

# Substrate selection by blue crab *Callinectes sapidus* megalopae and first juvenile instars

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**ABSTRACT:** Various marine and estuarine species utilize chemical cues during settlement. We investigated responses by megalopae and first juvenile (J1) blue crabs to common Chesapeake Bay substrates in mesocosm and field experiments. Mesocosm trials examined responses of megalopae or J1 crabs to sand, marsh mud, live oysters *Crassostrea virginica*, sun-bleached oyster shell, eel grass *Zostera marina* and artificial seagrass in replicate 160 l tanks. Either 10 megalopae or J1 crabs isolated in each of 6 substrates were allowed total access after acclimation to test the null hypothesis of equal distribution among substrates after 13 h. Thirty-five percent of megalopae were recovered from *Z. marina*, with the remaining substrates containing fewer than half that many. In contrast, 30 % of J1 crabs (with only 17% recovered from *Z. marina*) were found in live *C. virginica*. A field experiment quantified responses of ingressing megalopae to *Z. marina*, marsh mud, and *C. virginica*. Overnight settlement was significantly higher in *Z. marina* ( $\bar{x} = 3.3$  ind.; 60% of total) when compared to mud ( $\bar{x} = 0.9$ ; 16 %) or *C. virginica* ( $\bar{x} = 1.3$ ; 24 %). Likewise, J1 crabs were significantly more numerous in *Z. marina* ( $\bar{x} = 3.7$  ind.; 55% of total) than in *C. virginica* ( $\bar{x} = 1.8$ ; 27 %) and mud ( $\bar{x} = 1.2$ ; 18 %). J1 crab distribution in field plots likely reflected habitat selection by megalopae; laboratory results were equivocal and probably due to artifacts associated with density-dependent agonism. The initial non-random distribution of blue crabs in Chesapeake Bay may be deterministic and due to habitat-selection behavior by megalopae. Selection for seagrass assures the greatest likelihood of maximal survival and accelerated growth. Similar relationships may also exist in estuarine-dependent species with comparable habitat requirements and life-history characteristics.

**KEY WORDS:** Blue crab · Megalopae · First juvenile instar · Habitat selection · *Zostera marina* · *Crassostrea virginica* · Sand · Mud

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## INTRODUCTION

Many marine and estuarine organisms are patchily distributed by physical processes controlling the supply of recruits to suitable habitats. Others exhibit active larval/postlarval behavior during recruitment that assures a habitat-specific association upon settlement (Hadfield 1984, Scheltema 1974, 1986, Butman 1987, Butman et al. 1988, Morse 1990, Pechenick 1990, Young 1990, Rodriguez 1993). This behaviour may be particularly important in species that have both strong swimming capabilities and highly developed sensory systems (Connell 1985, Scheltema 1986, Butman 1987).

Among species of Brachyura and Palinura, for example, many exhibit life cycles with widely dispersing larvae (zoeae, glaucothoe) and postlarvae (megalopa, puerulus). These stages display swimming capabilities that increase ontogenetically, and often, the early juvenile stages are distributed non-randomly in nature (Botero & Atema 1982, Orth & van Montfrans 1987, Jensen 1989, Boudreau et al. 1990, O'Connor 1991, Fernandez et al. 1993). Such evidence suggests that the recruiting phase in the life cycle settles preferentially in specific (i.e. nursery) habitats.

Settling stages of decapods respond to various chemical and physical habitat characteristics that likely in-

volve the integration of multiple sensory modalities. Some decapods settle in response to (1) adult conspecifics (e.g. *Petrolisthes cinctipes* and *P. eriomerus*, Jensen 1989; *Uca pugilator*, O'Connor 1991), (2) light characteristics of crevices (e.g. *Homarus americanus*, Botero & Atema 1982, Boudreau et al. 1990), (3) habitat structural characteristics (e.g. *Homarus americanus*, Botero & Atema 1982, Boudreau et al. 1990; *Cancer magister*, Fernandez et al. 1993; *Panulirus argus*, Hernkind & Butler 1986; *Carcinus maenas*, Hedvall et al. 1998), (4) habitat-related chemical cues (*Callinectes sapidus*, Welch et al. 1997), (5) presence of an appropriate host in symbiotic species (e.g. *Echinoecus pentagonus*, Castro 1978) and (6) avoidance of potential predators (*C. sapidus*, Welch et al. 1997, Diaz et al. 1999). Larvae and postlarvae of several species delay metamorphosis in the absence of suitable cues (Pechenik 1990, O'Connor 1991, Harvey 1993). These studies imply that highly selective larval or postlarval behavior during recruitment, combined with strong mobility, likely plays a key role in selection of preferred nurseries during recruitment.

Habitat-specific associations for the blue crab *Callinectes sapidus* occur in many areas throughout its range. Within Chesapeake Bay, megalopae and smallest juvenile crabs occur principally in seagrass meadows (e.g. *Zostera marina* and *Ruppia maritima*; Orth & van Montfrans 1987, 1990) whereas elsewhere, they may be associated with marsh habitats (Thomas et al. 1990, Rozas & Minello 1998, Minello 1999). Whereas adults and juveniles are estuarine dependent (Williams 1984), larvae require high-salinity oceanic waters and are advected from the estuary in surface waters (Costlow & Bookhout 1959). The megalopa (postlarva) stage is the recruiting phase in the life cycle, with ingress into the Chesapeake Bay and its tributaries accomplished between July and the end of November each year (van Montfrans et al. 1990, 1995) via a combination of seasonal physical processes (Epifanio 1988a,b, Epifanio et al. 1984, 1989, Goodrich et al. 1989) and vertical migratory behavior of megalopae (Mense & Wenner 1989, De Vries et al. 1994, Olmi 1994, 1995, Tankersley & Forward 1994, Forward et al. 1995). Given the fact that estuarine cues accelerate megalopal metamorphosis (Forward et al. 1994, 1996, Wolcott & DeVries 1994), it is likely that sensory capabilities also exist for detecting the presence of specific estuarine habitats. When coupled with strong swimming capabilities of up to  $12.6 \text{ cm s}^{-1}$  (Luckenbach & Orth 1992), such sensory capacity may also enable the active selection of these habitats within the estuary. In this study, we investigate the ability of megalopae and first juvenile crabs to discriminate between commonly available habitats in Chesapeake Bay and examine the relative role of physical vs chemical cues in habitat selection via laboratory and manipulative field experiments.

## MATERIALS AND METHODS

**Laboratory experiments.** Experiments were conducted in a wet lab facility at the Virginia Institute of Marine Science, Gloucester Point, Virginia. We tested the response of megalopae or laboratory-metamorphosed first juvenile stage crabs (hereafter referred to as J1 crabs) to 6 habitat types. Five of the habitat types selected (natural sand, natural marsh mud, live oysters *Crassostrea virginica*, sun-bleached oyster shell, and live eelgrass *Zostera marina*) are common to Chesapeake Bay and 1 (artificial *Z. marina* constructed from polypropylene ribbon) was an inert analogue of *Z. marina* plants.

Live *Zostera marina* and oyster substrates were thoroughly cleaned with a cloth and brush, respectively, and therefore likely contained only a light complement of fouling organisms (e.g. diatoms) but differed from inert, unfouled substrates (artificial *Z. marina* and sun-bleached oyster shell) which were devoid of such influences. Additionally, the live and inert substrates (i.e. live vs artificial *Z. marina* and live vs sun-bleached oyster shell) were similar in overall dimension. Simulated (5 mm wide) and live *Z. marina* (3 to 4 mm wide) substrates spanned the height of the water column (~30 cm) in experimental tanks and were established at low densities equivalent to 180 shoots  $\text{m}^{-2}$ , characteristic of fall (Orth & Moore 1986). Live oysters ( $n = 8$ ) and oyster shells ( $n = 16$  half shells) were similar in length ( $\bar{x} = 74.7 \pm 5.6$ ) and width ( $\bar{x} = 53.1 \pm 5.8$ ), though sun-bleached oyster shells were not hinged.

Substrates were tested in replicate 160 l cylindrical fiberglass mesocosms (42 cm high  $\times$  70 cm wide) fitted with a central standpipe (Fig. 1). Mesocosm bottoms, filled to approximately 4 cm with sieved beach sand (grain size  $< 0.5 \text{ mm}$ ; total surface area available =  $0.38 \text{ m}^2$ ), were divided into 6 equal, contiguous pie-shaped sections (surface area =  $0.06 \text{ cm}^2$  each) into which substrates were randomly placed. The entire area of each pie-shaped tank section was covered by the experimental substrates being tested. Tanks were oriented randomly by compass heading within the laboratory prior to each trial to nullify tank orientation as a factor in laboratory experiments. A central standpipe (37.5 mm outside diameter) in each mesocosm was plugged with a rubber stopper at the bottom and fitted below the sediment surface with one screened (1 mm mesh; small enough to retain megalopae and J1 crabs but not the sand) drain plug per pie-shaped section. A series of similarly screened holes in the standpipe at the air-water interface facilitated water circulation and oxygenation via an air stone placed within the standpipe (Fig. 1).

Water circulation in each tank was minimal and considerably below the swimming capability of megalopae and J1 crabs (Luckenbach & Orth 1992, J. van

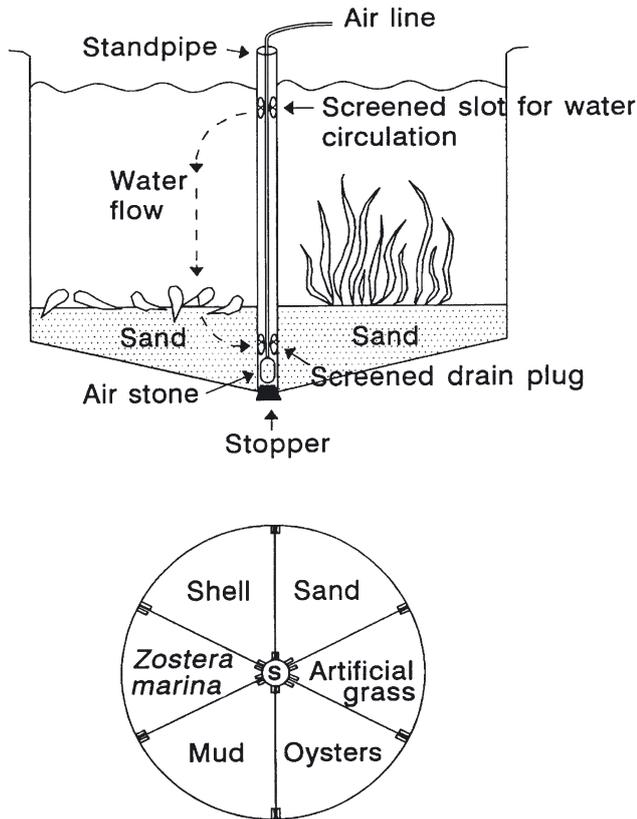


Fig. 1. Experimental mesocosm design. Top: tank cross section; bottom: top view. S: standpipe

Montfrans pers. obs.). Plastic sleeves attached to both the standpipe and opposing mesocosm sides enabled the removal (at the start of an experiment) and insertion (upon termination) of solid plastic partitions for either exposing or isolating adjacent mesocosm sections and associated experimental organisms, respectively. The 6 sections could thereby be isolated and the mesocosm emptied after partially removing the rubber stopper and allowing the water in each section to slowly drain via the screened drain plugs in the standpipe. Subsequently, upon complete removal of the stopper and the sequential removal of each screened drain plug, the contents of each randomly chosen section was individually rinsed through a 1 mm mesh sieve, thereby allowing experimental organisms, but not sediment, to be retained. Recovered individuals (88 to 100 % efficiency) were then enumerated and examined for indications of molting (e.g. metamorphosis of megalopae).

Experimental trials utilizing either megalopae (18 September,  $n = 4$  replicate tanks; 7 October,  $n = 5$ ) or J1 crabs (28 September,  $n = 7$ ; 7 November,  $n = 6$ ) were conducted to test the null hypothesis of uniform distribution among the 6 experimental substrates. All labo-

ratory experiments utilized either megalopae collected by a plankton net from the same site in the York River (Virginia Institute of Marine Science Ferry Pier; average salinity ~18 ppt) or J1 crabs that underwent the metamorphic molt from plankton-collected megalopae in laboratory mesocosms devoid of natural substrates. Within 48 h after ecdysis and exoskeleton hardening, J1 crabs were subjected to experimental conditions similar to those for megalopae to preclude further growth to the second juvenile instar and thereby ensure substrate selection behavior characteristic of J1 crabs.

Trials were initiated at 17:30 h by placing 10 ind. (either megalopae or J1 crabs) into each of the 6 sections per mesocosm with partitions in place (i.e. total of 60 ind. per mesocosm). Densities of megalopae ( $155 \text{ m}^{-2}$ ) used in our experiments approximated the maximum density ( $160 \text{ m}^{-2}$ ) of blue crabs (plus megalopae) ever quantified from a Chesapeake Bay sea-grass bed during the recruitment season (Orth & van Montfrans 1987, J. van Montfrans & R. J. Orth pers. obs.). After a 2 h acclimation period under fluorescent illumination, lights were turned off, partitions removed, and individuals allowed to redistribute among substrates. Trials were run under nocturnal conditions because megalopae ingress into settlement habitats during nighttime (Olimi 1994, 1995). Upon termination at 08:30 h the following morning, partitions between sections in each mesocosm were simultaneously reinserted to isolate adjacent substrates, lights were turned on and substrates in each mesocosm section were sampled. Thus, the post-acclimation experimental duration of 13 h slightly exceeded the natural period of nocturnal activity for megalopae and J1 crabs.

Data from laboratory experiments were analyzed using a replicated goodness of fit  $G$ -test (Sokal & Rohlf 1981), which examined the null hypothesis that experimental animals remained evenly distributed among substrates. Because some megalopae metamorphosed to J1 crabs overnight in megalopal trials, responses by megalopae and J1 crabs in these laboratory experiments were not independent; here, the total number of individuals (including megalopae that metamorphosed to J1 crabs) was used as the response variable. Given the short duration (13 h) of laboratory experiments and the even shorter time interval between metamorphosis of megalopae followed by shell hardening and termination of the experiment, this approach seemed reasonable. Variability in the rates of metamorphosis by megalopae between trials was analyzed using a 1-way ANOVA (Sokal & Rolph 1981).

**Field experiment.** A field experiment was conducted during full moon on 11/12 October 1989, a period of expected high settlement (van Montfrans et al. 1990, 1995). A total of 15 replicates of 3 experimental treat-

ments were established along 3 transects parallel to the shoreline (i.e. 5 treatments per transect) in the York River (1 m depth at mean low water) adjacent to the Virginia Institute of Marine Science (Fig. 2). Each replicate consisted of a plot containing 3 substrate treatments arranged in circular patches measuring 0.25 m in diameter ( $\sim 0.05 \text{ m}^2$ ). Substrates were randomly oriented by compass heading and equally spaced at a 2 m distance from a central stake marking each plot. Plots were separated by 4 to 5 m of bare sand along each transect. Substrate patches in each replicate were established by replacing natural sediment with each of 3 substrate types being tested (*Zostera marina*, marsh mud, and live *Crassostrea virginica*). *Z. marina* cores measuring 0.25 m in diameter were collected in a local (Allen's Island) grassbed, transported to the experimental site, and placed into excavated holes at the prescribed randomized location after careful examination and removal of any associated blue crabs. Densities of *Z. marina* in translocated plots were equivalent to low densities ( $\leq 180 \text{ shoots m}^{-2}$ ; Orth & Moore 1986) characteristic of natural inshore beds. Marsh mud was similarly translocated from a nearby marsh creek, whereas *C. virginica* treatments were established by placing 12 live oysters of medium size (similar to those used in laboratory experiments) within a 25 cm diameter circle to complete each experimental plot. These 3 substrates were selected because they contained the highest number of crabs overall during laboratory experiments utilizing megalopae or J1 crabs, and because they represented typical and readily available habitats in Chesapeake Bay.

Test substrates were collected from surrounding areas during the morning of 11 October and placed in the field between noon and 16:00 h. Substrates were randomly sampled early the following morning between 09:00 and 12:00 h. Thus, translocated substrates experienced a 12 h nocturnal period of megalopal recruitment activity and an average total duration in the field of about 21 h. Though experimental duration differed between lab and field experiments, settlement into field-deployed substrates during daylight hours was likely minimal, since megalopae and J1 crabs move about primarily during nocturnal flood tides (van Montfrans et al. 1990, Olmi 1994, 1995).

Sampling was accomplished by fitting a screened cylindrical sampling frame over each plot and removing

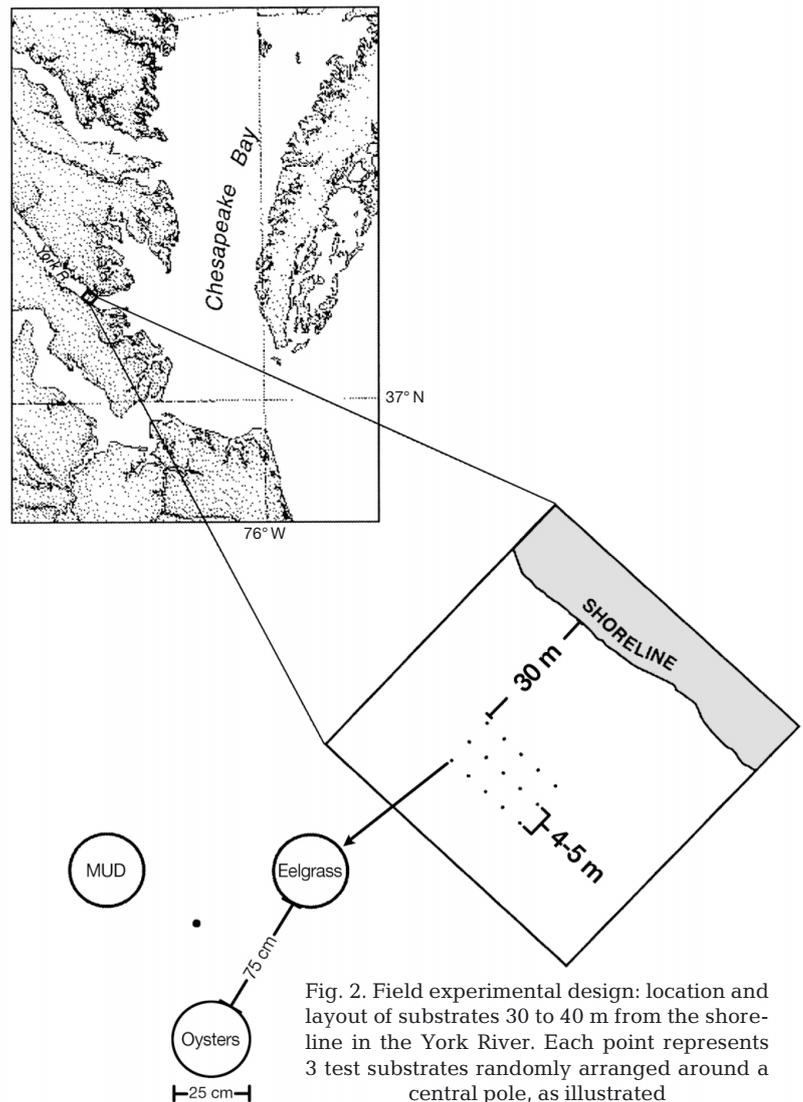


Fig. 2. Field experimental design: location and layout of substrates 30 to 40 m from the shoreline in the York River. Each point represents 3 test substrates randomly arranged around a central pole, as illustrated

colonized organisms using a suction sampler (Orth & van Montfrans 1987) equipped with a fine-mesh (0.50 mm) plankton-net cod end. Differences in the mean number of megalopae and J1 crabs (response variables) in each substrate type (dependent variable) were analyzed separately in a 1-way ANOVA. Differences between means were determined using a Student-Newman-Keuls post-hoc test (Sokal & Rohlf 1981).

## RESULTS

**Laboratory experiments.** At the end of the experiment—after 13 h of darkness, during which megalopae (plus metamorphosed J1 crabs) in each mesocosm were free to move about—individuals were unevenly distributed among the 6 substrates in the pooled data set ( $G_p [G \text{ for pooled data}] = 125.52, df =$

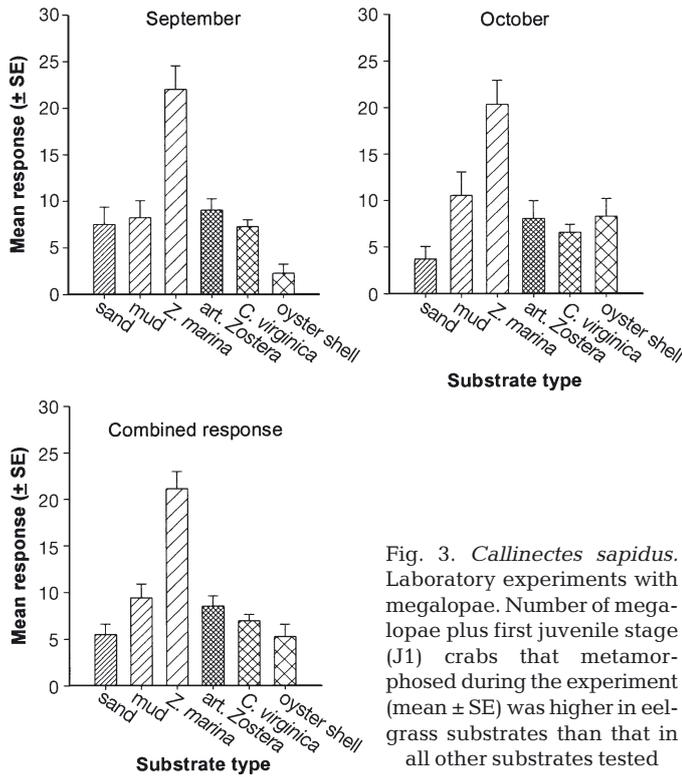


Fig. 3. *Callinectes sapidus*. Laboratory experiments with megalopae. Number of megalopae plus first juvenile stage (J1) crabs that metamorphosed during the experiment (mean ± SE) was higher in eelgrass substrates than that in all other substrates tested

5,  $p < 0.001$ ). Although the distribution among substrates differed somewhat between the 2 trial dates (Gh [G for heterogeneity] = 81.34,  $df = 35$ ,  $p < 0.001$ ), the number of individuals recovered from live *Zostera marina* was twice that found in any of the other substrates (Fig. 3). The mean rate of metamorphosis (± SE) by megalopae into J1 crabs differed between trial dates (September:  $\bar{x} = 37.0 \pm 5.0\%$ ; October:  $\bar{x} = 15.6 \pm 3.2\%$ ; ANOVA:  $F_{1,8} = 17.85$ ,  $p < 0.003$ ), suggesting greater megalopal settlement competency during the earlier trials.

Similar experiments with J1 crabs produced a different outcome. As in experiments testing megalopae, J1 crabs were unevenly distributed among the 6 substrates in the pooled data set ( $G_p = 114.82$ ,  $df = 5$ ,  $p < 0.001$ ), and some heterogeneity between trial dates ( $G_h = 166.58$ ,  $df = 84$ ,  $p < 0.001$ ) was evident. However in contrast to trials utilizing megalopae, the largest number of J1 crabs (Fig. 4) was recovered from live *Crassostrea virginica* ( $\bar{x} = 17.2$  ind.; ~30% of total) rather than live *Zostera marina* ( $\bar{x} = 9.6$  ind.; ~17% of total).

**Field experiments.** Both megalopae and J1 crabs preferred live *Zostera marina* when compared to live oysters and marsh mud in field experiments. Significantly more megalopae were recovered from live *Z. marina* ( $\bar{x} = 3.3$ ) than from either mud ( $\bar{x} = 0.9$ ) or live oyster substrates ( $\bar{x} = 1.3$ ; *Z. marina* > oyster = mud, SNK comparison,

ANOVA:  $F_{2,42} = 8.93$ ,  $p \leq 0.001$ ; Fig. 5a). Similarly, J1 crab abundance (Fig. 5b) was greatest in live *Z. marina* ( $\bar{x} = 3.7$ ) when compared to mud ( $\bar{x} = 1.2$ ) and oyster, ( $\bar{x} = 1.8$ ). substrates, which had equivalent abundances; SNK comparison, ANOVA:  $F_{2,24} = 12.88$ ,  $p < 0.001$ ). Overall, 60% of all megalopae and 55% of J1 crabs recovered from experimental field plots occurred in *Z. marina*.

**DISCUSSION**

We demonstrated in our experiments that blue crab megalopae are capable of discriminating between experimental substrates in both the laboratory and field. The ability of megalopae to discriminate between live *Zostera marina* over other substrates tested explains, in part, the high densities of early-stage juvenile crabs found in natural eelgrass habitats. Comparisons in laboratory trials suggest further that such behavior is probably mediated by chemical rather than structural cues associated with *Z. marina*, since megalopae consistently selected live, cleaned *Z. marina* over inert eelgrass mimics. Such behavior likely acts in concert with physical (e.g. hydrodynamic) processes to cause aggregations of individuals during settlement in nature.

Megalopae in our laboratory experiments did not choose live *Zostera marina* substrates simply because they were 3D, structurally complex and more readily encountered than other substrates offered. Artificial *Z. marina* was similar in gross morphology (though

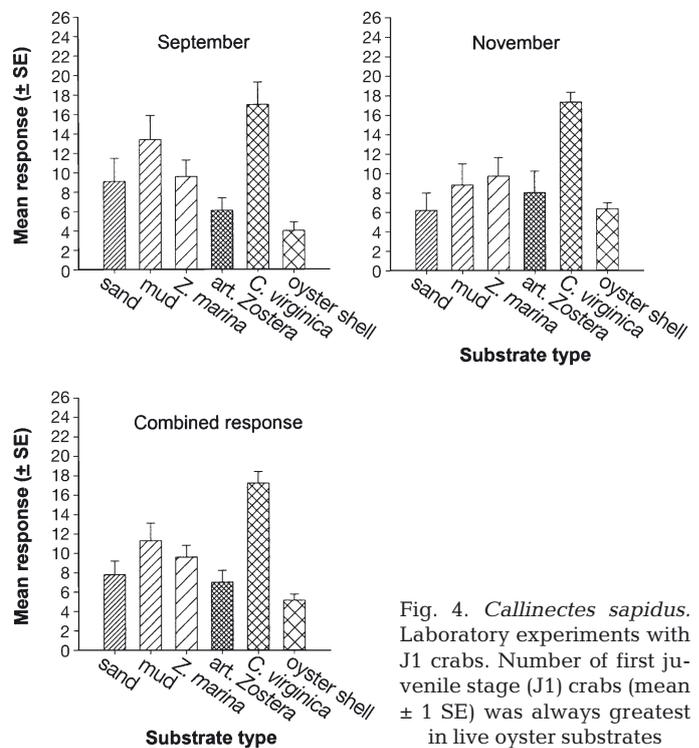


Fig. 4. *Callinectes sapidus*. Laboratory experiments with J1 crabs. Number of first juvenile stage (J1) crabs (mean ± 1 SE) was always greatest in live oyster substrates

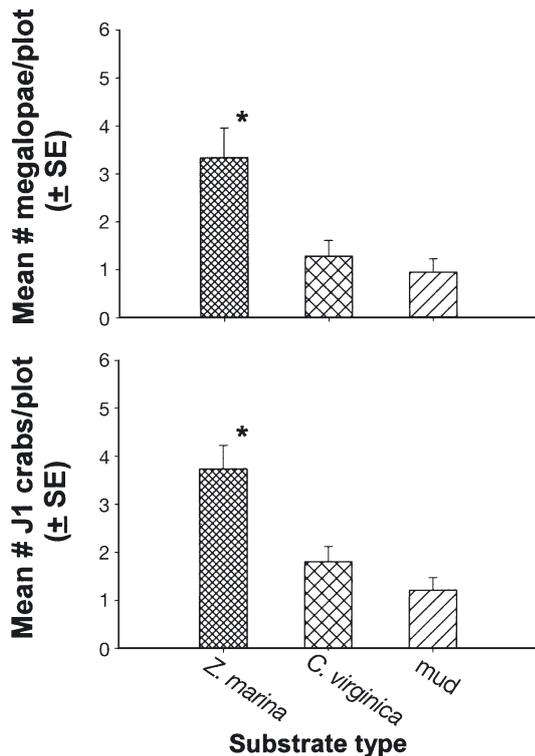


Fig. 5. *Callinectes sapidus*. Field experiment: number of (a) megalopae and (b) first juvenile stage (J1) crabs (mean  $\pm$  SE) found in substrates tested in nature. Megalopae and J1 crabs exhibited similar responses, with eelgrass containing significantly (\*) greater numbers of individuals than live oyster and mud substrates

blades were slightly wider and therefore overall surface area was somewhat greater) to live *Z. marina*; yet, on average, more than 3 times as many megalopae occurred in living, actively metabolizing plants than in artificial simulations. J1 crabs that metamorphosed during laboratory experiments showed similar responses to those in field experiments, suggesting that J1 crabs in field trials settled as megalopae, metamorphosed, and thereafter remained in the same habitat. Thus, the presence of recently metamorphosed J1 crabs probably reflected habitat selection while megalopae.

Our findings confirm suggestions by Orth & van Montfrans (1987) and Olmi et al. (1990) that colonization of seagrass beds in Chesapeake Bay occurs via the megalopa stage. Olmi et al. (1990) also indicated that J1 crab abundance reflected megalopal densities in the plankton, implying that the delivery of, and subsequent settlement by, megalopae are responsible for the initial densities of J1 crabs in seagrass beds. Physical forces that deliver megalopae to shallow-water areas undoubtedly act in concert with habitat-selection behavior to ultimately determine the initial distribution of blue crabs in nature.

Several investigations provide conflicting evidence for the ability of megalopae to actively orient toward and select settlement sites. Diaz et al. (1999) suggested that chemical and visual cues function in predator avoidance rather than habitat selection. Welch et al. (1997) found that blue crab megalopae are attracted to seagrass (*Zostera marina* and *Halodule wrightii*) cues, but avoid cues associated with salt marsh vegetation (*Spartina alterniflora*) and predators (*Uca* spp., *Panopeus herbstii*, *Palaemonetes pugio*). In contrast, Morgan et al. (1996) concluded that the ability of megalopae to discriminate between 3 types of experimentally transplanted vegetation (*Ruppia maritima*, *S. alterniflora* and *Juncus roemerianus*) was inconclusive due to low statistical power. However, strong non-significant trends in preference for seagrass (*R. maritima*) during periods of low megalopal abundance and *S. alterniflora* when settlement was high indicated that additional investigation into such processes is warranted.

Whereas megalopae preferred live *Zostera marina* substrates in our laboratory experiments, previously metamorphosed J1 stages of the blue crab did not. Rather, J1 crabs occurred predominantly in *Crassostrea virginica*, with more than 3 times the number of individuals found in live oysters than in sub-bleached shell substrates. Thus, like megalopae, J1 crabs also seem to respond to chemical rather than structural cues. Whether the apparent lack of preference by J1 crabs for live *Z. marina* is simply a laboratory artifact or an indication that J1 crabs actually change their habitat selection behavior is unclear.

Blue crabs are well known for their aggressive behavior (Mansour & Lipcius 1991) and cannibalistic tendencies (Mansour 1992, Moksnes et al. 1997) leading to density-dependent mortality or dispersal (Olmi et al. 1990, Pile et al. 1996, Moksnes et al. 1997, Etherington & Eggleston 2000, Heck et al. 2001). Although mortality (or loss) of megalopae and J1 crabs in our laboratory experiments was minimal, as evidenced by high recovery rates of experimental organisms, the limited amount of space available within each substrate offered ( $\sim 0.06 \text{ m}^2$ ) was likely too restrictive to accommodate the high densities of individuals. Thereby, their redistribution to other, potentially less desirable experimental substrates could have been affected by density-dependent interactions.

Density-dependent agonism as a mechanism for redistributing J1 crabs in our laboratory experimental treatments is likely. Olmi et al. (1990) evoked density-dependence as the cause of low spatial and temporal variability in natural juvenile crab densities, despite the occurrence of settlement peaks by megalopae at some sites but not others. Moksnes et al. (1997) suggested that relatively high rates of cannibalism and

agonism between J9 (9th juvenile) crabs and smaller (megalopae and J3) crabs could induce crab dispersal. Density-dependent agonism as a mechanism for post-settlement dispersal of newly settled crabs in North Carolina habitats was also evoked by Etherington & Eggleston (2000). Thus, density-dependent interactions can have a strong effect on post-settlement abundance patterns in nature (Olmi et al. 1990, Pile et al. 1996, Moksnes et al. 1997, Pardieck et al. 1999, Etherington & Eggleston 2000 (Moksnes 2002) and may also have been a factor in our experimental results.

Physiological state might also influence settlement of megalopae (Welch et al. 1997, Diaz et al. 1999). Previous studies conducted in the York River (Lipcius et al. 1990, Metcalf & Lipcius 1992) found that almost all individuals are in pre-molt by the time they reach our experimental field site. Though we did not quantify physiological state, the competency for settlement of the megalopae used in our laboratory experiments differed between trial dates, as evidenced by the significantly different rates of metamorphosis to J1 crabs (37% in September vs 16% in October). However, this factor did not substantially affect substrate selection behavior in our experiments (sensu Diaz et al. 1999).

Other factors such as predation (including cannibalism) could also affect post-settlement distribution. Mortality in our field experiment via fish or conspecific predation may have influenced the numbers of megalopae and J1 crabs found in experimental substrates, even though no small predatory fish such as gobies, blennies or shrimp (*Plaemonetes* spp., *Crangon septemspinosa*), or larger conspecifics, were found in our samples. Nevertheless, as local predators increase their feeding activity between dawn and dusk (Raffaelli & Hawkins 1996), habitat-specific predation might have confounded substrate selection results in the field. Cannibalism among recruited crabs, in particular, could have altered post-settlement survival (Moksnes et al. 1997, Moksnes 2002) in a habitat-specific manner. Cannibalism was minimal in our laboratory experiments, since a high percentage of experimental individuals were recovered and individuals were similar in size throughout the short experimental time period. It is likely that both habitat-selection behavior and predation interact in nature to influence initial distributions of early-stage juveniles.

The significantly greater number of newly recruited blue crabs quantified in previous studies from natural seagrass habitats relative to marsh creeks (Orth & van Montfrans 1987) can be explained, in part, by habitat preference behavior, and adds to the importance of vegetated habitats as nurseries (sensu Beck et al. 2001). Relatively high densities of crabs in seagrass habitats are maintained via reduced mortality of juvenile crabs (Pile et al. 1996, Schulman 1996, Orth &

van Montfrans 2002). Survival increases with crab size (Pile et al. 1996, Orth & van Montfrans 2002) as a function of shoot density (Schulman 1996). Thus, the accelerated growth rates exhibited by crabs in seagrass beds (Perkins-Visser et al. 1996) might impart an advantage for survival to that segment of the population in vegetated habitats.

Overall, the process of recruitment for blue crabs is complex and involves several intrinsic (i.e. physiological, behavioral) and extrinsic (i.e. currents, predation etc.) factors. Megalopae in the coastal ocean initiate vertical migration behavior when they encounter general, broad-scale estuarine cues (sensu Forward 1989, Forward et al. 1996, 1997), thereby enhancing their return from the coastal ocean to estuaries. Finer-scale habitat-specific cues (Welch et al. 1997, this study) determine, in part, the initial distribution of megalopae and J1 crabs within estuarine nursery habitats. Specific responses to estuarine nursery habitat types (e.g. seagrass beds, algal habitats) assure the greatest likelihood of recruitment success via accelerated metamorphosis to the J1 stage (Forward et al. 1994, 1996, Wolcott & DeVries 1994, Brumbaugh & McConaughy 1995), maximal survival (Pile et al. 1996, Orth & van Montfrans 2002) and accelerated growth (Perkins-Visser et al. 1996). Similar relationships may also occur in other estuarine-dependent species with comparable habitat requirements and similar life-history characteristics.

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