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Utilization Of Marsh And Seagrass Habitats By Early Stages Of Callinectes-aapidus - A Latitudinal Perspective

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UTILIZATION OF MARSH AND SEAGRASS HABITATS BY EARLY STAGES OF CALLINECTES SAPIDUS: A LATITUDINAL PERSPECTIVE

Robert J. Orth and Jacques van Montfrans

ABSTRACT

Seagrass beds and marshes have been identified as important nurseries for the blue crab, Callinectes sapidus. This nursery paradigm is based on blue crab abundance data from trawl, seine and drop-net sampling that has revealed greater abundances in these habitats than in adjacent unvegetated areas. Recently, more quantitative and intensive sampling in seagrass beds and marshes over broad latitudinal scales, combined with manipulative experiments, indicate that the same habitat may vary in utilization on regional scales. Mechanisms accounting for enhanced abundances in these nursery habitats have not been elucidated from a latitudinal perspective. Regional comparisons of blue crab catch data regressed on habitat area were not significant whereas similar comparisons within the Gulf region showed a significant positive relationship of crab harvest with total vegetated area. Thus, the quantity of habitat may be important over small latitudinal scales but other factors could affect population abundances across broad latitudinal distances. Latitudinal differences in habitat use may result from alternate modes of settlement via megalopae or recruitment by juveniles, active or passive habitat selection, post-settlement mortality and food quality and quantity. Tidal regimes and coastal morphology in relation to physical processes may influence the accessibility of important habitats by settling or recruiting individuals and thus be equally important. These factors are reviewed in an attempt to understand regional differences in the patterns of C. sapidus abundance.

Marshes and seagrasses support dense assemblages of both vertebrate and invertebrate species (Orth et al., 1984b). These wetland habitats vary in areal coverage and configuration, are found at different depths, and are influenced by varying tidal regimes, depending on latitude. Wetlands are reported nursery areas for several species of commercial significance, e.g., penaeid shrimp, Penaeus spp., and blue crabs, Callinectes sapidus (Boesch and Turner, 1984; Heck and Thoman, 1984; Zimmerman and Minello, 1984; Zimmerman et al., 1984; Coles and Long, 1985; Staples et al., 1985; Turner and Boesch, 1988). Yet, the degree to which wetland habitats contribute to the overall abundance of commercial species remains speculative (Nixon, 1980).

This paper focuses on the blue crab, C. sapidus, which occurs over a wide range of estuarine, coastal and lagoonal habitats from Cape Cod, Massachusetts, to the Caribbean. It is both ecologically significant (Virnstein, 1977) and commercially important in the United States from the mid-Atlantic to the Gulf coast (Fig. 1) (Williams, 1974; Perry, 1984).

The marsh and seagrass nursery paradigm proposed for C. sapidus has been based principally on abundance data from trawl and seine surveys (Heck and Orth, 1980; Weinstein and Brooks, 1983; Heck and Thoman, 1984). More recently, quantitative drop net sampling (Zimmerman and Minello, 1984; Orth and van Montfrans, 1987; Thomas et al., in press; Wilson et al., in press) revealed greater abundances of early crab stages than was previously reported. These studies and manipulative experimental research (Heck and Wilson, 1987; Wilson et al., 1987), conducted from New Jersey to Texas, indicate that vegetated habitats are characterized by higher overall abundances of blue crabs and lower predation rates than unvegetated habitats. Furthermore, a major proportion of the crabs in veg-
etated habitats are <20 mm in carapace width and utilize these habitats, especially seagrasses, in the winter. Significantly fewer crabs occur in New Jersey wetland habitats than in those in the Chesapeake Bay or Texas. Although greater densities occur in seagrass habitats than marsh creeks, the marsh surface in Texas supports greater densities than marsh creeks in Virginia and New Jersey.

The mechanisms which account for the increased abundances of juveniles in vegetated systems remain relatively unclear. We attempt to examine: 1) habitat area versus blue crab fisheries relationships; 2) factors influencing habitat utilization by blue crabs; and, 3) how these factors may vary latitudinally, and potentially explain observed abundance patterns.

**HABITAT AREA—FISHERIES PRODUCTION RELATIONSHIPS**

Evidence that the quantity of wetlands may contribute to stock size of particular species by providing food and refuge for early juvenile stages is accumulating (Boesch and Turner, 1984; Turner and Boesch, 1988). A significant, positive and linear relationship between penaeid shrimp yield and area of vegetated wetlands was found not only in the northern Gulf of Mexico (Turner, 1977) but also on a more global scale (Turner and Boesch, 1988). A positive relationship between commercial landings of estuarine-dependent species and the ratio of marsh to open water area was reported among major regions of the U.S. Atlantic and Gulf coasts, with the Chesapeake Bay having a substantially higher production per unit habitat area than other regions (Nixon, 1980). Although the data reported in these studies suggest that the penaeid shrimp population may be limited by the quantity of wetland habitats, similar data have not been shown for other commercial species.

We examined this relationship for the blue crab by comparing the average hard blue crab landings (1960–1980, all gear and seasons included) for four major reporting regions (Mid-Atlantic, Chesapeake Bay, South Atlantic and Gulf as...
Table 1. Salt marsh and seagrass coverage (hectares) by state. Wetland areas identified as containing salt tolerant vegetation (categorized as "salt marsh" or "non-fresh" in data reports or published papers) were used and listed in the totals above. Estimates for seagrass or submerged vegetation coverage in most states may be underestimated because of the lack of adequate mapping surveys.

<table>
<thead>
<tr>
<th>State</th>
<th>Salt Marsh</th>
<th>Seagrass</th>
</tr>
</thead>
<tbody>
<tr>
<td>New Jersey</td>
<td>83,989</td>
<td>12,624*</td>
</tr>
<tr>
<td>Delaware</td>
<td>26,183</td>
<td>0</td>
</tr>
<tr>
<td>Virginia-Maryland</td>
<td>145,813*3</td>
<td>17,353*11</td>
</tr>
<tr>
<td>North Carolina</td>
<td>64,291*4</td>
<td>80,972*12</td>
</tr>
<tr>
<td>South Carolina</td>
<td>149,580*</td>
<td>0</td>
</tr>
<tr>
<td>Georgia</td>
<td>151,538*</td>
<td>0</td>
</tr>
<tr>
<td>Florida-Atlantic Coast</td>
<td>38,826*</td>
<td>2,800*13</td>
</tr>
<tr>
<td>Florida-Gulf Coast*</td>
<td>137,455*7</td>
<td>913,700*13</td>
</tr>
<tr>
<td>Alabama</td>
<td>11,855*</td>
<td>12,300*13</td>
</tr>
<tr>
<td>Mississippi</td>
<td>24,919*</td>
<td>2,000*13</td>
</tr>
<tr>
<td>Louisiana</td>
<td>720,648*</td>
<td>4,100*13</td>
</tr>
<tr>
<td>Texas</td>
<td>174,899*</td>
<td>68,500*13</td>
</tr>
</tbody>
</table>

* Includes 34,540 hectares of mangroves listed in Perry, 1984. 1, Tiner, 1983a; 2, Tiner, 1983b; 3, Silberhorn, VIMS, pers. comm.; 4, Field et al., 1988; 5, Tiner, 1977; 6, Reyer et al., 1988; 7, Perry, 1984; 8, Rosch et al., 1987; 9, Pendleton, USF&WS, Slidell, LA, pers. comm.; 10, Macomber and Allen, 1979; 11, Orth et al., 1989 (Lower and Middle Chesapeake Bay + Chincoteague Bay); 12, Ferguson et al., 1988 and 13, Iverson and Bittaker, 1986.

Figure 2. Comparison of total salt marsh area for the four reporting regions versus hard blue crab landings (1960–1980 average). Data for 1981 through 1986 were not included in the analysis in this and subsequent figures because of significant changes in the reporting of landings data in the Maryland section of the Chesapeake Bay beginning in 1981.
identified by the National Marine Fisheries Service (NOAA: Fisheries of the United States, 1960–1980: Current fishery statistics) with total marsh (Fig. 2, Table 1), total seagrass (Fig. 3, Table 1) and total vegetated area. The Gulf coast contained the greatest abundance of both marsh and seagrass habitats. Seagrasses were absent from Delaware (including Delaware Bay), South Carolina and Georgia. There was no significant relationship between landings and habitat quantity (Fig. 4). Despite the small area of available habitat, the Chesapeake Bay had the highest landings relative to other regions. We realize that conclusions based on fishery dependent landings may be problematic because: 1) data were not standardized as catch per unit effort; 2) fishing pressure differs between regions and blue crabs may be under-exploited in some regions (Gulf and South Atlantic) where more lucrative species (shrimp and lobster) occur; and, 3) reporting variations occur between regions. Few standardized fisheries-independent data on such relationships are available for making further comparisons. However, it is likely that multiple factors affect the size of crab populations on such broad geographic scales rather than simply the quantity of nursery habitat.

We also examined landings and habitat relationships within the Gulf coast region assuming that the constraints on fisheries dependent data listed above...
would not vary as much within a region. We chose the Gulf region, both because of the large number of states that reported landings, and the potential for comparison with Turner’s (1977) conclusions on the relationship of vegetated habitat and shrimp landings in the northern Gulf of Mexico. Landings for blue crabs (averaged for the period of 1960–1980) were regressed on habitat area. The relationship was not significant for total marsh \( (r^2 = 0.478, P = 0.196) \) or total seagrass \( (r^2 = 0.365, P = 0.281) \) area but was significant for total vegetated area \( (r^2 = 0.943, P = 0.006, \text{Fig. 5}) \). These results are similar to Turner’s (1977) and are particularly interesting since Turner’s regression statistics were not significant until seagrass area in Florida was also included in the analysis.

These comparisons suggest that habitat quantity may be a good indicator of potential abundance within a region but such relationships are more complex between regions. Marshes and seagrass beds are undoubtedly important nursery areas for \( C. \text{sapidus} \) throughout its range. However, the utilization of structurally similar habitats may differ between latitudes, primarily because mechanisms affecting recruitment, settlement, and survival may vary. Habitat value will depend on the interaction of one or more of the following factors which, in addition to overall habitat quantity, will ultimately determine population abundances of blue crabs in a region: 1) proximity to and rate, duration and magnitude of larval supply; 2) post-larval settlement factors which may entail active behavior (i.e., response to chemical cues) or passive deposition; 3) frequency and duration of tidal inundation, and habitat accessibility; 4) physical factors, e.g., temperature, salinity and hydrodynamics; 5) quantity and quality of food; 6) architectural complexity, e.g., biomass, leaf area, and shoot density; and, 7) predation intensity resulting from the density and diversity of predators.

Below, we focus on each of these factors and finally attempt to integrate their effects on \( C. \text{sapidus} \) abundance throughout its range.

**Larval Supply Related Factors.**—The life cycle of the blue crab generally entails the migration of egg-bearing females to the seaward portions of estuaries or lagoons, release of zoeae and export from the estuary, zoeal development and metamorphosis to the megalopal stage on the nearshore continental shelf, and reinvasion of the estuary by megalopae (Perry, 1984; Sulkin, 1984; Sulkin and Epifanio, 1986; McConaugha, 1988). The seasonal duration of megalopal ingress
Figure 5. Relationship between hard blue crab landings (1960–1980 average) and total marsh (A), total seagrass (B) and total vegetated habitat (C) for the Gulf coast states (TX—Texas, LA—Louisiana, MS—Mississippi, AL—Alabama, FL—west coast Florida).
<table>
<thead>
<tr>
<th>Locality</th>
<th>Methods</th>
<th>Sampling frequency</th>
<th>Vertical distribution</th>
<th>Abundance and temporal patterns</th>
<th>Diel-tidal patterns</th>
</tr>
</thead>
<tbody>
<tr>
<td>Delaware</td>
<td>Clarke-Bumpus or neuston net, 0.24-mm mesh, surface/mid/bottom, day/night</td>
<td>weekly VI–IX/79; summer–fall cruises 1980–1981</td>
<td>greatest conc. in bottom although density shifts with stage of tide</td>
<td>1–2 m⁻³, Aug–Sept.</td>
<td>megalopae most common in water column on flooding tidal currents, suggesting a tidally related vertical migration abundant on flood tides, both day and night</td>
</tr>
<tr>
<td>Delaware</td>
<td>Pump sampler into Clarke-Bumpus net, 0.24-mm mesh, surface/bottom, day/night</td>
<td>every 2 h over 6 tidal cycles, IX/6–9/83</td>
<td>5 occurrences in bottom samples only</td>
<td>0.5–2 m⁻³</td>
<td></td>
</tr>
<tr>
<td>Canary Creek, near mouth of Delaware Bay, Meredith, 1982</td>
<td>Plankton net, 1.0-mm mesh, sampling integrates entire water column</td>
<td>Semi-monthly sampling during night time flood IX/76–IX/77 (Diel sampling in VI, VII &amp; VIII/76)</td>
<td>N/A</td>
<td>0–60 m⁻³, Max. density mid-Sept to mid-Octtober</td>
<td>much greater abundance on flood tides</td>
</tr>
<tr>
<td>Virginia</td>
<td>Clarke-Bumpus net, 0.24-mm mesh, surface/bottom, day only</td>
<td>monthly, I/68–XII/69</td>
<td>bottom, none in surface</td>
<td>0.4–0.9 m⁻³ Sept–Nov.</td>
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<tr>
<td>Chesapeake Bay and York River, Sandifer, 1972, 1975</td>
<td>Clarke-Bumpus and neuston net, epibenthic sled, 0.24-mm mesh, 5 depths from surface to bottom, day only</td>
<td>bi-weekly, VII/1/80–IX/30/80</td>
<td>surface at bay mouth and shelf, bottom in bay and river</td>
<td>0–345 m⁻³, 2% collected at inner bay stations</td>
<td></td>
</tr>
<tr>
<td>Virginia</td>
<td>Clarke-Bumpus and neuston net, epibenthic sled, 0.24-mm mesh, 5 depths from neuston to epibenthic</td>
<td>bay mouth IX/1983, river VII/1984, shelf VIII/1985, every 3 h for 72 h. One station each area</td>
<td>74% of all megalopae in neuston</td>
<td>max. density in ocean—345 m⁻³</td>
<td>greater conc. at surface during night</td>
</tr>
<tr>
<td>shelf, bay, York River, Johnson, 1982, 1985</td>
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<tr>
<td>Virginia</td>
<td>Clarke-Bumpus and neuston net, epibenthic sled, 0.24-mm mesh, 5 depths from neuston to epibenthic</td>
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<tr>
<td>York River, bay mouth, shelf, Maris, 1986</td>
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<tr>
<td>Locality</td>
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<tr>
<td>Virginia bay mouth and shelf,</td>
<td>Clarke-Bumpus and neuston net, epibenthic sled, 0.24-mm mesh, 5 depths from surface to bottom, day only</td>
<td>bi-weekly V/15/80 IX/30/80</td>
<td>not presented in paper</td>
<td>July–Sept. with 2 peaks (Abundance data not presented)</td>
<td>N/A</td>
</tr>
<tr>
<td>McConaugha et al., 1983</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Virginia Gloucester Point</td>
<td>stationary traps at surface for 24 h</td>
<td>daily, VII–XII in 85, 86,</td>
<td>N/A</td>
<td>0–50 trap$^{-1}$ all months peaks in Sept. through Nov. associated with full moon</td>
<td>N/A</td>
</tr>
<tr>
<td>55 km from bay mouth, van Montfrans et al., in press</td>
<td></td>
<td>87</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>North Carolina</td>
<td>plankton net, 1.0-mm mesh, surface/bottom at night</td>
<td>monthly to semi-monthly, new and full moon, 1957 to 1967</td>
<td>greatest conc. at surface</td>
<td>10’s–1,000’s 30 min tow, all year with peaks in late summer and fall</td>
<td>N/A</td>
</tr>
<tr>
<td>Pamlico River complex, Williams, 1971</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>South Carolina</td>
<td>stationary plankton nets, 0.5-mm mesh, day/night</td>
<td>weekly (night) to monthly (day/night) I/85–VI/84</td>
<td>N/A</td>
<td>0–3.9 m$^{-3}$ Feb and May to Dec. highest densities Sept. to Nov.</td>
<td>densities much greater on flood tide and at night</td>
</tr>
<tr>
<td>marsh creeks, ~10 km from ocean inlet, Olmi, 1986</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>South Carolina</td>
<td>plankton net 1.0-mm mesh surface/bottom day/night</td>
<td>biweekly, daytime II/86–VI/87, 6 night sampling periods</td>
<td>63–95% in daytime bottom samples</td>
<td>max. density of 0.3 m$^{-3}$ Peak ingress—Aug. to Nov. Smaller peak in March. Decreasing conc. upriver</td>
<td>densities greatest at surface at night, bottom during day</td>
</tr>
<tr>
<td>3 sites, 2, 24, and 38 Run from mouth of Charleston Harbor, Mense and Wenner, 1989</td>
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Table 2. Continued

<table>
<thead>
<tr>
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</tr>
</thead>
<tbody>
<tr>
<td>Florida</td>
<td>Clarke-Bumpus samplers, surface/bottom, day</td>
<td>monthly, I/61–XII/62</td>
<td>96% of megalopae in bottom samples</td>
<td>summer peaks, July–September, no densities given</td>
<td>N/A</td>
</tr>
<tr>
<td>St. Johns River, Tagatz, 1968</td>
<td>nekton net, 1.0-mm mesh, surface/bottom</td>
<td>monthly, VII/74–IX/79</td>
<td>equal distri. at surface and bottom</td>
<td>max. density of 2.5 m⁻³ March–December, peaks in spring–early summer and late summer–fall; greatest nos. at stations with lower salinities</td>
<td>largest catches taken on rising or peak tides</td>
</tr>
<tr>
<td>Mississippi coastal water, Stuck and Perry, 1981</td>
<td>plankton nets; 1.0-mm mesh; integrated entire water column, day</td>
<td>monthly to semi-monthly I/63–XI/65</td>
<td>N/A</td>
<td>0–25,553·6 min tow⁻¹; Jan–Nov; winter &amp; summer peaks</td>
<td>N/A</td>
</tr>
<tr>
<td>Texas major Gulf passes, More, 1969</td>
<td>stationary plankton net, 1.0-mm mesh, surface/bottom day/night</td>
<td>flood tide, 3 days/wk, I/68–VII/69</td>
<td>greatest conc. at surface</td>
<td>12–194 m⁻¹, all year with 3 peaks: early winter, late spring, fall</td>
<td>52% collected during daylight</td>
</tr>
<tr>
<td>Texas mouth of bayou, King, 1971</td>
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</table>
increases with decreasing latitude (Table 2), reflecting a longer period conducive for reproduction and larval development at lower latitudes. Megalopae can be transported long distances up an estuary (van Montfrans et al., in press; Mense and Wenner, 1989), and primary habitats into which settlement appears to occur are in marshes and seagrass beds (Zimmerman and Minello, 1984; Orth and van Montfrans, 1987; Mense and Wenner, 1989; Olmi et al., in press; Thomas et al., in press).

Habitats in close proximity to a supply source of competent recruits (i.e., mouths of estuaries or coastal lagoons) will be potentially more valuable as settlement sites than those far removed from the source. The abundance of recruiting post-larvae alone may determine the relative importance of a particular estuary or region. Mense and Wenner (1989) found the largest quantity of *C. sapidus* megalopae at a polyhaline marsh site (75% of total) compared to a mesohaline (23%) or oligohaline (2%) site. This pattern was similar for megalopal settlement on artificial substrates in the York River, Virginia, where abundance decreased with increasing distance from the river mouth (van Montfrans and Orth, unpubl. data). Staples and Vance (1987) found that the abundance of juvenile banana prawns, *Penaeus merguiensis*, was directly related to the magnitude of post-larval settlement in several Australian estuaries. The consistency in post-larval immigration appeared to be more important than the relative strength of an immigration pulse within a river.

If intense meteorological events (e.g., hurricanes, which increase non-tidal volume flux) occur when megalopae are reinvading estuaries, additional megalopae could be transported into an estuary (Goodrich et al., 1989) resulting in a strong year class. Matlock (1987) suggested that hurricanes may have been responsible for increased year-class strength of red drum, *Sciaenops ocellatus*, through above average transport of larvae from the Gulf of Mexico to estuarine nurseries. Non-local forcing at mouths of estuaries affected transport of larval fish through the inlets (Pietrafesa and Janowitz, 1988), and could similarly affect transport of megalopae.

The supply of megalopae which are competent to metamorphose will, in part, determine which habitats are colonized by post-larvae. Furthermore, the magnitude of settlement will be partially influenced by extreme meteorological events during periods of megalopal availability.

**Post-larval Settlement Factors.**—Larvae of many marine invertebrates exhibit preferences for specific substrates under static laboratory conditions (see Crisp, 1974; Butman, 1987, for reviews). Cues inducing settlement, i.e., a “change in venue from a planktonic to a benthic existence” (Butman, 1987, p. 116), may be either physical (e.g., sediment grain size or variations in surface characteristics, such as texture or degree of contouring), or chemical (e.g., organic molecules derived from biological substrates). Current debate centers on the relative role of active selection and passive deposition under more natural, turbulent flows in determining settlement patterns (Butman, 1986; 1987). Recently, Butman et al. (1988) demonstrated that larvae of a polychaete can actively select specific substrates under turbulent flow conditions, indicating that such selection establishes initial concentrations of settlers prior to post-settlement mortality influences. Similar data for decapod crustaceans are lacking.

Substrate choice experiments with megalopae and first stage crabs under static laboratory conditions demonstrated that megalopae prefer live seagrass, *Zostera marina*, over other substrates offered, while first stage crabs were associated more with live oysters and mud (van Montfrans and Orth, unpubl.). Such choice by
megalopae implies a chemically mediated or tactile mechanism. Pueruli and juvenile lobsters (both *Panulirus argus* and *Homarus americanus*) prefer living algal substrates (Marx and Herrnkind, 1985; Johns and Mann, 1987) suggesting a chemical attractant, although plant architecture is also an important component of habitat selection (Herrnkind and Butler, 1986) (see section below on plant architecture).

Physiological state may control the degree of choice a megalopa can exhibit. If a preferred habitat is not in close proximity when molting to the first stage crab becomes obligatory, settlement and metamorphosis could occur anywhere. Postponement of metamorphosis could improve the individual's chance of surviving by encountering a favorable habitat.

*Tidal Inundation and Habitat Accessibility.*—Tides affecting estuaries and coastal lagoons along the distributional range of *C. sapidus* are either semi-diurnal (Atlantic coast) or diurnal (Gulf coast, NOAA tide tables). Tidal amplitude, which would have the greatest effect on habitat availability, ranges from less than 1 meter in the Gulf coast states to greater than 2 m in Georgia and South Carolina with monthly and seasonal variations in these ranges (Hicks et al., 1983). Tidal periodicity coupled with tidal amplitude results in marshes being inundated for different lengths of time (e.g., up to 70% of the day for many northwest Gulf marshes, Zimmerman, pers. comm.). Prevailing seasonal wind patterns can affect tidal inundation and thus habitat availability. When periods of extended marsh inundation coincide with megalop ingress into nursery habitats such as in the Gulf coast region, these marshes may play a more important role in blue crab population dynamics than Atlantic coast marshes (Zimmerman and Minello, 1984; Mense and Wenner, 1989).

In contrast to marshes, seagrass beds along both the Atlantic and Gulf coast are not as affected by tides or winds, and generally remain continuously submerged. When seasonal, astronomical, or meteorological conditions result in marshes, such as those in Texas along the Gulf coast, being inundated for much longer periods, they are utilized similarly to seagrasses by juvenile blue crabs (Thomas et al., in press). In Chesapeake Bay, Virginia, along the Atlantic coast, marsh inundation is limited and crab abundances are at least an order of magnitude greater in seagrass beds (Orth and van Montfrans, 1987).

Vast tidal marshes or subtidal seagrass beds behind coastal barrier islands such as those in New Jersey, Virginia, North Carolina and Texas may not be as available to megalopae as similar habitats in large estuaries with wide ocean connections. These habitats are accessible via narrow, shallow channels only tens to hundreds of meters across which could restrict megalop transport. This contrasts with the Chesapeake Bay, which is approximately 30 km in width. The width, as well as the cross-sectional area of the opening, affects the volume flux of water passing into nursery areas, and may thus be an important consideration in regulating the number of recruiting megalopae entering estuarine nursery areas.

Some potential nursery areas may not be accessible to settling megalopae. Higher elevations which are infrequently flooded within a marsh system or have poor access may be less valuable as blue crab settlement habitat because of transport restrictions. The extent of fringing marsh in direct contact with open water of the appropriate salinity (Zimmerman and Minello, 1984) may determine the importance for recruiting blue crab, rather than total marsh area. Together, these factors may have a major influence on the local abundance of blue crabs and could, in part, explain latitudinal differences in crab abundance.
Physical Factors.—Shallow marsh and seagrass habitats experience large daily, seasonal and annual fluctuations in temperature and salinity. Temperatures often exceed 30°C in these habitats (Kneib, 1984b; Zimmerman and Minello, 1984) and may extend beyond the physiological limits of tolerance for *C. sapidus*. Adult blue crabs segregate by size and sex in different habitats, especially after reproduction (Van Engel, 1958; Hines et al., 1987). This may be physiologically controlled by salinity tolerance. Excessive rainfall can rapidly alter salinity levels in marsh creeks and adjacent habitats. However, little is known about the temperature and salinity tolerances of settling megalopae and early juveniles. Stranding of megalopae and early stage juveniles on marsh surfaces may result in death through thermal stress, desiccation, or increased predation. Temperature can also influence the length of the megalopausal stage (Costlow and Bookhout, 1959) and, thus, the duration of estuarine reinvasion or the distance of transport within the estuary (Sulkin and Van Heuvelen, 1986).

Hydrodynamics are affected by seagrasses and marshes which reduce current velocity (Fonseca et al., 1982) thereby increasing the deposition of fine, particulate material (Scoffin, 1970; Ward et al., 1984) and recruiting fauna associated with these habitats (Eckman, 1983; 1987; Fonseca and Fisher, 1986). Seagrass species have different friction values (Fonseca and Fisher, 1986) and even within a meadow, hydrodynamic gradients can exist that could result in differential post-larval settlement. Because megalopausal swimming speeds are low relative to most tidal currents (Luckenbach and Orth, unpublished data), active selection by megalopae may be limited to periods of reduced current velocity. Seagrass beds may have a filtering or shadow effect (Connell, 1985; Roughgarden et al., 1988) if the height of the water column is similar to the height of the vegetation. Alternatively, if water column height is large, such as during nighttime flood tides when megalopae are in surface layers (Epifanio et al., 1984; Mense and Wenner, 1989; Olmi, unpubl. data), megalopae may pass over a bed and not settle.

Thus, the value of a particular marsh as a settlement habitat may vary depending upon the presence or absence of adjacent seagrass beds. Hydrodynamics and tidal inundation may act in concert to determine the relative influence of structure on settlement and magnitude of year class strength.

Food Considerations.—Marshes and seagrass beds support dense concentrations of meiofaunal, macrofaunal and natant components (Kneib, 1984a; 1984b; Orth et al., 1984a) and are sites of high secondary production (Currin et al., 1984; Weinstein et al., 1984; Fredette and Diaz, 1986; Fredette et al., in press). Differential settlement by *C. sapidus* into various habitats could be related to both quantity and quality of food items. Although data on the effect of food on settlement are unavailable for *C. sapidus* post-larvae, studies on habitat selection by *Panulirus argus* pueruli and juveniles showed that pueruli settled in complex habitats regardless of food but that juveniles preferred food-rich complex habitats (Herrnkind and Butler, 1986).

Both diel and tidal differences in intertidal marsh habitats and submerged seagrass beds could affect food availability. Laughlin (1982) found no day–night differences in diet or in total food consumption by *C. sapidus* in subtidal habitats. However, a 24-hour study comparing feeding by larger *C. sapidus* (60–130 mm) in a marsh creek and seagrass bed in the lower Chesapeake Bay showed greater overall stomach fullness for crabs in the grassbed than for crabs in the marsh creek. Feeding was related to tidal cycle in the marsh creek, with guts being fullest at high tide and decreasing to lows just prior to the next high tide (Ryer, 1987).
Architectural Complexity.—Seagrass beds and marshes along the latitudinal range of *C. sapidus* are present in single species stands or complex, multi-species assemblages. The plant species forming these communities exhibit a variety of morphologies, biomass, density and patchiness. Vegetation may exist in clumps of various sizes and shapes interspersed with unvegetated zones. Such variation is important because of increased habitat complexity (Zimmerman et al., 1984) for settling and juvenile *C. sapidus*.

Associated with different architectural types are different amounts of food, refuge and living space. Predator–prey relationships are influenced by plant structure, habitat complexity, and behavioral characteristics and relative sizes of predators and prey (Main, 1985; 1987; Heck and Crowder, in press).

Bell and Westoby (1986a) suggest that architectural effects are secondary in determining initial abundances of fish species that settle from planktonic populations. They state that settlement is a random, stochastic event, and that initial densities are set by availability (i.e., supply) of settlers. Larvae do not discriminate among beds while settling, but rather choose sites they first encounter. Herrnkind and Butler (1986), however, showed that post-larval spiny lobsters, *P. argus*, use intricate algal architecture as a cue for settlement, while juveniles respond to both food and architecture when selecting habitats. The developmental state of post-larvae may play a key role in determining when and where settlement occurs, although few supportive data are available. The relationship between post-larval availability in the plankton, settlement in benthic habitats, and the role of structure in mediating this relationship may explain deviations from proposed models of increasing faunal abundance with increasing structural complexity of vegetation (Hicks, 1980; Orth et al., 1984a; Bell and Westoby, 1986a; 1986b; Bell et al., 1987; Lewis, 1987; Heck and Crowder, in press).

Predation Effects.—Marshes and seagrasses serve as important refuges from predation for many species of finfish and invertebrates. Experimental laboratory and field studies have shown increased prey survivorship in these habitats (Vince et al., 1976; van Dolah, 1978; Minello and Zimmerman, 1983; Orth et al., 1984b; and papers cited therein; Kneib, 1987; Heck and Wilson, 1987). Threshold or minimum plant density was required to significantly reduce predation (Nelson, 1979; Heck and Thoman, 1981; Savino and Stein, 1982; Gotceitas and Colgan, 1987; Wilson et al., 1987).

Predator diversity and respective predator densities must be considered in analyzing spatial and temporal patterns of blue crab abundance, especially along latitudinal gradients where diversity of predators increases with decreasing latitude (Bertness et al., 1981; Menge and Lubchenco, 1981). Heck and Wilson (1987) found higher predation rates on brachyuran crabs with decreasing latitude in seagrass habitats, but not in unvegetated areas. They suggested that predation rates in unstructured habitats may not be as dependent on predator diversity as they are in structured habitats.

Regional differences in *C. sapidus* abundance may be closely linked to predation on the early life history stages, especially post-larvae and early juveniles. Interregional differences in predator guilds may be important in determining post-settlement mortality rates. The sparid, *Lagodon rhomboides* (pinfish), and the haemulid, *Orthopristis chrysoptera* (pigfish), found throughout the Gulf coast and on the Atlantic coast from Florida to North Carolina, are major consumers of decapod crustaceans (Adams, 1976; Stoner, 1980; Stoner and Livingston, 1984). Absence
of *L. rhomboides* and similar predator types in the Chesapeake Bay has been suggested as one reason for the high densities of epifaunal isopods and amphipods in seagrass beds when compared to more southern areas (Ryer and Orth, 1987). This could be important in post-settlement survival of *C. sapidus*.

Predation rates vary tidally and seasonally both within and between latitudes. Intensity of predation is high in marsh creeks at ebb tide when both prey and predators are concentrated (Kneib, 1984a; 1987), and the refuge effect of structure is temporally unavailable. In contrast subtidal seagrass habitats should retain their refuge value throughout a tidal cycle. Gulf coast marsh surfaces, because of more continuous inundation than their Atlantic counterparts, may offer a more stable refuge to blue crabs. Seasonal movements of predators to deeper water related to declining fall temperatures, especially in the mid-Atlantic region, may result in increased survivorship of post-larvae since megalopal recruitment continues through late November (van Montfrans et al., in press).

Predation is an important element in structuring marine benthic communities and has a strong latitudinal component that could have a major role in determining blue crab post-settlement mortalities and thus population size.

**Conclusions**

We have reviewed several (though not all) factors likely to affect blue crab population size. Some are predictable and vary more between than within latitudes (e.g., predation, tidal inundation, duration of recruiting season). Other factors (e.g., meteorological, inlet geomorphology, food and habitat availability) are likely to vary as much within as between latitudes.

The relationship between vegetated (total marsh and seagrass) area and landings within the Gulf region emphasizes the importance of this habitat type for blue crabs. The lack of a similar relationship across latitudes stresses the potential importance of other factors. Marsh physiography, for example, may be unique to a region (e.g., reticulated marshes of Texas and Louisiana resulting from an interaction of various factors such as tidal amplitude and subsidence). Longer periods of tidal inundation experienced by Gulf coast marshes relative to Atlantic coast marshes (Zimmerman and Minello, 1984) during megalopal ingress may be a primary factor contributing to the greater importance of these habitats along the Gulf coast. This fact coupled with the greater overall abundance of both marshes and seagrass beds in the Gulf coast region would argue that blue crab population size should greatly exceed that of other areas. Although this may be the case, landings data (with their aforementioned limitations) do not support this contention. Additional effects of more intensive predation could negate the influence of greater habitat area on population size. Pre- and post-settlement mortality effects are largely unknown but likely have a major impact on blue crab abundance. Along the eastern seaboard, post-larval supply rates, habitat availability coupled with varying restrictions on megalopal transport (i.e., inlet size), and especially predation, may have a major influence on population size depending on latitude.

High blue crab abundance in the Chesapeake Bay may result from a combination of high supply rates via physical mechanisms for larval and post-larval population maintenance in nearby coastal waters, a non-restrictive entrance, somewhat lower predation rates relative to areas in more southerly latitudes, and the proximity of abundant seagrass nursery habitats to post-larvae. Delaware Bay has a non-restrictive entrance and similar transport mechanisms as the Chesapeake Bay to facilitate larval and post-larval reinvasion, but, in contrast to the Chesapeake Bay,
lacks seagrasses and is smaller in size. We expect these differences contribute to the substantially lower abundances of blue crabs in Delaware Bay relative to the Chesapeake Bay. Furthermore, we suggest that levels of blue crab population abundances in North Carolina, South Carolina and Georgia are strongly affected by the presence or absence of seagrass beds. North Carolina estuaries, which are characterized by extensive seagrass habitats associated with barrier island lagoonal systems should support considerably higher numbers of blue crabs than South Carolina and Georgia estuaries which lack seagrass beds and associated lagoons. We expect that blue crab abundance in the latter two states, which have relatively high tidal ranges and comparable marsh physiography, would be similar since populations appear to be regulated by similar factors. States such as North Carolina and New Jersey, which are latitudinally separated but have somewhat similar lagoonal-estuarine habitats, might exhibit differences in blue crab abundances due to other influences. For example, both North Carolina and New Jersey have an abundance of seagrass habitat behind a barrier island system. Although differences in the extent of available habitat occur, the longer duration of recruitment in North Carolina might also contribute to predicted higher blue crab abundances relative to New Jersey. Additionally, New Jersey approaches the northern range extent of *C. sapidus*, whereas North Carolina is more centrally located. Various physical constraints (particularly temperature) on the population near its northern range extent could negatively affect population size in New Jersey.

A critical assessment of relative adult population size for various regions will require concurrently collected fisheries independent data using standardized methods across regions. Comparisons of such data along with standardized and quantitative field surveys and experimental research on the distribution and abundance of planktonic and juvenile life history stages, physical transport processes, settlement and predation will allow more accurate insights into the regulation of blue crab population size in the future.

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