

Species group IV (Table 3) was generally the most ubiquitously distributed assemblage over the range of environmental factors (particularly...
TABLE 3.—Two-way coincidence table comparing stations (Groups A-D) and species (groups I-VI) associations at York River estuary sites. Clustering by unweighted-pair group-average; similarity index = Canberra metric, all data log_{10}(x + 1) transformed, single station occurrences dropped. G = Goalders Creek, B = Blevins Creek, U = upstream, D = downstream, S = shoal stations, W = Wegener ring samples.

<table>
<thead>
<tr>
<th>Group</th>
<th>Species</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
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</thead>
<tbody>
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<td>I</td>
<td>Paralichthys dentatus</td>
<td>3</td>
<td>12</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Micropogonias undulatus</td>
<td>3</td>
<td>91</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Opsanus tau</td>
<td>3</td>
<td>26</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Anchoa hector</td>
<td>3</td>
<td>26</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Gymnosomia regalis</td>
<td>16</td>
<td>77</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Syngnathus tuscus</td>
<td></td>
<td>1</td>
<td>2</td>
<td></td>
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<tr>
<td>II</td>
<td>Pomatomus saltatrix</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Peprilus alepidotus</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Anguilla rostrata</td>
<td>1</td>
<td>1</td>
<td>8</td>
<td></td>
</tr>
<tr>
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<td>Morone saxatilis</td>
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<td>8</td>
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<td>Brevoria tyvanus</td>
<td>3</td>
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<td>1</td>
<td>23</td>
</tr>
<tr>
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<td>3</td>
<td></td>
<td>1</td>
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<td>Fundulus heteroclitus</td>
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<td>1</td>
<td>3</td>
<td>23</td>
</tr>
<tr>
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<td>Menidia beryllina</td>
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<td>6</td>
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<td></td>
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<td>48</td>
<td>57</td>
<td>57</td>
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</tr>
<tr>
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<td>Leiostomus xanthinus</td>
<td>709</td>
<td>1,646</td>
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<td>1,301</td>
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<td></td>
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<td>39</td>
<td>373</td>
<td>310</td>
<td>1,248</td>
</tr>
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<td></td>
<td>Trinectes maculatus</td>
<td>1</td>
<td>385</td>
<td>1,439</td>
<td>35</td>
</tr>
<tr>
<td></td>
<td>Callinectes sapidus</td>
<td>83</td>
<td>144</td>
<td>308</td>
<td>1,248</td>
</tr>
<tr>
<td></td>
<td>Gobiosoma bosci</td>
<td>1</td>
<td>3</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Menidia menidia</td>
<td>17</td>
<td>5</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>V</td>
<td>Fundulus majalis</td>
<td></td>
<td>2</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>VI</td>
<td>Microgobius thalassinus</td>
<td></td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
</tbody>
</table>

salinity) examined. Nonetheless, within this group were several species which displayed area-specific distributions, in either relative numbers or presence/absence in a given creek system. Examples of the former include the hogchoker and bay anchovy and of the latter, white perch, which was far more prevalent upstream. The Goalders Creek nekton community was also dominated by members of groups I and II, whose members were rare or absent at downstream localities. Remaining species were generally not captured in sufficient numbers to depict their role in defining community structure in each area.

Trophic Analysis

Six species (Fig. 4) were sufficiently abundant in time and space to allow a comparative trophic analysis to be undertaken. Collectively, they exceeded 98% of the total number of individuals captured during this study. Prey taxa were defined on the basis of 39 categories (Table 4). All but two—miscellaneous (MISC) and unidentified (UID)—were mutually exclusive. These two did not exceed 17% of the total diet composition of any one species and were generally much lower than this amount. The dietary relationships of these six species are summarized across all sampling strata by the dendrograms appearing in Figure 4. With the exception of summer flounder, Paralichthys dentatus, sufficient numbers of individuals were captured to also allow partitioning by size classes. Such ontogenetic summaries are shown in Figure 5.

Although more than 2,600 specimens were examined for diet composition, sample sizes were not sufficient in the first year of the study to examine details of seasonal or spatial food utilization in all species except spot (O'Neil 1983). In addition, several species were only abundant in a restricted area (Table 1) or attained peak abundance in a relatively narrow time frame, precluding dietary comparison of dominant species (Fig. 6).

Diet overlap was greatest between white perch and hogchoker (Fig. 4). Dietary items shared by these species included clam siphons, Leoptochirus plumulosus, and other gammarid amphipods. Both predators were generally habitat-specific, with young-of-year white perch more abundant in the creeks and hogchoker prevalent on the river shoals (Table 1). Largely because of fish (TEL) included in the diet of larger individuals, white catfish displayed somewhat less overlap in its diet compared with the former species, but because of its partial piscivorous habits shared this similarity with the major fish predator captured in our trawl samples—the summer flounder. Both small summer flounder and white perch (<61 mm) also consumed substantial quantities of the mysid shrimp Neomysis americana.
Among the six species examined, spot and bay anchovy displayed the least dietary overlap, with the former exhibiting the greatest dietary diversity (consisting mainly of benthic prey items), and the latter including a greater percentage of planktonic food items in its diet. However, the large variety of prey items consumed by all species indicates that each is a trophic opportunist (Darnell 1958, 1961; Carr and Adams 1973; Sheridan and Livingston 1979; Livingston 1982).

Ontogenetic shifts in diet were evident for each of the species examined (Fig. 5). In spot, dietary importance of calanoid copepods declined in fish >20 mm SL, while harpacticoid copepods increased in importance in fish 21-80 mm SL. Concurrently, the percentage of various polychaetes and gammarid amphipods slowly increased in their diet. Nematodes also became less important with increasing size. Interestingly, spot stomachs at all sizes contained clam siphons and maldanid tails, indicating that specific parts of larger prey were important dietary items.

Ostracods and crab zoea were abundant food items for small (<21 mm SL) bay anchovy; larger
FIGURE 5.—Ontogenetic comparisons in diet among the five most dominant species captured in this study. Sample size (stomachs with food) appear below histograms, size increment (standard length) above. Prey designations are defined in Table 4.
individuals incorporated more *Neomysis americana*, calanoid copepods, and gammaridean amphipods into their diet. In hogchokers, however, gammarids predominated in smaller individuals, <61 mm SL, but with increasing size became somewhat less important and were replaced by nereid polychaetes and clam siphons. Hogchokers had the highest proportion of unidentified remains (UID) of any predator examined due to the high level of maceration characteristic of this species.

*Neomysis americana* was clearly the dominant prey item of small (<60 mm SL) white perch, but became less important in the diets of larger individuals which fed increasingly on gammarid amphipods and clam siphons. White catfish <120 mm SL also fed conspicuously on amphipods but, uniquely among the predators examined, also fed upon xanthid crabs, and at larger sizes incorporated a substantial proportion of fishes into their diet.

Relative fullness indices displayed varying trends on a species-specific basis (Table 5). Values declined in the later part of the study for white perch and white catfish, whereas no apparent trends were observed for other species.

### DISCUSSION

#### Species Composition and Abundance

Along with other recent studies of shallow-water nekton (Orth and Heck 1980; Weinstein and Brooks 1983; Heck and Thoman 1984), the present effort provides additional information on the use of inshore habitats of the lower Chesapeake Bay. A striking characteristic of the marsh nekton community in the lower Chesapeake Bay is the generally low diversity of the constituent fauna and the high level of dominance of only a few species. On both the eastern shore of Virginia (Delmarva Peninsula) (Weinstein and Brooks 1983) and in the
York River estuary, no more than two species comprised >90% of the total number of individuals captured at polyhaline tidal creek stations. On the average, spot comprised 71.8% of this total. Only in the oligomesohaline Goulders Creek was species dominance shared by more than two species (Table 1), but once again, spot predominated with 65.4% of the total. By comparison, Hackney et al. (1976) reported a mean of seven species totaling >90.0% at four trawl stations in their study of a mesopolyhaline tidal creek in Georgia, while in several studies in South and North Carolina (Cain and Dean 1976; Bozeman and Dean 1980; Weinstein et al. 1980) three to nine species (\( \bar{x} = 7 \)) comprised this total. Species richness was significantly greater in Goulders Creek than in the polyhaline Blevins Creek system. This is somewhat surprising since previous studies have often shown that diversity decreases for both fishes and invertebrates in the upstream direction (Dahlberg 1972; Boesch 1977; Gainey and Greenberg 1977; Weinstein et al. 1980). The absence or scarcity of stenohaline marine species derived largely from the seasonally abundant southern Carolinian ichthyofauna may partially explain this difference in the York River estuary. In North Carolina, for example, these taxa increased species richness in polyhaline tidal creeks, especially near the estuary mouth (Weinstein 1979; Weinstein et al. 1980). Also present in estuaries below the Chesapeake Bay are species with warm-temperate affinities which share dominance with spot and bay anchovy, including Mugil cephalus, M. curema, Lagodon rhomboides, Paralichthys lethostigma, Bairdiella chrysura, and the brown shrimp, Penaeus aztecus. These species are much less common in the Chesapeake Bay.

Another noteworthy finding is that species replacement does not occur from regional and northerly taxa. For example, Ophidion marginata, Stenotomus chrysops, Urophysis regia, and Centropristis striata were only rarely encountered in our studies (Weinstein and Brooks 1983). In the present investigation, these species were restricted to shoal stations outside of the tidal creek mouths (Table 1). Thus, there appears to be an underutilization of shallow nursery habitats by transient marine fishes in the Chesapeake Bay compared with the lower latitude estuaries (for more detailed discussion see Weinstein and Brooks 1983 and Heck and Thoman 1984). This difference is perhaps due partly to the unique location of the Chesapeake Bay in the transition zone between faunal provinces (Briggs 1974) with neither taxonomic group able to adapt fully to conditions (primarily temperature regimes and their variance?) associated with this transition zone. The recent geological and evolutionary history of northern estuaries, including the Chesapeake Bay (Shubel and Hirschberg 1978), may also play a role in determining the degree of estuarine dependency of local faunas.

A unique aspect of this study was the opportunity to compare utilization of the tidal creeks with adjacent shoal areas. Previously, these comparisons had to be made among collections with different gears (and their associated selectivity and efficiency) or in different years or by different investigators (Chao and Musick 1977; Markle 1976). The results for spot are of interest because of the general dominance of this species in many estuaries along the Atlantic and Gulf coasts.

Recently, Weinstein and Walters (1981), Weinstein and Brooks (1983), and Weinstein (1983) described the importance of marshes, specifically tidal creeks, to this species and the relationship between productivity and energy export via several fish vectors—from the marshes ultimately to the marine environment (Weinstein 1981). Spot were recruited into upstream marshes of the York River estuary earlier than to downriver sites and tended to remain there longer (Fig. 3). Once recruited into the marshes (by June) spot reside here until fall, when they emigrated into deeper water, and finally (for most individuals) return to the marine environment. As expected, however, there is an upstream limit to utilization in oligohaline tidal creeks where we found densities of spot decreased (Table 2) as salinities became more variable (approaching 0%) and where temperature regimes became more unstable (Hackney et al. 1976). Whether the lower abundance of spot outside of the creeks is due to differential mortality and/or habitat selection remains unknown. Other taxa, e.g., young-of-year Atlantic croaker, weakfish, and hogchoker, apparently prefer the shoals and generally deeper water. There is little question that they are more abundant outside of the marshes (Chao and Musick 1977; Orth and Heck 1980; Weinstein and Brooks 1983; Middleton, unpubl. data). If, as many would argue, predation is a major regulator of local abundance and ultimately community structure, what protection would the homogenous, relatively unstructured shoals and flats afford these species? Considering the apparent physical and behavioral similarities, as well as recruitment dynamics between spot and Atlantic croaker, there does not seem to be any
significant adaptive feature of the latter that would provide better survivorship in open waters (at least with regard to predation). Just how this species and others minimize the effects of predation in open waters is an important research question for the future.

Trophic Comparisons

The six species examined in detail are clearly trophic opportunists and overlap in many food categories. In addition, each goes through distinct ontogenetic stages in feeding which include significant shifts in the portions of the water column searched. The prey taxa have been categorized by Darnell (1961), Qasim (1972), and Chao and Musick (1977) according to their vertical occurrence in the water column from open waters to the bottom: fishes, macrozooplankton (e.g., Neomysis americana), microzooplankton (e.g., calanoid copepods), epibenthos (e.g., harpacticoid copepods), infauna, and organic matter. At sizes <21 mm SL all five of the species examined apparently spent considerable periods foraging in the water column. Between 21 and 40 mm SL several species continued to feed on "pelagic" prey, although by this size the transition to benthic feeding was nearly complete in spot and hogchoker.

Whether resource partitioning or dietary specialization (Chao and Musick 1977) occurs in these taxa as a means of reducing interspecific interactions is a matter of speculation. Without question, there are differences in feeding localities of the fishes examined—e.g., white perch and white catfish are generally restricted to oligohaline habitats, while Atlantic croaker and hogchoker are more abundant on the shoals. Also noted are differences in seasonal abundance (Fig. 6), size related feeding distributions reflecting ontogenetic shifts (Fig. 5), morphological differences among predators (Chao and Musick 1977), etc. But whether or not any of these traits reflect past or present competitive pressures remains unknown. Food that is generally limiting for several of these species and others is currently an area of controversy. Currin et al. (in press) have suggested that predation, not resources, limits production rates of spot and Atlantic croaker in shallow marsh embayments in Albermarle Sound, N.C. In contrast, Weisberg and Lotrich (1980) found that growth rates of the mummichog, Fundulus heteroclitus, could be altered by manipulating fish density. Increased growth rates were also demonstrated with food enrichment experiments in sub-tidal areas. Similar findings were reported by Miklas and Reed (in press) for F. heteroclitus populations in a tidal tributary of the Rhode River, Del. Our own findings of a seasonal decline in relative fullness index values in several species, along with a parallel decline in benthic biomass (T. Fredette6), tend to support the possibility of periodic food scarcity.

Trophic opportunism has often been cited in studies of estuarine fishes (Darnell 1958, 1961; Livingston 1982). Several investigators have pointed to the importance of omnivorous and ontogenetic progressions in feeding stages (Sheridan 1979; Stoner 1980; Livingston 1982) as obscuring distinct trophic relationships in nektonic food webs. Along with these difficulties are problems associated with the "snapshot" view often gained of the system. Numerically abundant species are likely to play the major role in conversion and production of organic materials in estuaries (and are, therefore, mainly responsible for the construct of food webs and energy flow therein), yet the identification of these species often comes from the sampling program itself.

Thus, although the dominant species in this study, spot, is undoubtedly important in this regard, the selective nature of our sampling effort does not allow us to place this importance in proper perspective. It is probable that dominance, expressed in numbers and/or biomass of those species captured in this study, is shared and sometimes surpassed by other local species not sampled quantitatively by this program. These include young-of-year bluefish, Pomatomus saltatrix; various cyprinodonts, especially F. heteroclitus; anchovies; and silversides. On an estuary-wide basis, we also do not completely "track" species distributions in time and space (Purvis 1976) so that our already distorted view of local habitats cannot easily be extrapolated to system-wide considerations. Such difficulties occur in most studies and must be recognized and eventually accounted for in considerations of fish community ecology in estuaries.

SUMMARY

Tidal creeks of the York River estuary were characterized by distinct nekton communities displaying low diversity and dominated by relatively

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few taxa. Of the many transient marine species (Weinstein 1979; Weinstein et al. 1980) that utilize marsh creeks along the Atlantic coast, only the spot, *Leiostomus xanthurus*, seemed to actively select this habitat. Within creeks there also was an apparent upstream limit in abundance of this species at low salinities. Although not captured quantitatively in this study, Atlantic menhaden, *Brevoortia tyrannus*, were often observed in large numbers in the creeks, especially upstream. Other species, particularly Atlantic croaker, weakfish, and hogchoker were captured in greater numbers in low salinity shoal waters (<5 m) adjacent to the species mentioned above, white perch; striped bass, *Morone saxatilis*; and white catfish were seasonally present as young-of-year in the area.

Dietary composition of the six species examined in detail reflected that of trophic opportunism, with maximum dietary diversity displayed by spot. Ontogenetic progressions in diet also were observed in all species. Two species, summer flounder and white catfish, were piscivorous at larger sizes, feeding mainly on *Anchoa* spp. The apparent absence of specialization in any of these predators may reflect the general adequacy of food supplies in the primary nurseries.

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