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Robert J. Orth
Virginia Institute of Marine Science

Jacques Van Montfrans
Virginia Institute of Marine Science

Romuald N. Lipcius
Virginia Institute of Marine Science

Karen S. Metcalf
Virginia Institute of Marine Science

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Utilization of Seagrass Habitat by the Blue Crab, *Callinectes sapidus* Rathbun, in Chesapeake Bay: A Review

ROBERT J. ORTH, JACQUES VAN MONTFRANS, ROMUALD N. LIPCIUS and KAREN S. METCALF
*School of Marine Science, Virginia Institute of Marine Science, College of William and Mary,
Gloucester Point, Virginia, 23062, USA*

Key words: Seagrass, habitat, blue crab, *Callinectes sapidus*, nursery

Abstract

Seagrasses are generally presumed to provide important habitats for numerous species of vertebrates and invertebrates, serving as a nursery, structure for attachment, or foraging area. However, few species appear directly dependent on seagrass, one notable exception being the bay scallop, *Argopecten irradians* Lamarck. Research in Chesapeake Bay on the abundant, and commercially exploitable blue crab, *Callinectes sapidus* Rathbun, over the last decade, focused on the relevance of seagrass habitat for the overall population. Our research has demonstrated: 1. higher densities of juvenile blue crabs in seagrass habitats compared to adjacent marsh and unvegetated areas, 2. seagrasses to be an important settlement habitat for recruiting post-larval blue crabs, and 3. mediated predator-prey interactions related to seagrass abundance and increasing crab size.

Our current research focuses on the importance of restored areas for blue crab survival and relevance of seagrass habitat baywide in the context of landscape distributional patterns and metapopulation dynamics. Our findings suggest that similar habitats may differentially affect the numerical abundance of juvenile blue crabs. Elucidating the mechanistic reasons for the value of seagrass habitat for blue crabs, one of the last remaining, viable commercial fisheries in Chesapeake Bay, will be crucial in developing strategies for protecting and restoring seagrass habitat in Chesapeake Bay.

INTRODUCTION

Seagrasses have long been recognized as important habitats for numerous species of invertebrates and vertebrates. Quantitative faunal studies reported more species and individuals in seagrass compared to adjacent unvegetated areas (Orth, Heck and van Montfrans, 1984). This richness, first described for eelgrass communities in European coastal waters by the Danish scientist Peterson (1918), led to the early hypothesis that eelgrass communities formed the base of the food web and the productive commercial fisheries in these areas. The pandemic decline of eelgrass in the North Atlantic in the 1930's (Rasmussen, 1973) resulted in dramatic reductions in the associated faunal communities but apparently did not result in significant changes in coastal fisheries. This led to the development of alternative hypotheses for the possible mechanisms that fueled the high finfish

production, with waning interest in seagrass habitats for almost half a century.

Seagrass beds are often cited as critical nursery grounds for some commercially exploitable species, e.g. the bay scallop, *Argopecten irradians* Lamarck, from the North Atlantic coast of the United States, and some penaeid shrimp species in Australia (Loneragan *et al.*, 1994; O'Brien, 1994). However, estimating the dependency of a particular species on seagrass is difficult for several reasons. Firstly, many seagrass associated species are found in other habitats (e.g. marshes), or in other geographical locations that do not contain seagrass. Secondly, commercial exploitation generally occurs outside the boundaries of the seagrass bed. The degree of dependence may also be a function of other biological or physical factors, unrelated to the presence of seagrass, e.g. meteorological processes that determine abundance of larval or post-larval recruits entering a nursery habitat, the location

of critical seagrass area, or other critical nursery area in relation to larval supply (Roughgarden, Gaines and Possingham, 1988).

Our research in Chesapeake Bay focuses on the relevance of seagrass habitat for the abundant, and commercially exploited blue crab, *Callinectes sapidus*. Despite oceanographic discontinuities at biogeographical boundaries, varying climatic regimes, and a diversity of estuarine habitats, this species is distributed across a wide geographic range from Maine in the northwestern Atlantic throughout the Gulf of Mexico and Caribbean to northern Argentina (Williams, 1984). Blue crabs are commercially important from the mid-Atlantic to the Gulf Coast, and the Chesapeake Bay region accounts for approximately 50% of the total hard crab catch in the United States.

Although wetland habitats have been regarded as critical for the support of many commercial fisheries (Boesch and Turner, 1984), our analysis of blue crab harvest data regressed on marsh and seagrass area did not find significant latitudinal trends with either habitat type (Fig. 1). However, within the Gulf Coast region, a significant ($r^2 = 0.943$, $P = 0.006$) relationship was evident with total vegetated area (Orth and van Montfrans, 1990). Despite Chesapeake Bay having a relatively small acreage of seagrass and marsh compared to other regions, we hypothesized that the

relatively higher blue crab abundance is, in part, related to the presence of seagrass in critical areas of Chesapeake Bay.

Seagrass Habitat in Chesapeake Bay

Chesapeake Bay contains numerous species of rooted, submersed macrophytes, including several exotic species, which have undergone sometimes dramatic fluctuations in distribution and abundance, during the past century (Orth and Moore, 1984; Orth, Batiuk and Nowak, 1995). Two species, *Zostera marina* L. (eelgrass) and *Ruppia maritima* L. *sensu lato* (widgeongrass), grow in the higher salinity regions of this estuary where recruitment and settlement of blue crab postlarvae occurs (see life history aspects below). Both species co-occur in shoal areas of the bay and its tributaries and are generally found in water depths of 2m or less (at mean low water - MLW) with greatest coverage in waters 1m or less. Typical depth distributions in Chesapeake Bay indicate that monospecific widgeongrass is found in the shallowest depths (<0.3 m MLW), mixed widgeongrass and eelgrass at intermediate depths (0.3-0.6 m MLW), and monospecific eelgrass at deeper depths (>0.6 m MLW) (Orth and Moore, 1988).

A baywide decline of all species in all sections of the bay was evident by the early 1970's and was correlated to deteriorating water quality related to

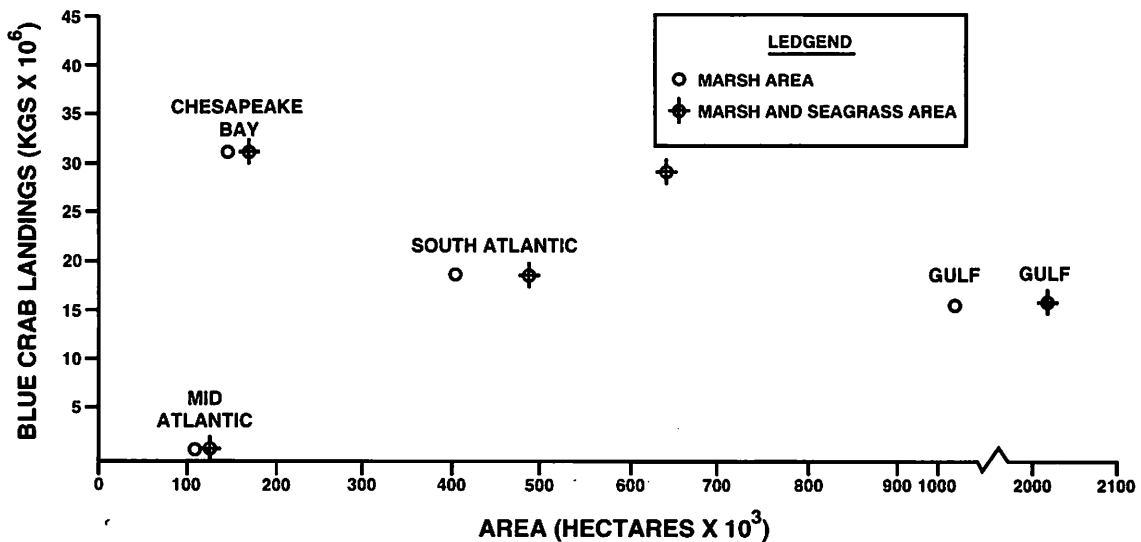


Figure 1: Relationship between hard blue crab landings and area of vegetated habitat for marsh area and marsh plus seagrass area for the four reporting regions (from Orth and van Montfrans, 1990).

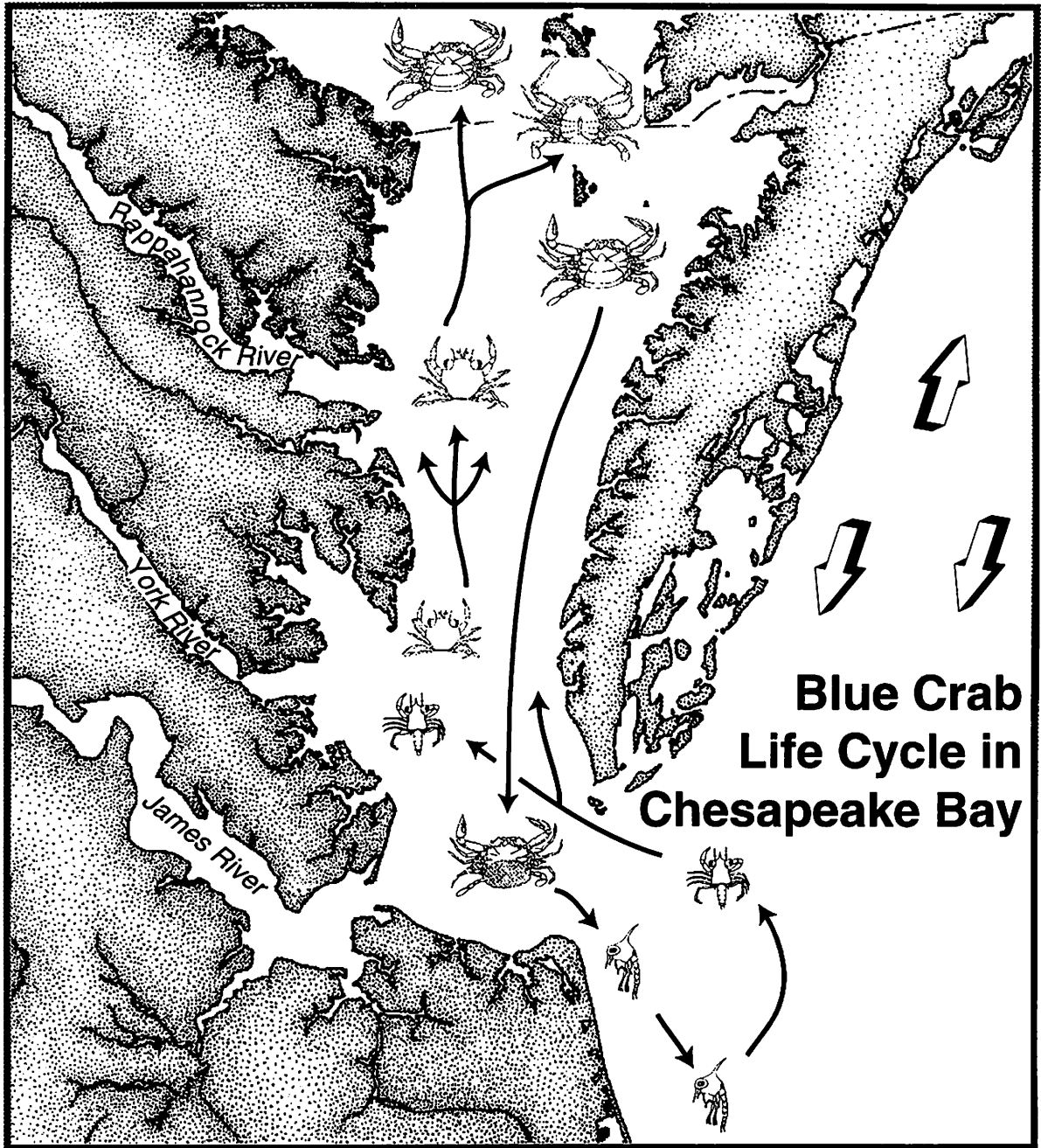


Figure 2: Life cycle of the blue crab in the Chesapeake Bay region (see text for details - arrows between blue crab life history stages, which are not to scale, indicate general movement within the bay and nearshore shelf region; large, open arrows indicate nearshore ocean circulation patterns).

anthropogenic inputs of nutrients and sediments (Orth and Moore, 1983; Kemp *et al.*, 1983). Declines were most evident in upbay, lower salinity regions, and the shoals of the major tributaries (James, York, Rappahannock, Potomac, and Patuxent rivers). Despite

some recovery over the last decade (Orth *et al.*, 1995), many areas previously vegetated remain devoid of vegetation. These areas include riverine and mid-bay shoal areas where eelgrass and widgeongrass once were abundant (Orth *et al.*, 1995) and undoubtedly served

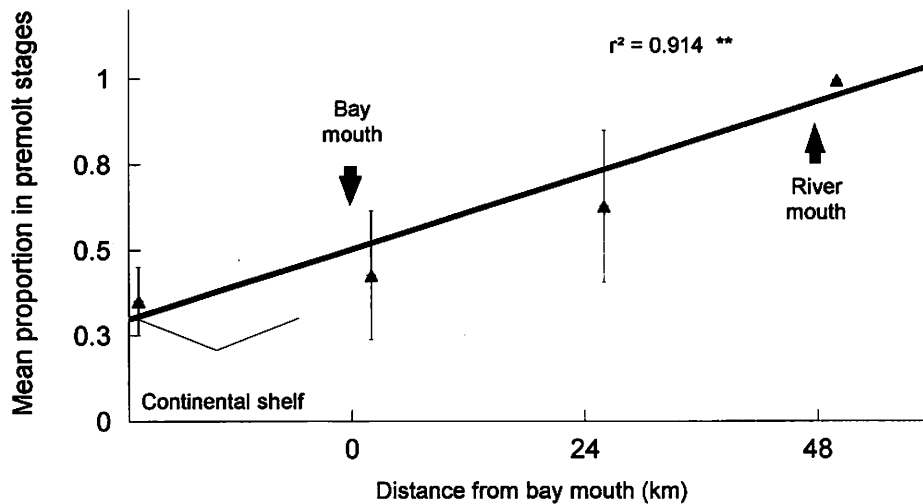


Figure 3: Mean proportion of blue crab megalopae collected in premolt versus distance from the mouth of Chesapeake Bay for a transect from the continental shelf to the mouth of the York River (from Metcalf and Lipcius, 1992).

as critical nursery areas for the early life history stages of the blue crab. An analysis of adult female abundance for the last four decades revealed significantly lower abundances over the last two decades compared to the previous two decades (Lipcius, unpubl. data) coinciding with this baywide submerged aquatic vegetation (SAV) decline.

Life History of the Blue Crab in Chesapeake Bay

The life cycle of the blue crab in Chesapeake Bay involves complex ontogenetic shifts in habitat use (Fig. 2). Following mating, ovigerous females move to the mouth of Chesapeake Bay where up to 8 million larvae (zoea) per individual are released on night-time ebb tides. Zoea are transported on ebb tides to offshore coastal waters where development through seven or eight larval stages lasts at least 30 days (Costlow and Bookhout, 1959; Provenzano *et al.*, 1983; McConaugha *et al.*, 1983). Zoeae are generally retained in the vicinity of the bay mouth against the general drift of shelf waters by wind-driven surface currents during the summer (Boicourt, 1982; Johnson, Hester and McConaugha, 1984). Metamorphosis to the postlarva (megalopa) stage, which reinvades the Chesapeake Bay, occurs on the inner shelf. Duration of the megalops is at least 15 days prior to metamorphosis into the first juvenile instar (Sulkin and Van Heukelem, 1986). Thus, overall development through the dispersive larval and postlarval phase in the blue crab life history is at least 45 days. Successful reinvasion is aided by postlarva behavior (Sulkin, 1984;

Forward and Rittschof, 1994), in concert with physical and meteorological conditions of the mid-Atlantic Bight (Goodrich, van Montfrans and Orth, 1989). Precise forcing functions on the reinvasion process still remain problematic.

As postlarvae ingress the bay and subestuaries, physiological changes (Lipcius, Olmi and van Montfrans, 1990; Metcalf and Lipcius, 1990) (Fig. 3), coupled to an active upward swimming movement in the water column on night-time flood tides (Olmi, 1994; De Vries, *et al.*, 1994; Forward and Rittschof, 1994; Tankersley and Forward, 1994), place postlarvae most competent to settle (i.e. molting to first instar blue crabs) in close proximity to their primary settlement habitat - seagrass beds in shoal areas less than 2 meters (Lipcius *et al.*, 1990; Olmi *et al.*, 1990). The strong swimming abilities of blue crab postlarvae (Luckenbach and Orth, 1990) can potentially enhance habitat selection at the time of settlement. Settlement of postlarvae is highly episodic with a distinct lunar component (Fig. 4; van Montfrans, Peery and Orth, 1990, van Montfrans *et al.*, 1995). Limits of active settlement decrease with increasing distance from the mouth (Fig. 5) with up-estuary areas colonized by migration of early instar crabs (Hines, Lipcius and Haddon, 1987).

Our past research has also focused on potential cues for settlement of blue crab postlarvae since larvae of many invertebrates have been shown to be attracted to specific substrata by different chemical stimuli (Crisp, 1974; Butman, 1987). We conducted field tests of

postlarvae responses to three substratum types (mud, live oysters, and live eelgrass) and found a significant preference for eelgrass over the other substrata. These results corroborated those of laboratory experiments for postlarvae but not first instar crabs (van Montfrans and Orth, unpubl. data). Forward, Frankel and Rittschof (1994) also found that blue crab postlarvae molted fastest in estuarine water especially when eelgrass was present, compared to offshore, continental shelf water, suggesting chemical (as well as tactile) cues in inducing metamorphosis.

Seagrass Habitat - Blue Crab Relationships

Intensive sampling in seagrass and other shallow water habitats (mud, sand, marsh creek) using a drop net and suction sampler over the last decade has generally shown significantly higher densities of blue crabs in seagrass than in other habitats (Penry, 1982; Orth and van Montfrans, 1987; Montane *et al.*, 1995). This is particularly true for early instar crabs which are up to two orders of magnitude more abundant in

vegetated than adjacent, unvegetated habitats (Figs. 6 and 7). Although postlarvae settle on artificial substrates in these unvegetated areas (substrata are constructed of "hogs hair" air-conditioning filter material), first and second instar crabs are rare or absent. We hypothesized that predation was a critical process affecting abundance among adjacent habitats and that abundance of later stage crabs (greater than third instar) were the result of movement of crabs from seagrass to other habitats. The reduction in density of later stage crabs (greater than 10 - 15 mm carapace width) in the seagrass beds suggested a possible shift in habitat use triggered by attainment of a size refuge from predation. Our studies have also shown that blue crabs less than 25 mm appear to overwinter in seagrass beds while larger crabs overwinter in deep water sand and mud habitats (Orth and van Montfrans, 1987; Montane *et al.*, 1995).

We examined fish predation on settling postlarvae and early instar crabs in grassbeds by quantifying the gut contents of resident fish during postlarval

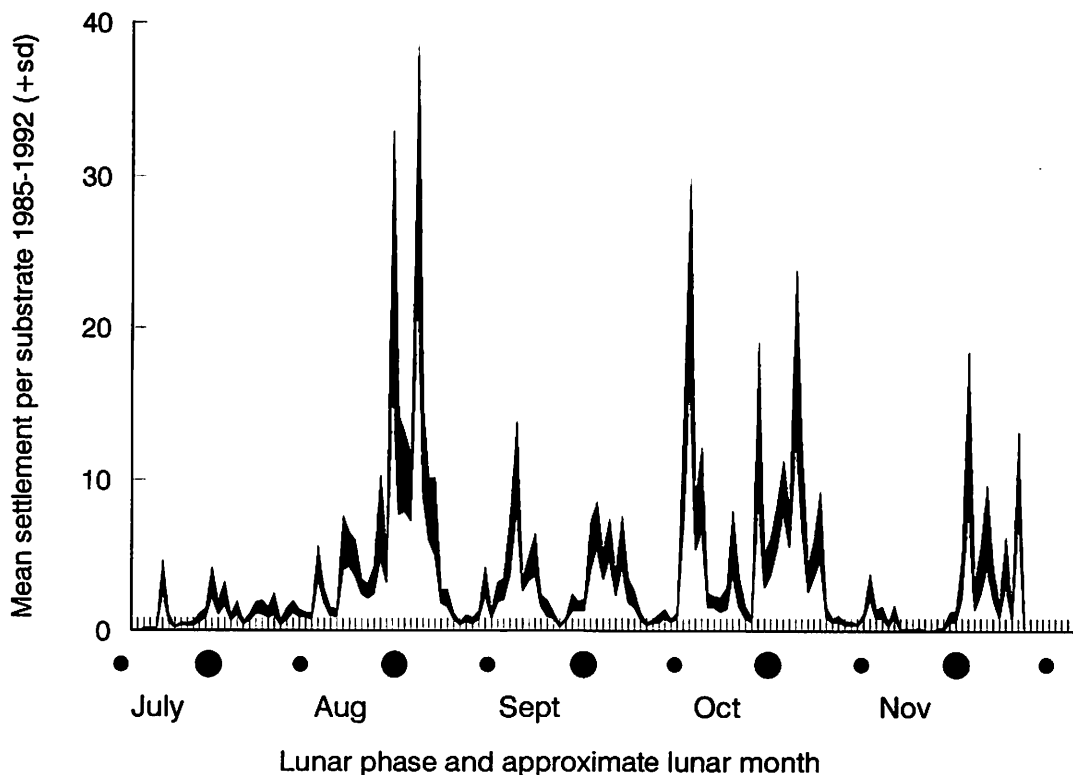


Figure 4: Daily settlement (mean and standard deviation - unshaded and shaded portion of figure) of blue crab postlarvae on artificial substrates in the York River averaged from 1984-1992 (small, closed circles on x-axis represent the new moon, while the large, closed circles represent the full moon).

settlement. Predation was most evident during the morning hours when postlarvae settle from the plankton, while predation on juveniles was most evident during night-time. Although the contribution of blue crabs to the overall diet of individual fish was small, the high density of fish in grassbeds could potentially have a significant impact on blue crab abundance. We suggest that the density of postlarval pulses in these grassbeds may increase the proportional survival of postlarvae during settlement (Metcalf *et*

al., unpubl. data).

Results from a variety of predator-prey studies in both vegetated and unvegetated habitats support the refuge-from-predation hypothesis attributed to complex structured habitats such as seagrasses. Our early work with simulated seagrass and marsh creek habitats with postlarvae and first instar crabs and a fish predator showed higher survival in simulated seagrass and with increasing density of seagrass shoots (Orth and van Montfrans, unpubl. data). Tethering experiments under

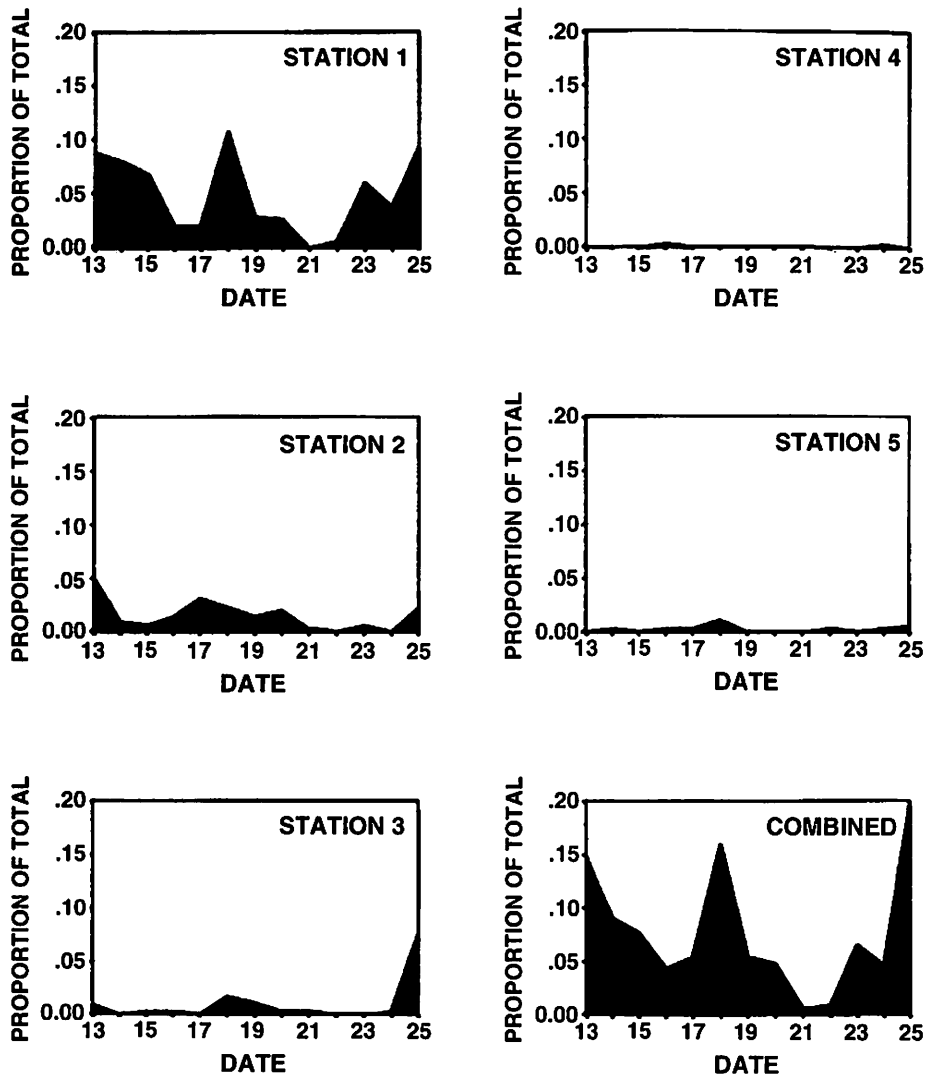


Figure 5: Settlement of blue crab postlarvae on artificial substrates with increasing distance from the mouth of the York River estuary (the distances of station 1-5 from the river mouth, as measured linearly from the river axis, were 0.0, 10.7, 20.2, 33.1, and 40.8 km, respectively).

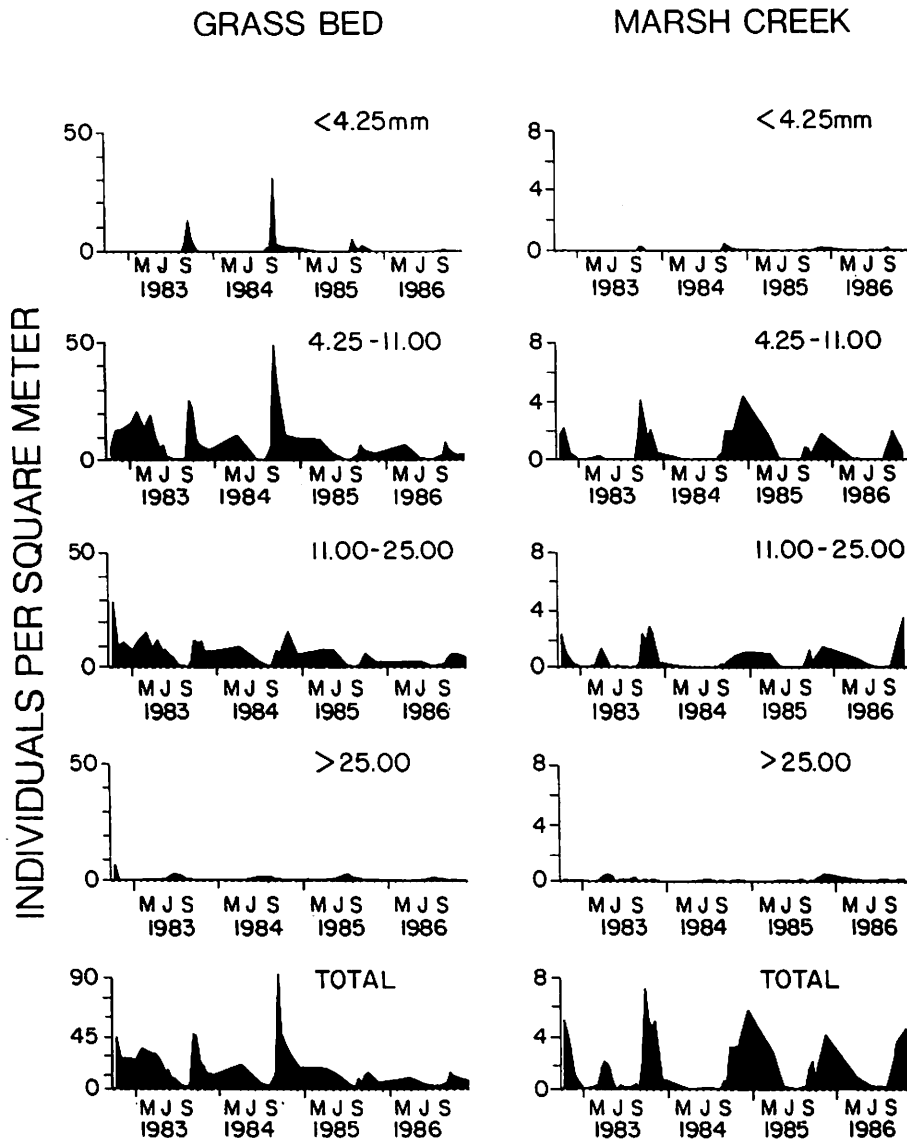


Figure 6: Annual and seasonal abundance patterns of four size groups of blue crabs residing in a seagrass bed and tidal marsh habitat, 1982-1986 (from Orth and van Montfrans, 1987).

field and laboratory settings in vegetated and unvegetated habitats with first through ninth instar crabs showed that survival increased significantly in vegetated habitats and with increasing crab size until the ninth instar when survival in vegetated and unvegetated habitats did not differ significantly (Pile, 1993). A conceptual model was developed which indicated an ontogenetic shift in habitat occurred from vegetated to unvegetated areas between the fifth and seventh instars of newly settled crabs due to size and

habitat specific changes in survival (Pile, 1993).

Cannibalism by larger juveniles and adults upon young juveniles has been convincingly demonstrated in the field for the blue crab through stomach content analysis, direct observations, and predation experiments (Mansour and Lipcius, 1991). Cannibalism experiments conducted with postlarvae and early instar crabs, testing the effects of size, density, and habitat type (sand and seagrass), showed mortality of postlarvae to be inversely density dependent in sand

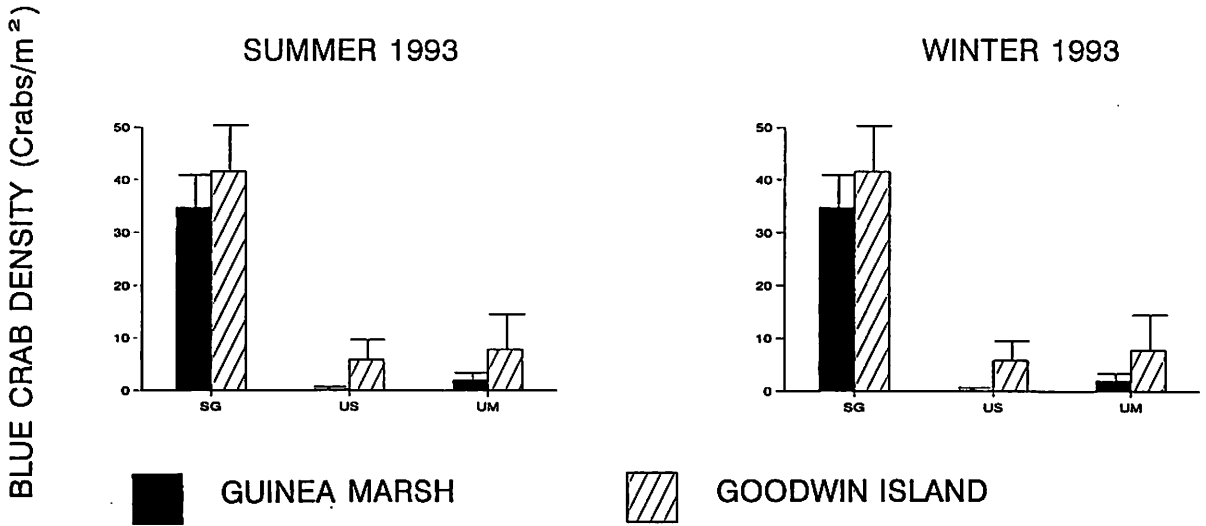
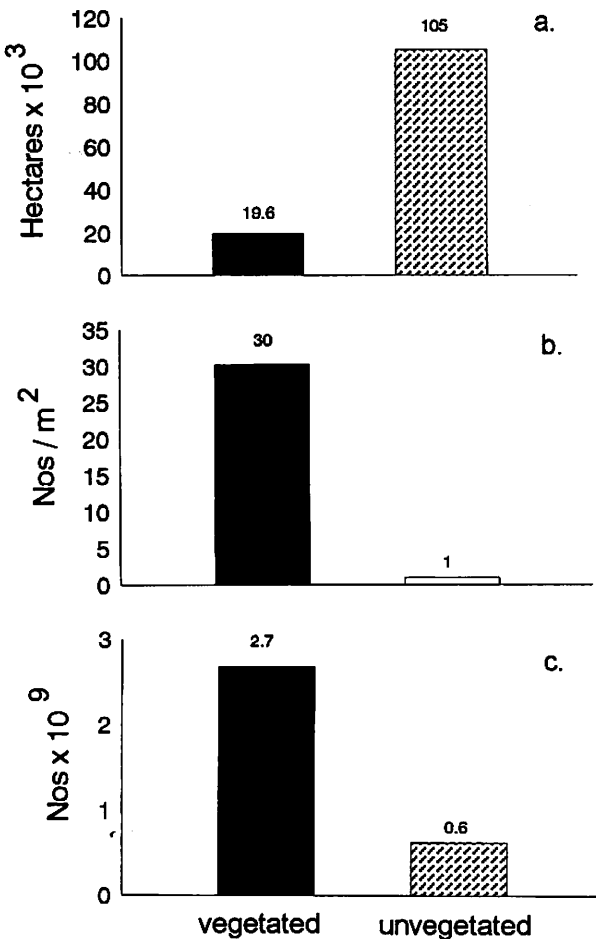


Figure 7: Density of blue crabs from seagrass (SG) and adjacent unvegetated mud (UM) and sand (US) areas from two locations at the mouth of the York River (Guinea Marsh and Goodwin Island) in summer and winter, 1993 (from Montane, *et al.*, 1995).



but independent of prey density in seagrasses where mortality was significantly lower than in sand. In the size experiments, mortality was higher in sand than seagrasses for all instars, and higher for postlarvae than third and fifth instars (Moksnes *et al.*, unpubl. data).

The significantly higher densities and higher survival rates of early instar crabs in seagrass habitats compared to unvegetated areas suggest that, on a relative scale, seagrasses may be vital to the overall stock size of blue crabs in Chesapeake Bay. We are currently focusing on seagrass habitat from a baywide perspective in the context of landscape distributional patterns and metapopulation dynamics for juvenile blue crabs. We concurrently examined abundance and size distribution of blue crabs in 12 broad zones throughout lower and mid-Chesapeake Bay characterized by shallow vegetated and unvegetated habitats less than 2 meters (MLW). Sampling in August, 1994, showed higher abundance of blue crabs in vegetated than

Figure 8: a) Comparison of total areal coverage (hectares) of shoal areas in lower Chesapeake Bay (see stippled and crosshatched areas in Fig. 9) less than two meters (MLW) both vegetated and unvegetated in 1994. b) Blue crab density in 1994 from a quantitative random survey throughout lower Chesapeake Bay in both habitat types less than two meters deep (MLW), and c) Estimates of total crabs contributed by lower Chesapeake Bay vegetated and unvegetated habitats extrapolated from available habitat area (a) and blue crab density (b).

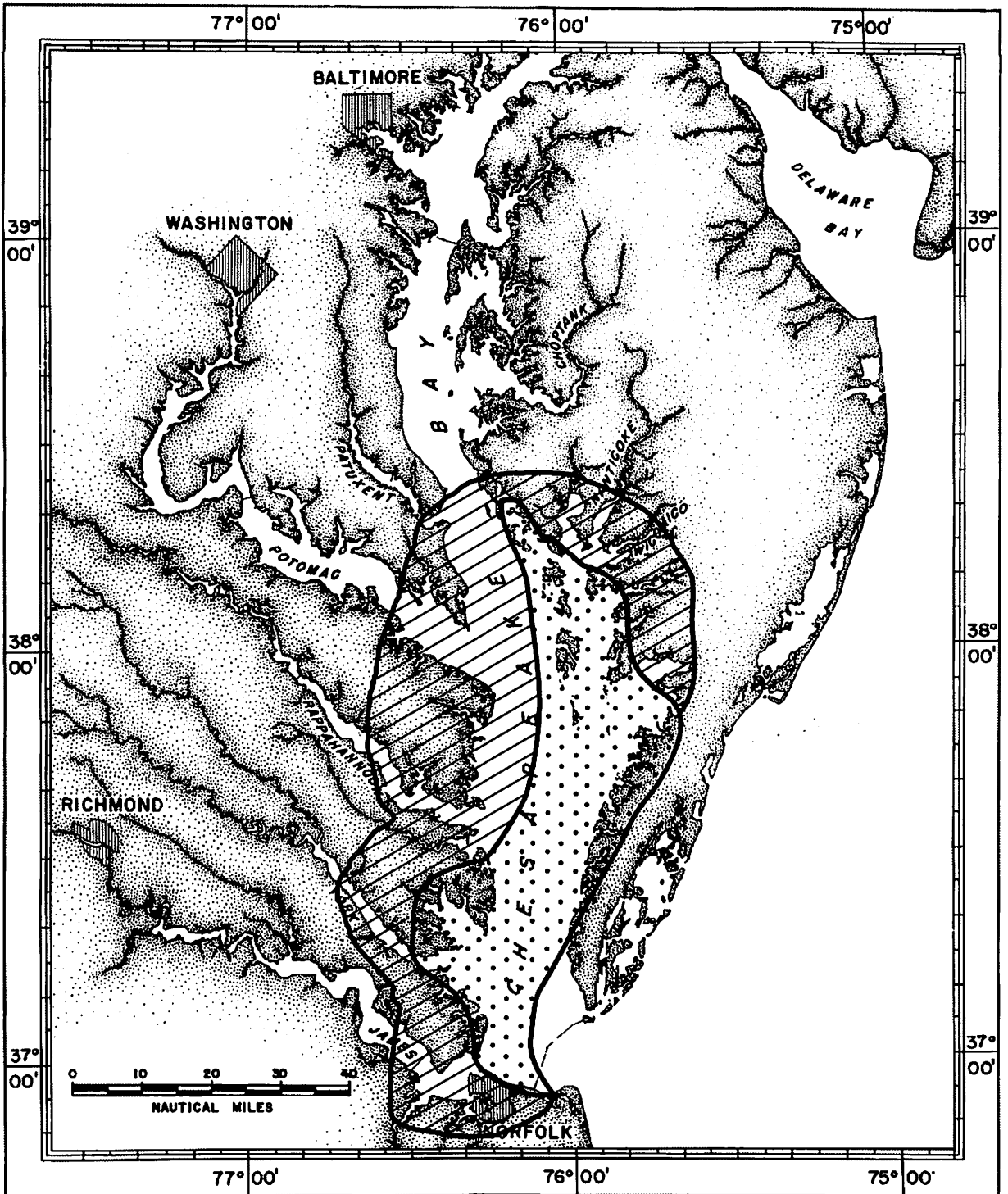


Figure 9: Map of Chesapeake Bay depicting critical seagrass habitat for blue crab postlarval settlement (stippled and crosshatched area). The stippled section represents areas currently vegetated, while the crosshatched section represents areas that historically supported dense seagrass beds but are currently unvegetated or sparsely vegetated.

unvegetated habitats in all zones. Overall, when comparing blue crab density for total vegetated vs unvegetated area (Fig. 8), the abundance of crabs in vegetated areas is almost 5 times that of the unvegetated area. These data strongly indicate the importance of seagrass beds in lower Chesapeake Bay for blue crabs. Some seagrass zones had significantly higher densities than others suggesting that natural processes (e.g. recruitment, migration, predation) may differentially structure the juvenile crab population in these zones (Lipcius *et al.*, unpubl. data). These data illustrate that similar habitats may differentially affect the numerical abundance of juvenile blue crabs on a baywide basis and strongly points to the need for broad-scale ecological sampling, even in similar habitats.

The relevance of seagrasses on blue crab abundance (Fig. 8) is highlighted in Figure 9, depicting current (stippled) and historic (crosshatched) upbay and upriver limits of seagrass habitat for blue crab postlarvae and early instars. These historic upbay and upriver limits of seagrasses also coincide with approximate limits of settlement of postlarvae (see Fig. 5). Our data (van Montfrans *et al.*, unpubl. data, 19??) show settlement continues in these historic areas but postlarvae most likely experience significant mortality because of the absence of vegetation. This habitat loss is hypothesized to have an effect on the adult population size.

CONCLUSIONS

Our research has shown: 1. higher densities of juvenile blue crabs in a seagrass habitat compared to adjacent marsh and unvegetated areas, 2. some seagrass areas are potentially more important because of location relative to settlement of postlarvae or differential predation effects, 3. seagrasses to be an important settlement habitat for postlarval blue crabs, the life history stage that recruits into Chesapeake Bay from the offshore continental shelf, 4. generally higher survival rates of early instar crabs in vegetated areas compared to unvegetated areas and with increasing size until the ninth instar where survival in vegetated and unvegetated habitats is not significantly different, and 5. an ontogenetic shift in habitat use from vegetated to unvegetated areas between the fifth and seventh instars of newly settled crabs due to size and habitat specific changes in survival.

The loss of seagrass habitat in upriver and upbay areas where survival of settling postlarvae has been

significantly altered because of shifting predator-prey dynamics may have profound implications for blue crab stocks in Chesapeake Bay. Elucidating these mechanistic reasons for the value of seagrass habitat for the blue crab, one of the last remaining, viable commercial fisheries in Chesapeake Bay, is crucial in developing strategies for protecting and restoring seagrass habitat in Chesapeake Bay.

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REFERENCES

- Boesch D F and Turner R E 1984 Dependence of fishery species on salt marshes: The role of food and refuge. *Estuaries* 7: 460-468.
- Boicourt W C 1982 Estuarine larval retention mechanisms on two scales. *In: Estuarine Comparisons*. Ed V Kennedy. pp 445-457. Academic Press, New York.
- Butman C L 1987 Larval settlement of soft-sediment invertebrates: The spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. *Oceanogr. Mar. Biol. Ann. Rev.* 25: 113-161.
- Costlow J D Jr and Bookhout C G 1959 The larval development of *Callinectes sapidus* reared in the laboratory. *Biol. Bull.* 116: 373-396.
- Crisp D J 1974 Factors influencing the settlement of marine invertebrate larvae. *In: Chemoreception in marine organisms*. Eds P T Grant and A. M. Mackie. pp 177-265. Academic Press, New York.
- DeVries M C, Tankersley R A, Forward R B Jr, Kirby-Smith W W, and Luettich R A Jr 1994 Abundance of estuarine crab larvae is associated with tidal hydrologic variables. *Mar. Biol.* 118: 403-413.
- Forward R B Jr and Rittschoff D 1994 Photoresponses of crab megalopae in offshore and estuarine waters: Implications for transport. *J. Exp. Mar. Biol. Ecol.* 182: 183-192.

- Forward R B Jr, Frankel D A Z and Rittschof 1994 Molting of megalopae from the blue crab *Callinectes sapidus*: effects of offshore and estuarine cues. *Mar. Ecol. Prog. Ser.* 113: 55-59.
- Goodrich D M, van Montfrans J and Orth R J 1989 Blue crab megalopal influx to Chesapeake Bay: evidence for a wind-driven mechanism. *Estuar. Coast. Shelf Sci.* 29: 247-260.
- Hines A H, Lipcius R N and 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.
- Johnson D R, Hester B S and McConaughy J R 1984 Studies of a wind mechanism influencing the recruitment of blue crabs in Middle Atlantic Bight. *Cont. Shelf Res.* 3: 425-437.
- Kemp W M, Boynton W R, Twilley R R, Stevenson J C and Means J C 1983 The decline of submerged vascular plants in upper Chesapeake Bay: Summary of results concerning possible causes. *Mar. Tech. Soc. J.* 17: 78-89.
- Lipcius R N, Olmi E J III and van Montfrans J 1990 Planktonic availability, molt stage and settlement of blue crab postlarvae. *Mar. Ecol. Prog. Ser.* 58: 235-242.
- Loneragan N R, Kenyon R A, Haywood M D E and Staples D J 1994 Population dynamics of juvenile tiger prawns (*Penaeus esculentus* and *P. semisulcatus*) in seagrass habitats of the western Gulf of Carpentaria, Australia. *Mar. Biol.* 119: 133-143.
- Luckenbach M W and Orth R J 1990 Swimming velocities and behavior of blue crab (*Callinectes sapidus* Rathbun) megalopae in still and flowing water. *Estuaries* 15: 186-192.
- Mansour R A and Lipcius R N 1991 Density dependent foraging and mutual interference in blue crabs preying on infaunal clams. *Mar. Ecol. Prog. Ser.* 72: 239-246.
- McConaughy J R, Johnson D F, Provenzano A J and Maris R C 1983 Seasonal distribution of larvae of *Callinectes sapidus* (Crustacea; Decapoda) in the waters adjacent to Chesapeake Bay. *J. Crust. Biol.* 3: 582-591.
- Metcalf K S and Lipcius R N 1992 Relationships of habitat and spatial scale with physiological state and settlement of blue crab postlarvae in Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 82: 143-150.
- Montane M M, Lipcius R N, Haner J L, Seebo M S, Pile A J, van Montfrans J, Orth, R J, Gibs, D, Mosknes P and Pihl L 1995 A field study of the population dynamics of the blue crab *Callinectes sapidus* Rathbun, in Chesapeake Bay. Final Report, 285 p. Chesapeake Bay Stock Assessment Committee, NOAA.
- O'Brien C J 1994 Ontogenetic changes in the diet of juvenile drown tiger prawns *Penaeus esculentus*. *Mar. Ecol. Prog. Ser.* 112: 195-200.
- Olmi E J III 1994 Vertical migration of blue crab, *Callinectes sapidus* megalopae: implications for transport in estuaries. *Mar. Ecol. Prog. Ser.* 13: 39-54.
- Olmi E J III, van Montfrans J, Lipcius R N, Orth R J and 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.
- Orth R J and Moore K A 1983 Chesapeake Bay: An unprecedented decline in submerged aquatic vegetation. *Science* 222: 51-53.
- Orth R J and Moore K A 1984 Distribution and abundance of submerged aquatic vegetation in Chesapeake Bay: An historical perspective. *Estuaries* 7: 531-540.
- Orth R J and Moore K A 1988 Distribution of *Zostera marina* L. and *Ruppia maritima* L. sensu lato along depth gradients in the lower Chesapeake Bay. *Aquat. Bot.* 32: 291-305.
- Orth R J and van Montfrans J 1987 Utilization of a seagrass meadow and tidal marsh creek by blue crabs *Callinectes sapidus*. I. Seasonal and annual variations in abundance with emphasis on post-settlement juveniles. *Mar. Ecol. Prog. Ser.* 41: 283-294.
- Orth R J and van Montfrans J 1990 Utilization of marsh and seagrass habitats by early stages of *Callinectes sapidus*: a latitudinal perspective. *Bull. Mar. Sci.* 46: 126-144.
- Orth R J, Batiuk R and Nowak J F 1995 Trends in the distribution and abundance of submerged aquatic vegetation in Chesapeake Bay and tributaries - 1970-1991. U.S.E.P.A. Final Report. 240 p.
- Orth R J, Heck K L Jr and van Montfrans J 1984 Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. *Estuaries* 7: 339-350.
- Orth R J, Nowak J F, Anderson, G F, Wilcox D J, Whiting J R, and Nagey L S 1995 Distribution of submerged aquatic vegetation in the Chesapeake Bay and tributaries and Chincoteague Bay -1994. U.S.E.P.A. Final Report. 258 p.
- Penry D L 1982 Utilization of a *Zostera marina* and *Ruppia maritima* by four decapods with an emphasis on *Callinectes sapidus*. Master's thesis. College of William and Mary, Williamsburg, Virginia. 95 p.
- Peterson C G L 1918 The sea bottom and its production of fish foods; a survey of the work done in connection with valuation of Danish waters from 1883-1917. Report of the Danish Biological Station. 25: 1-62.
- Pile A J 1993 Effects of habitat and size-specific predation on the ontogenetic shift in habitat use by newly settled blue crabs. Master's thesis. College of William and Mary, Williamsburg, Virginia. 84 p.
- Provenzano A J Jr, McConaughy J R, Phillips K B, Johnson D F and Clark J 1983 Vertical distribution of first stage larvae of the blue crab, *Callinectes sapidus*, at the mouth of Chesapeake Bay. *Est. Coast. Shelf. Sci.* 16: 489-499.
- Rasmussen E 1973 Systematics and ecology of the Isefjord marine fauna (Denmark). *Ophelia* 11: 1-495.
- Roughgarden J, Gaines S D and Possingham H 1988 Recruitment dynamics in complex life cycles. *Sci.* 241: 1460-1466.
- Sulkin S D 1984 Behavioral basis of depth regulation in the larvae of brachyuran crabs. *Mar. Ecol. Prog. Ser.* 15: 181-205.
- Sulkin S D and Van Heukelem 1986 Variability in the length of the megalopal stage and its consequences to dispersal and recruitment in the portunid crab, *Callinectes sapidus* Rathbun. *Bull. Mar. Sci.* 39: 269-278.
- Tankersley R A and Forward R B Jr 1994 Endogenous swimming rhythms in estuarine crab megalopae: implications for flood-tide transport. *Mar. Biol.* 118: 415-423.

van Montfrans J, Peery C A and Orth R J 1990 Daily, monthly and annual settlement patterns by *Callinectes sapidus* and *Neopanope sayi* on artificial collectors deployed in the York River, Virginia. Bull. Mar. Sci. 46: 214-228.

van Montfrans J, Epifanio C E, Knott D M, Lipcius R N, Mense D J, Metcalf K S, Olmi E J III, Orth R J, Posey M H, Wenner

E L and West T L 1995 Settlement of blue crab postlarvae in western North Atlantic estuaries. Bull. Mar. Sci. 57: 834-854.

Williams A B 1984 Shrimp, lobsters and crabs of the Atlantic Coast of the United States, Maine to Florida. Smithsonian Institution Press, Washington D. C. 550 p.