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VARIATION IN PLANKTONIC AVAILABILITY AND SETTLEMENT OF BLUE CRAB MEGALOPAE IN THE YORK RIVER, VIRGINIA

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ABSTRACT

Blue crab, *Callinectes sapidus,* megalopae and juveniles were sampled in the plankton and on natural (grassbeds) and artificial settlement substrates (collectors) at two sites in each of two areas of a lower Chesapeake Bay tributary (York River, Virginia) to examine spatial variability in blue crab recruitment. Spatial patterns of abundance were not consistent across habitats (plankton, artificial collectors and grassbeds) or time. Densities of planktonic mega-lopae were homogeneous at 1–2 m (within site) but varied at spatial scales of hundreds of meters (between sites) and kilometers (between areas). Settled megalopae were distributed unevenly within and between sites, but their abundance did not differ between areas. Densities of megalopae and first-stage juveniles in grassbeds correlated with megalopal abundance in the plankton. Settlement on collectors, however, was not correlated with planktonic density, probably because of low sample size. Total juvenile abundance exhibited lower spatial and temporal variability in grassbeds than that of megalopae or first-stage juveniles, suggesting high post-settlement mortality or migration from areas of high settlement.

Population levels and distributions of marine species with planktonic larvae are determined in part by recruitment dynamics, including those processes that affect the transport and survival of pelagic and settlement stages. Relationships between settlement and subsequent population size have been demonstrated for tropical reef fishes (Sale, 1980; Sale et al., 1984; Victor, 1986; Doherty, 1987) and sessile invertebrates (Keough, 1984; Connell, 1985; Gaines et al., 1985; Sutherland, 1987; Judge et al., 1988). The structure of intertidal communities reflects a composite of density dependent and independent factors that determines the supply rate of potential settlers to a location and post-settlement mortality (Connell, 1985; Roughgarden et al., 1988). Definition of the spatial and temporal scales at which significant recruitment variability occurs is critical to an understanding of the demography and dynamics of marine populations (Judge et al., 1988; Roughgarden et al., 1988).

In Chesapeake Bay, young juvenile blue crabs, *Callinectes sapidus* Rathbun (Decapoda: Portunidae), are not distributed evenly over available habitat, but are concentrated in certain areas, particularly seagrass beds (Heck and Orth, 1980; Penry, 1982; Heck and Thoman, 1984; Orth and van Montfrans, 1987). Such uneven distribution may result from (1) differential settlement of immigrating postlarvae because of hydrography (i.e., supply rate) or habitat selection, (2) differential mortality of settled megalopae and juveniles, and (3) migration among habitats by young juveniles.

Large variability in blue crab recruitment is not unexpected, given its early life-history features. Timing of larval release (Provenzano et al., 1983; Salmon et al., 1986) and behavior of stage I zoeae (Sulkin et al., 1980) promote larval advection from the estuary, followed by larval development (seven zoeal stages and the megalopa) in continental shelf waters (Nichols and Keney, 1963; Dudley and Judy, 1971; Smyth, 1980; Johnson, 1982; 1985; McConaugha et al., 1983; Epifanio et al., 1984). Megalopae or early juveniles reinvade estuaries via wind-

driven surface currents, residual inflowing bottom waters, tidally-related vertical migrations, or wind-driven water mass exchange (see Epifanio, 1988, and Mc-Conaugha, 1988, for recent reviews). Some investigators (Sandifer, 1972; 1973; 1975; Goy, 1976; Johnson, 1982; 1985) collected relatively few blue crab megalopae in Chesapeake Bay, leading Johnson (1982; 1985) to doubt the importance of reinvasion by megalopae. Williams (1971), however, noted that significant numbers of megalopae moved toward the upper reaches of North Carolina estuaries, and other investigators concluded that colonization of shallow water habitats was primarily by the megalopal stage (Meredith, 1982; Olmi, 1986; Mense and Wenner, 1989). At a site in the York River, Virginia (~50 km from the Chesapeake Bay mouth) blue crab megalopae have been collected regularly during late summer and fall in the plankton (E. J. Olmi, unpubl. data) and on artificial settlement substrates (van Montfrans et al., in press). Thus, the megalopal stage is likely the major reinvasive stage to the lower Chesapeake Bay and its tributaries. Low catch rates in previous studies may have resulted from sampling at times when blue crab megalopae were not abundant in the water column.

In offshore waters, blue crab megalopae are concentrated near the surface (Smyth, 1980; Johnson, 1982; 1985; Maris, 1986), but within estuaries their vertical position varies (Sandifer, 1975; Johnson, 1982; Epifanio et al., 1984; Maris, 1986) due in part to diel (Maris, 1986; Mense and Wenner, 1989; E. J. Olmi, unpubl. data) or tidal (Epifanio et al., 1984) vertical migrations. Peak abundance of megalopae occurs during night-time flood tides (Meredith, 1982; Epifanio et al., 1984; Olmi, 1986) suggesting that both tidal and diel influences are important.

The magnitude of megalopal variability and its temporal and spatial scales in the estuary are poorly defined. Further, little is known of the relationship between megalopal abundance and settlement. In this study we examine variation in (1) abundance of blue crab megalopae in the plankton, (2) their settlement on artificial substrates and in natural seagrass beds, and (3) abundance of juveniles in seagrass beds on scales of meters, hundreds of meters, and kilometers. Also, we relate patterns in the abundance of potential settlers (plankton) to those of megalopae settling on natural and artificial substrates.

METHODS

Study Areas.—We sampled blue crab megalopae and juveniles in the lower York River, Virginia (lower Chesapeake Bay) on 8–9 September, 6–7 October and 9–10 October 1987 (each 2-day period is considered one sampling date). Sampling was conducted within 3 days of full moon, when settlement is normally highest (van Montfrans et al., in press). On each date we sampled two sites within either of two areas near the river mouth (Area B or C) and two sites at an upriver area (Area A) (Fig. 1). Area A, located approximately 12 km from the York River mouth, was sampled on all three dates. Area B, located in Mobjack Bay 4 km north of the mouth of the York River and the site of previous investigations of blue crab habitat utilization (Orth and van Montfrans, 1987), was sampled on 9–10 September, but later abandoned because of weak tidal currents. Area C, located in the York River about 5 km from the mouth (Fig. 1), was sampled on 6–7 and 8–9 October. Sites within each area were 200–400 m apart, and each contained shallow (<2 m) seagrass beds (*Zostera marina* with *Ruppia maritima*), which serve as settlement and nursery habitats for postlarval and juvenile blue crabs (Orth and van Montfrans, 1987).

Collections.—On each sampling date, three collection methods were used: plankton nets, artificial substrates (collectors), and benthic suction sampling in seagrass beds. Paired plankton nets 1 m apart were deployed at each site for 20 min during mid-flood tide at night. Each net (0.75-mm mesh) filtered an area 50 cm wide from the surface to a depth of 80 cm. One net of each pair was equipped with a flowmeter (General Oceanics model 2030). Nets were fished passively except on three occasions (9 September, sites B-1 and B-2; 9 October, site C-1) when they were pushed at idle speed by boat during part of the sampling period because currents were weak. Water volumes filtered per sample varied from 34.5 to 161.8 m³. Plankton samples were collected sequentially at sites within an area, but concurrently among areas. Plankton samples were preserved in diluted (5–10%) formalin, and blue
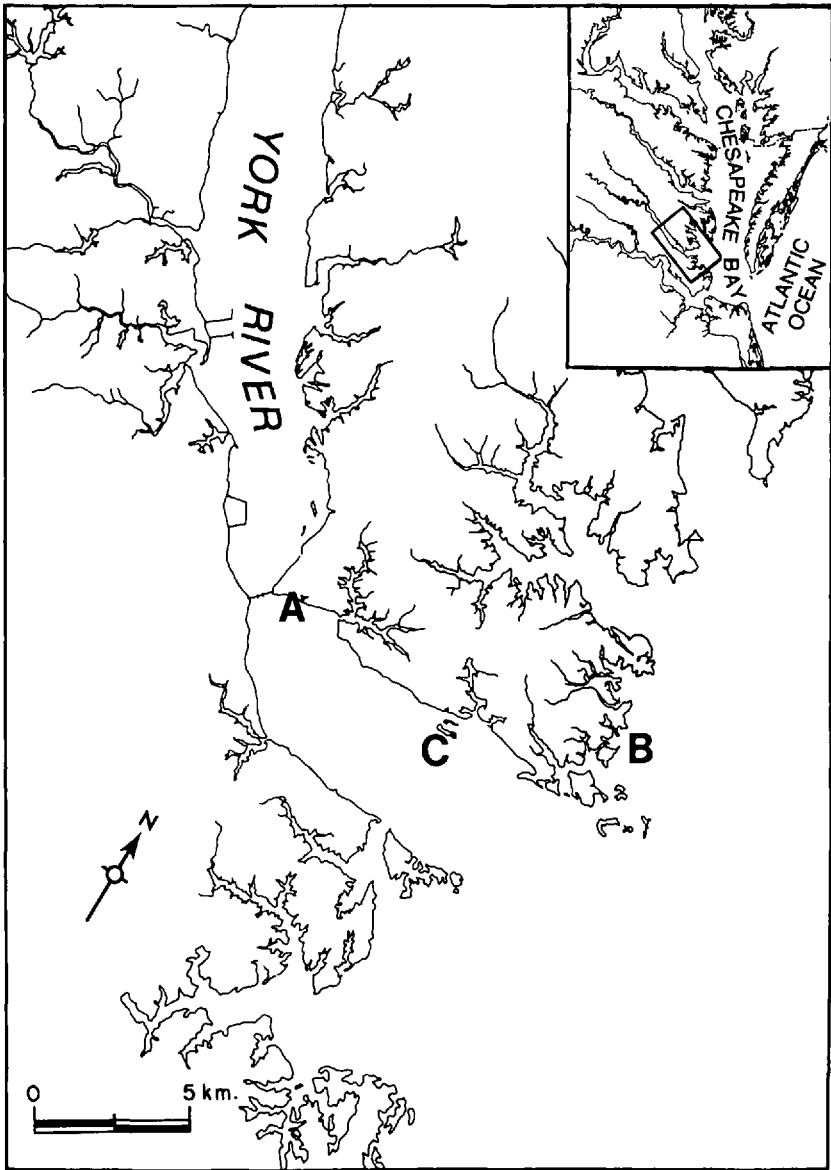
Figure 1.   Map of the lower York River, Virginia showing sampling stations for blue crab megalopae and juveniles. Stations A and B were sampled 9–10 September and stations A and C were sampled 6–7 and 8–9 October, 1987.

crab megalopae and juveniles were sorted and identified in the laboratory. Collections were standardized as number of megalopae per 10 m³ of water filtered, with the reported density for each site representing the mean for the paired net samples.

Artificial substrates have been used successfully to study patterns of settlement of several decapod crustaceans (Phillips, 1972; Shanks, 1983; Beninger et al., 1986; van Montfrans et al., in press). Four collectors, synthetic fiber air-conditioning filters (47 × 39 × 1 cm), were spaced 2–3 m apart at each site, and deployed during early flood tide in the evening, remaining submersed 15 cm below the surface for 12–14 h. Collectors were suspended from floats and weighted to maintain vertical position in the water column. Each was retrieved by dip net, and blue crab megalopae and juveniles were recovered by rinsing with fresh water through a 1-mm sieve. On 6–7 and 8–9 October, a flowmeter (General Oceanics model 2030) was deployed with collectors at each site to estimate tidal flow.

The day following deployment of collectors and plankton nets, we sampled the surviving recruits in grassbeds at each site. A plastic cylinder with mouth opening of 0.055 m² was pushed into the sediment and the contents of the cylinder, including the upper few cm of the sediment, were suctioned for 30 sec with a venturi-type suction sampler (Orth and van Montfrans, 1987). Cloth mesh (0.5 mm) covered the top of the cylinder and prevented escape. Suction sampling was shown to be 88% efficient in collecting juvenile blue crabs from grassbeds (Orth and van Montfrans, 1987). Four cylinder collections within a 2-m radius were combined to form one of three replicate samples in each area. Megalopae and juveniles were sorted live from suction samples, and their abundances were standardized as number of individuals per m². We considered megalopae collected from substrata (artificial substrates or grass beds) to be settled.

Statistical Analyses.—Megalopal abundance in each habitat (i.e., density (ind· 10 m^{-3}) in the plankton, number of individuals per collector and density (ind·m^{-2}) in grassbeds) was analyzed (ANOVA; SPSS, 1986) separately for September and October because sampling areas were not consistent over the 2 months. Juvenile abundance was analyzed only for grassbed samples. The data for 9 September (Areas A and B) were analyzed with a two-factor nested design (Site within Area). Data from 7 and 9 October were analyzed in a three-factor nested design with Date and Area as main factors and Site nested within Area. When interaction terms were significant, we conducted one-way analyses of main factors (each of Areas A and C by Date and each Date by Area) with an experiment-wise error rate of 0.05 (Underwood, 1981). Abundance data were log-transformed as necessary to eliminate heterogeneity of variance. Multiple comparisons were conducted with Student-Newman-Keuls tests.

RESULTS

Plankton.—Mean megalopal densities in the plankton varied from 0.4 to 57.9 per 10 m³, and variability between paired nets (i.e., within each site) was generally low (CV: average 28%, range 2–71%) (Fig. 2A). Mean megalopal densities were greater upriver (Area A) than at areas near the York River mouth (Areas B and C), but the significance of Site within Area varied among dates. On 10 September, when planktonic densities were highest, abundance differed significantly among all sites (Table 1, Fig. 2A).

There was a significant Date × Site within Area interaction on 7 and 9 October (Table 1). On 7 October, megalopal densities were greater at Area A than Area C, and variability within areas was not significant. On 9 October, however, densities differed significantly between sites at Area A (Table 1). Megalopal densities were similar between lower river sites on both dates.

At both upriver sites, megalopal densities were significantly greater on 10 September than on either sampling date in October (Table 2). Between 7 and 9 October densities decreased significantly at one upriver site (A-1) and increased significantly at one lower river site (C-1), resulting in a significant date by site interaction (Tables 1, 2, Fig. 2A).

Juvenile *C. sapidus* (predominately first- and second-stage crabs) were too infrequent in plankton samples (≤0.5· 10 m^{-3} or ≤5·collection^{-1}) to warrant statistical analysis of their abundance.

Collectors.—The mean number of megalopae per collector ranged from 0 to 20, with moderate variability among collectors at a site (CV: average 83%, range 23–200%) (Fig. 2B). Abundance did not differ by Area, but Site within Area was significant on all dates, generally because of greater numbers of megalopae at site A-1 (Table 1). At the lower river area, sites differed only on 7 October. At all sites, megalopae were more abundant on collectors on 7 October than other dates (Table 2).

Abundance of megalopae on collectors was not correlated with abundance in the plankton ($r = -0.02$, $P > 0.50$) (see Fig. 2A, B). Settlement on collectors was low on 10 September when planktonic abundance was high, but on 7 October when settlement was greatest, megalopae were not abundant in plankton samples.

Table 1. Results of analysis of variance comparisons of megalopal and juvenile abundance by Area, Site within Area and Date. Table values are exact probabilities for calculated F ratios. Comparisons among sites for each date were one way analyses followed by Student-Newman-Keuls multiple comparisons. Measures of abundance were: plankton, ind·10 m⁻³; collectors, ind.·collector⁻¹; grassbeds, ind·m⁻²

Date	Areas	Factor	Plankton Megalopae	Collectors Megalopae	Grass beds Megalopae[1]	Grass beds First crab	Grass beds Total crab
10 Sept	A, B	Site within area	0.000**	0.000**	0.638	0.512	0.212
		Area	0.041*	0.575	0.160	0.090	0.840
		Site (SNK comparison)	$A_1 > A_2 > B_1 > B_2$	$A_1 > B_2 = B_1 = A_2$			
7, 9 Oct	A, C	Site within area	0.608	0.000**		0.390	0.428
		Area	0.009**	0.654	0.423	0.099	0.800
		Date	0.489	0.026*		0.423	0.313
		Date × site within area	0.012*	0.234		0.390	0.488
		Date × area	0.209	0.701		0.423	
7 Oct	A, C	Site within area	0.304	0.000**			
		Area	0.031*	0.760			
		Site (SNK comparison)	$A_1 = A_2 > C_1 = C_2$	$A_1 > C_1 > C_2 = A_2$			
9 Oct	A, C	Site within area	0.013*	0.001**			
		Area	0.580	0.515			
		Site (SNK comparison)	$A_2 > C_1 = A_1 = C_2$	$A_1 > C_1 = A_2 = C_2$			

[1] Within site error estimates of megalopal abundance not available for grass bed samples from 7 and 9 October.
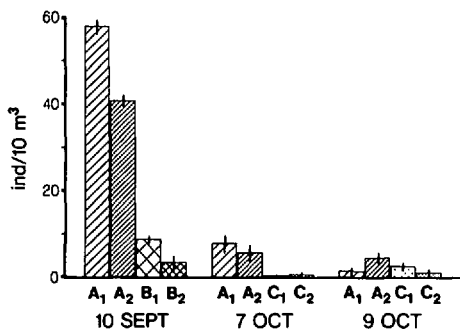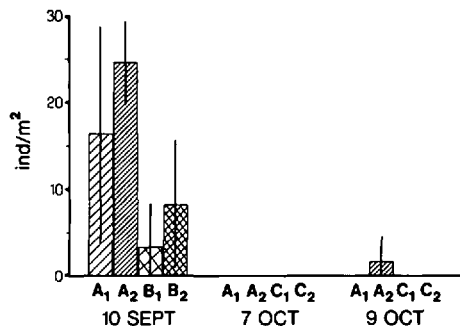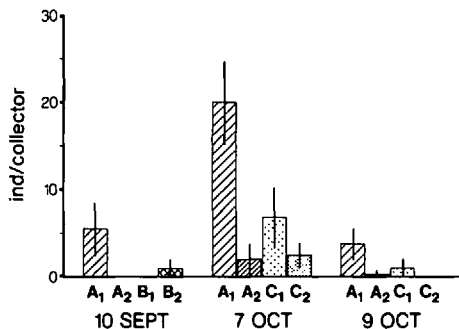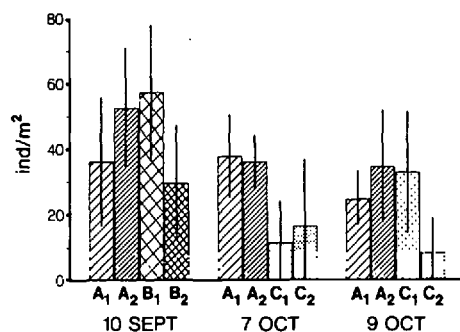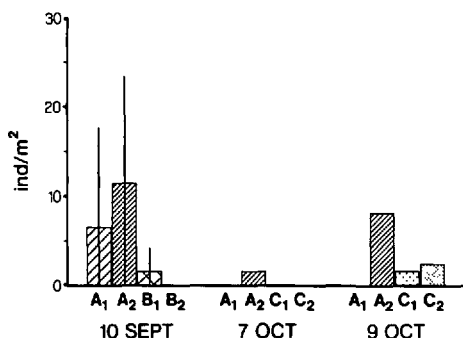
Figure 2.   Mean abundance of *C. sapidus* megalopae and juveniles by Site and Date. Sites A-1, A-2, B-1 and B-2 were sampled 10 September and sites A-1, A-2, C-1 and C-2 were sampled 7 and 9 October. Error bars represent + and − one standard deviation. A. Mean density (ind · 10 m⁻³) of megalopae from paired plankton collections. B. Mean number of megalopae per artificial collector. C. Mean density (ind · m⁻²) of megalopae from grassbeds (no estimate of SD from 7 October or 9 October). D. Mean density (ind · m⁻²) of first-stage juveniles from grassbeds. E. Mean density (ind · m⁻²) of all juveniles from grassbeds.

Table 2. Comparisons (one-way ANOVA) of abundance by date for sites A_1, A_2, C_1 and C_2, followed by Student-Newman-Keuls multiple comparisons. Table values are exact probabilities for calculated F ratios. Dates 1 = 10 Sept., 2 = 7 Oct., 3 = 9 Oct. Measures of abundance were: plankton, ind.·10 m^{-3}; collectors, ind.·collector^{-1}; grassbeds, ind.·m^{-2}

Site	Dates	Plankton Megalopae	Collectors Megalopae	Grass beds Megalopae*	Grass beds First crab	Total crab
A_1	10 Sept., 7 Oct., 9 Oct.	0.000** 1 > 2 > 3	0.001** 2 > 1 = 3	0.422 1 = 2 = 3	0.001** 1 > 2 = 3	0.570
A_2	10 Sept., 7 Oct., 9 Oct.	0.000** 1 > 2 = 3	0.046* 2 > 3 = 1		0.001** 1 > 3 = 2	0.347
C_1	7 Oct., 9 Oct.	0.035* 3 > 2	0.014* 2 > 3		none collected	0.174
C_2	7 Oct., 9 Oct.	0.339 2 = 3	0.000** 2 > 3		none collected	0.569

* Within site error estimates of megalopal abundance in grass beds 7 and 9 Oct. available only for site A-1.

Twenty-one juvenile *C. sapidus* were found on artificial collectors on 10 September (Areas A and B). Of these, 60% (12) were first-stage crabs. Although no megalopae were collected at site A-2 on this date, 7 of 11 juveniles collected there were first crabs. Juveniles were not quantified in subsequent samples from these substrates.

Grassbeds.—Highest densities of megalopae and first-stage juveniles (11.5 and 26.4·m^{-2}, respectively) were collected in grassbeds at site A-2 on 10 September, but Area and Site within Area were not significant because within site variability was high (CV: average 152%, range 108%–175%) (Table 1, Fig. 2C, D). Megalopae were generally less abundant in October (Fig. 2C), but variance estimates are available only for collections at site A-1. Only one first-stage crab was collected in grassbeds in October (Fig. 2D). Abundance of megalopae in grassbeds was positively correlated with megalopal abundance in the plankton ($r = 0.71$, $P < 0.05$), but not with abundance on collectors ($r = -0.32$, $P > 0.20$) (see Fig. 2A–C).

Total densities of juvenile blue crab (including first-stage crabs) in grassbeds ranged from 8.20 to 57.4·m^{-2} and did not differ significantly by Date, Area or Site (Tables 1 and 2, Fig. 2E). First-stage crabs constituted approximately 30% of the juveniles collected on 10 September, but were virtually absent in later collections. Total juvenile abundance in grassbeds exhibited less within site variability (CV: average 61%, range 21–125%) than first-stage crabs (CV: average 107%, range 20–173%) or megalopae. These juveniles were probably all from the 1987 spawning season (largest, 51.4 mm carapace width) and their mean widths varied from 6.6 to 15.6 mm (Table 3).

DISCUSSION

Judge et al. (1988) commented: "It would be comforting if most of the variation in the recruitment of benthic populations could be ascribed to particular temporal or spatial scales. This would help identify the principal physical mechanisms controlling larval supply and simplify attempts to explicitly model the population dynamics in space and time." In this paper we report on spatial variability in recruitment of blue crab and the relationships between abundance of megalopae in the plankton and abundance of megalopae and juveniles on settlement substrates.

Table 3. Number (in parentheses) and mean total carapace width (mm) ± one standard deviation of juvenile blue crabs collected from grass beds, by date and site

Site	10 September	7 October	9 October
A_1	(22) 7.7 ± 5.5	(23) 9.8 ± 9.4	(15) 11.7 ± 7.2
A_2	(32) 6.6 ± 4.7	(22) 14.2 ± 8.7	(21) 8.1 ± 5.8
B_1	(34) 10.4 ± 3.6		
B_2	(18) 10.0 ± 6.9		
C_1		(8) 7.3 ± 2.3	(23) 15.6 ± 11.1
C_2		(10) 7.1 ± 3.2	(5) 12.3 ± 7.6

Settlement refers to the termination of a pelagic larval (or postlarval) existence and assumption of a benthic life (Scheltema, 1974), usually associated with metamorphosis. If post-settlement survival of non-motile organisms is independent of the density of settlers, then abundance of recruits will be correlated with settlement intensity (Connell, 1985; Sutherland, 1987). Recruitment dynamics of motile organisms are complicated by migration of post-settlement individuals. Certainly some benthic organisms return to the water column after settlement (Butman, 1987), and relocation by fishes may play an important role in structuring coral reef communities (Robertson, 1988). Settlement of benthic decapod crustaceans occurs when the postlarva becomes associated with substratum prior to metamorphosis. Although we considered megalopae collected from natural or artificial substrates to be settled, we could not rule out the possibility that this association was temporary. Indeed, megalopae likely descend to and rise from the bottom to avoid ebb currents (Meredith, 1982; Epifanio et al., 1984; Olmi, 1986) and search for suitable settlement sites. Thus, our measures of settlement incorporate temporary and permanent settlement.

Spatial Variability. — Heterogeneous distributions of larval and postlarval decapod crustaceans in the plankton have been observed in several species (Chace and Barnish, 1975; Rice and Kristensen, 1982; Booth et al., 1985; Shanks, 1985; Epifanio, 1987), including the blue crab (Johnson, 1982; Provenzano et al., 1983; Maris, 1986), but rarely have the limits of these distributions (i.e., patch size) been quantified. Booth et al. (1985) estimated patch size of *Cancer magister* megalopae at 2–4 km. Ichthyoplankton in Biscayne Bay, Florida was often randomly or uniformly distributed, but occasionally patches existed at scales of 10–1,000 m (Houde and Lovdal, 1985).

Planktonic blue crab megalopae in the York River were fairly homogeneous at spatial scales of 1–2 m. Differences in abundance between sites (hundreds of meters) and between areas (kilometers) were not consistent over time, and greatest differences among sites occurred when densities were highest. Inconsistent spatial patterns likely reflect variability in the system but may have resulted from low abundance of megalopae in October plankton collections or low sample sizes. Mense and Wenner (1989) examined abundance of blue crab megalopae along a salinity gradient in South Carolina and observed decreasing abundance from the polyhaline (75% of total), to mesohaline (23%) to oligohaline (2%) zones.

Settlement of megalopae on artificial and natural substrates exhibited greater local (1–3 m) heterogeneity than was observed in the plankton. Despite the within-site variability, mean number of megalopae per collector was greater at Site A-1 than other sites on all dates, suggesting greater supply of megalopae to that site. Settlement of blue crab megalopae on collectors was greater in the lower 12 km of the York River than at up-river stations (P. W. Sadler, J. van Montfrans and

R. J. Orth, unpubl. data). The present study was confined to the lower 12 km of the York River, and settlement did not differ between areas (several km).   High within-site variability of megalopae in grassbeds may have resulted from post-settlement microhabitat selection (Bell and Westoby, 1986) or mortality. Densities of megalopae in seagrass were generally higher at Site A-2 than A-1, in contrast to patterns observed in the plankton and on collectors. One possible explanation for lower densities of megalopae in seagrass at Site A-1 is a filtering effect of grassbeds immediately in the path of the flood current reaching that site. Gaines et al. (1985) observed that settlement intensity of barnacles decreased with distance away from the delivery source—fewer cyprids remained in the water column to settle at the "down-current" sites.

Although megalopal abundance differed significantly across the spatial scales examined, the magnitude of these differences ($\leq 20 \times$) was considerably less than has been observed in barnacle settlement (up to several orders of magnitude) (Caffey, 1985; Connell, 1985; Gaines et al., 1985; Judge et al., 1988).

Temporal Variability.—Temporal variability in settlement is related to spawning patterns of adults, transport processes and the physiology and behavior of potential recruits. Settlement of intertidal barnacles may show considerable daily variability at a single site (Wethey, 1984; Shanks, 1986), and over time the relative importance of settlement sites varies (Caffey, 1985; Connell, 1985; Gaines et al., 1985; Sutherland, 1987; Judge et al., 1988). Abundance of blue crab megalopae in the York River differed significantly among sampling dates (i.e., over periods of 2 days and also over 1 month), but temporal changes were not consistent among habitats (plankton, collectors or seagrass) or among sites for a given habitat. Although this study was not designed to examine temporal scales of recruitment in detail, it is important that spatial patterns of abundance changed significantly over two days. Thus, frequent sampling is necessary to detect temporal patterns in the immigration and settlement of blue crab megalopae.

Daily sampling of plankton (E. J. Olmi, unpubl. data) and artificial substrates (van Montfrans et al., in press) in the York River indicates that planktonic densities and settlement may vary greatly from one day to the next. Settlement appears to be episodic (van Montfrans et al., 1990). Orth and van Montfrans (1987) observed discrete peaks of abundance of early juveniles (<4.25 mm carapace width) in seagrass beds and attributed this variability to pulsed settlement of megalopae. Similarly, Doherty (1987) found that the major portion of a year class of damselfish on patch-reefs resulted from occasional, brief periods of intense settlement.

Planktonic Availability vs. Settlement.—Several studies have shown a relationship between the abundance of pre-settlement individuals in the water column and settlement (Wethey, 1984; Gaines et al., 1985; Victor, 1986), and Grosberg (1982) observed that the vertical zonation of barnacles paralleled the distribution of their cyprids in the water column.

We found that density of megalopae in the plankton was positively correlated with settlement in grassbeds, but not on artificial collectors. Although the average density of megalopae during a night-time flood tide may be approximated by a single collection during maximum flood at night (E. J. Olmi, unpubl. data), a single plankton sample may not reflect accurately numbers of megalopae contacting grassbeds and collectors over longer periods (≥ 12 h). The correlation observed between plankton and grassbed collections was encouraging, and although settlement on collectors was not correlated with planktonic abundance, both are highly variable (van Montfrans et al., 1990; E. J. Olmi, unpubl. data)
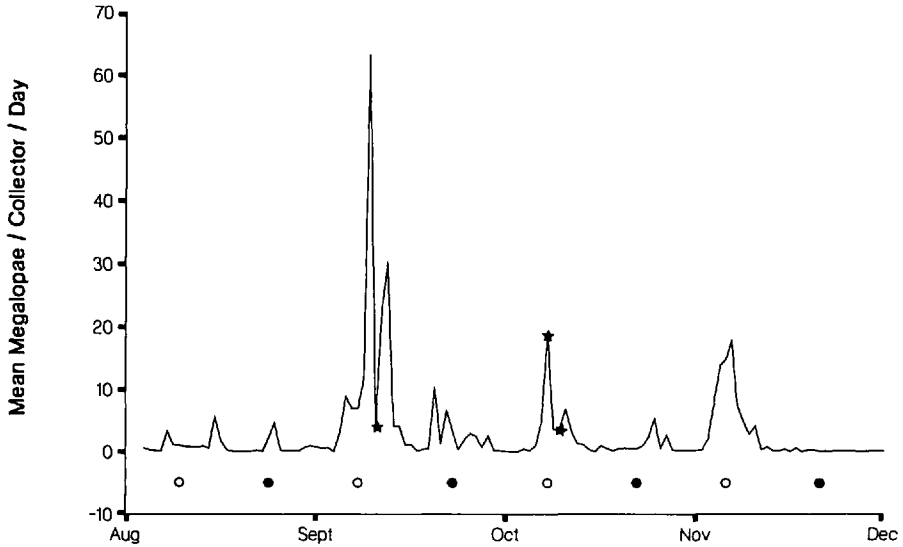
Figure 3. Daily settlement of blue crab megalopae on artificial collectors at site A-1 during 1987 (from van Montfrans et al., in review). Stars indicate dates of the present study.

and a single day may not represent general patterns. For instance, Figure 3 illustrates that settlement at Site A-1 on 10 September and 7 October represented low and high peaks, respectively, within periods of generally high (10 September) and low (7 October) settlement. Thus, average settlement on collectors generally corresponded with abundance in the plankton, but settlement on the days of our study did not, emphasizing the need for frequent sampling in a highly variable system.

Megalopae on collectors were found to be in a developmental state intermediate between those of planktonic megalopae and megalopae in grass beds (Lipcius et al., in press). We believe that settlement on collectors is a useful index of natural settlement and the lack of correlation between the two resulted from low sample size. The use of postlarval collectors to predict commercial stocks of the western rock lobster (*Panulirus longipes*) (Phillips, 1972) and in ecological studies of other species including blue crab (Shanks, 1983, Beninger et al., 1986; van Montfrans et al., 1990) attests to their utility.

Density is typically used as a measure of planktonic abundance because it allows comparison among samples collected in different flow regimes (i.e., current or tow speeds). Our objective was to examine spatial variability in abundance of immigrating and settling megalopae so we followed convention and used density as our measure of planktonic abundance. Delivery rate of potential settlers to an area, however, is a function of the density of propagules in the adjacent water *and* the flow rate past the settlement substrate. In this study, delivery rate (mean number of megalopae per 20-min stationary set of paired nets) was influenced by flow regime (e.g., densities were similar between sites, but greater numbers of megalopae were collected at the site with greater tidal flow). However, correlations between availability and settlement using the two measures of planktonic abundance (density and absolute numbers) differed little. Between-site differences in settlement on collectors on 7 and 9 October were accounted for by adjusting settlement (ind/collector) for relative flow regimes among areas (from flowmeters

deployed with collectors on 7 and 9 October). There is little doubt that flow regimes can affect settlement rates, and it appears that measuring the density of potential settlers in adjacent waters may not always be sufficient to estimate delivery rates to settlement sites.

Finally, it has been shown that settlement of blue crab megalopae is correlated with their developmental state (molt stage) (Lipcius et al., in press). If the majority of megalopae in the plankton are in an early developmental state and not ready to settle, then settlement may not reflect availability. Also, the response of megalopae to different settlement substrates may change as developmental state progresses towards metamorphosis.

Recruitment. — Juvenile blue crabs were present in all grassbed samples, reaching densities of $57 \cdot m^{-2}$. This is consistent with the paradigm that these areas serve as nursery habitat (Heck and Orth, 1980; Penry, 1982; Heck and Thoman, 1984; Orth and van Montfrans, 1987). First-stage crabs were abundant (up to $24 \cdot m^{-2}$) on 10 September, corresponding in time and space with megalopal abundance in the plankton and grassbeds. This strongly suggests that initial colonization of seagrass habitats was by megalopae, with subsequent metamorphosis to the first juvenile instar, as suggested by Orth and van Montfrans (1987). First-stage juveniles constituted approximately 30% of all juveniles collected on 10 September, but were rare in October collections.

Juvenile densities observed in this study were among the highest reported for blue crabs (Orth and van Montfrans, 1987). In contrast to the apparent localized, episodic occurrence of megalopae and first stage juveniles, total juvenile densities in grassbeds exhibited moderate stability over time and space. Either: (1) recruitment to the different sites was random over time, such that over longer time periods recruitment was similar among sites, or (2) settlement was localized, but recruitment was density-dependent, such that new recruits in high densities experienced proportionally greater mortality or emigration. The juveniles collected were small (2.4–51.4 mm) and probably all came from the 1987 spawning season. Larger crabs move out of grassbeds to other habitats (Orth and van Montfrans, 1987). These populations represent a dynamic balance between recruitment, mortality and emigration.

Conclusions

Although this study was of limited duration, it illustrates the highly variable nature of blue crab recruitment and the necessity for frequent sampling on multiple temporal and spatial scales. Abundance of planktonic megalopae in the York River was heterogeneously distributed across hundreds of meters and kilometers, but not at small scales (1–2 m). Local variation was greater for settlement on natural and artificial settlement substrates. Significant variability in immigration and settlement was observed over two days and also over one month, but likely occurs at finer temporal scales. The similarity of juvenile densities across sites and time contrasted the localized, episodic settlement by megalopae.

Settlement in grassbeds correlated positively with abundance of megalopae in the plankton, but settlement on artificial substrates did not correlate with planktonic abundance or settlement in grassbeds. This lack of correlation was attributed to infrequent sampling, and we believe that collectors are a usefull method of measuring relative settlement rates. Factors such as developmental state and substrate selection may mediate relationships between availability of propagules and settlement. We suggest that flow regime as well as density of pre-settlement individuals in the plankton be measured to estimate adequately delivery rate to

a site. Few habitats have been documented as settlement sites for immigrating blue crab megalopae, and recruitment dynamics of blue crab may vary among habitats.

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