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Title: Shelter bottlenecks and self-regulation in blue crab populations: Assessing the roles of nursery habitats and juvenile interactions for shelter dependent organisms
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Research Category:
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Background and Objectives of the Research Project:

In many marine fish and crustaceans, young juvenile stages are vulnerable to predation, and their survival may be dependent on the availability of habitats that provide shelter from predators. In areas where the supply of the larval stages is high, such nursery habitats may become overcrowded and limiting for juvenile populations, resulting in density-dependent processes that can regulate their numbers. However, little is presently known regarding processes that can act as regulating mechanisms in juvenile marine organisms.

In the present project we studied the blue crab *Callinectes sapidus* in the Mobile Bay Estuary, Alabama, an area with documented high supply of blue crab postlarvae. The aim of the project was to determine if the availability of seagrass habitats can become a limiting resource for juvenile populations of blue crabs, and to test if competition and cannibalism between juveniles within seagrass beds can be important population regulating mechanisms. We hypothesized: (1) that competition for space or food within grass beds will result in density-dependent emigration from these habitats into unvegetated areas where mortality is higher, and (2) that cannibalism between juveniles is common and increases with either cannibal or prey densities. These hypotheses were tested at Dauphin Island Sea Lab and the surrounding area, and assessed on several spatio-temporal scales using both laboratory and field experimental techniques.

We believe this work could significantly improve our basic understanding of recruitment regulation in benthic organisms, and be broadly applicable to the management of shelter-dependent fishery species. Understanding whether a marine population is limited by the supply of larvae, or regulated by density-dependent processes after settlement is central for efficient conservation and management of marine habitats and organisms. If juvenile blue crabs are limited by nursery habitats, and not by larval supply in the Mobile Bay Estuary, the species may be better managed by protecting the seagrass and marsh habitats in the area, than by increasing the regulations on the fishery.

Progress Summary/Accomplishments

In the first year of the project (2001) the results from two extensive laboratory mesocosms experiments did not provide support of the hypothesis that competition within grass beds creates density-dependent emigration from the nursery habitats, but suggested that density-dependent juvenile cannibalism may act as a regulating mechanism. To further investigate the effect of cannibalism and also to test the influence of different juvenile habitats on the recruitment of juvenile blue crabs, two field experiments were performed in 2002.

In the first study a cage experiment was performed to assess the relative importance of postlarval habitat selection and predation on abundance and distribution of juvenile blue crabs among 4 different habitats: live oysters, seagrass (*Halodule wrightii*), artificial seagrass, and open mud. The experimental setup consisted of empty habitat patches provided with or without cages that would allow settling megalopae and the smallest juvenile crabs to pass through the mesh but stop predators. After a period 3 d the number of crabs that had colonized the habitats were sampled. High and similar numbers of blue crab settlers (megalopae and first instar crabs) colonized the oysters and natural and artificial seagrass habitats (140-350 settlers m^{-2}) whereas significantly lower numbers were found on the open mud habitat (35 to 70 settlers m^{-2}). This habitat specific settlement pattern was found also in cages where predators were excluded, suggesting that active habitat selection at settlement was responsible for the distribution. Similar settlement and survival in the three structurally complex habitats demonstrated that oysters constitute a potential important habitat for juvenile crabs, and that artificial grass could be used in the second experiment as a substitute for natural grass.

In the second experiment we enclosed different densities of juvenile blue crabs and assessed density-dependent effects on blue crab recruits (megalopae and first to third instar crabs) that colonized artificial seagrass patches inside the cages. High densities of blue crab recruits colonized the predator exclusion cages (466 recruits m^{-2} $3d^{-1}$), whereas densities of recruits were up to 7 times lower in cages containing cannibalistic crabs, in uncaged seagrass plots and in natural seagrass. A negative correlation was found between the number of enclosed cannibals and number of new recruits suggesting that early juvenile mortality is directly related to cannibal densities, and therefore to the survival of earlier cohorts. Further, proportional losses of megalopae and J1 crabs in cannibal inclusion cages were higher during periods of high compared to low settlement (70-86% and 31-54% loss $3d^{-1}$, respectively), indicating that the functional response of juvenile cannibals may decrease cannibalism at low prey densities. Laboratory experiments demonstrated that blue crabs settlers did not emigrate in response to juvenile cannibals, suggesting that the high loss rates in the field experiment represent settlement mortality.

The study demonstrates that density-dependent cannibalism between juvenile blue crabs can be a major source of early benthic mortality with large effects on local recruitment patterns. These results suggest that juvenile crabs can regulate new cohorts by cannibalizing more efficiently when smaller crabs are abundant, and by creating higher mortality rates on new settlers when cannibal densities are high. This regulating mechanism would limit the densities of crabs within nursery habitats, making the availability of seagrass, marsh, and oysters habitats a critical factor in the recruitment of juvenile blue crabs.

Publications/Presentations: (none yet)

Future Activities: Presentation of the results at the Benthic Ecology Meeting 2003. Publication of three manuscript from results of the project.

Supplemental Keywords: Habitat bottlenecks, Recruitment regulation, Post-settlement processes

Relevant Web Sites: None

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The relative importance of habitat selection and predation for the distribution of blue crab megalopae and young juveniles

Per-Olav Moksnes and Kenneth L. Heck Jr.

Abstract: Early benthic stages of many fish and mobile invertebrates are concentrated in structurally complex habitats, but the proximate causes of this distribution are usually not known. We assessed the relative role of three potentially important processes affecting the distribution of young juvenile blue crabs *Callinectes sapidus* Rathbun: (1) habitat selection at settlement, (2) selection of habitats by dispersing juveniles, and (3) habitat-specific predation rates. These processes were assessed concurrently over 2 to 3 days during summer and fall in a shallow nursery area in Alabama, using cage techniques.

Densities of blue crab settlers (megalopae and first instar crabs) in uncaged habitat patches were high and similar in artificial seagrass, live shoal grass *Halodule wrightii*, and live oyster habitats (on average 54-115 settlers m^{-2}), but significantly lower in mud (14 settlers m^{-2}). The same settlement pattern was found in habitats provided with predator exclusion cages, suggesting that habitat selection by megalopae was responsible for the distribution of settlers, and that predation had little effect on settlement. High settlement and survival in the oyster habitat indicate that oyster beds may constitute important nursery habitats for juvenile blue crabs. Active selection of several structurally complex habitats, including artificial habitats, suggests that blue crab megalopae are opportunistic rather than habitat specific in their choice of a settlement habitat, and indicate that flow or tactile cues from the physical structure are

more important than chemical cues when selecting between habitats. In contrast, settlement of a small panopeid megalopae (c.f. *Eurypanopeus* sp.) occurred almost exclusively in the oyster habitat where densities were on average 160x higher than in the other habitats. The specific selection of the adult habitat in the panopeid megalopae may reflect a more limited ability to redistribute after settlement, in comparison to juvenile blue crabs.

Second and third instar (J2-3) blue crabs also colonized the caged patches in high numbers, resulting in similar crab densities in the structurally complex habitats (on average 28 to 75 crabs m^{-2}) and significantly lower densities on mud (13 crabs m^{-2}) compared to natural shoal grass. Densities of J2-3 crabs were significantly lower in uncaged habitats (on average 44% loss), suggesting high predation mortality. However, the distribution of J2-3 crabs did not change significantly in the presence of local predators, demonstrating that habitat selection was the dominant process responsible for the habitat specific pattern. Densities of potential predators (mainly grass shrimp and juvenile cannibals) were on average 5 times higher in the structurally complex habitats compared to the mud habitat. The aggregation of small benthic predators and young juvenile blue crabs in the same habitats, coupled with density-dependent predation rates, appear to decrease the proximate effect of predation on the distribution of juvenile blue crabs. The distribution of colonizing J4-10 blue crabs in uncaged habitats differed from the distribution of settlers and J2-3 crabs by having low and similar densities in mud, oyster and natural shoal grass (on average 8 crabs m^{-2}), and significantly higher densities in the artificial seagrass (45 crabs m^{-2}), indicating an ontogentic change in habitat preference and distribution in older juveniles. These results suggest that active habitat selection at settlement followed by a dynamic redistribution of young juvenile crabs are the dominant proximate processes responsible for the habitat- and size-specific distribution of juvenile blue crabs.

Keyword: Early post-settlement mortality; Migration; Nursery habitats; Xanthid crab; *Palaemontets* sp.; *Crassostrea virginia*;

INTRODUCTION

In marine benthic organisms with pelagic larvae, settlement and early juvenile stages are a critical phase in the life-cycle because of high mortality that can substantially alter their abundance and distribution (see Ólafsson et al. 1994, Gosselin &Qan 1997, Hunt &Scheibling 1997, Olafsson et al. 1994 for review). Young juveniles of motile epibenthic organisms are often concentrated in structurally complex microhabitats that are thought to provide refuge from predation (e.g. crabs in mussel and seagrass beds [Klein-Breteler 1976, Heck &Orth 1980], lobsters in macroalgae and cobblestones [Herrnkind &Butler 1986, Wahle &Steneck 1991], bivalves in macroalgae [Bayne 1964, Petersen 1984], fish in macroalgae [Carr 1994, Eggleston 1995]). Decreased predation mortality in structurally complex habitats in comparison to unstructured sand or mud bottoms has been demonstrated for settling postlarvae of several decapod species in the laboratory (Johns &Mann 1987, Dittel et al. 1996, Moksnes et al. 1997, Moksnes et al. 1998) and for juvenile stages using tethering techniques (Wilson et al. 1987, Barshaw &Able 1990, Smith &Herrnkind 1992, Fernandez et al. 1993, Moksnes et al. 1998) and is often suggested as the process responsible for the non-random distribution of juveniles. However, since most field studies assessing juvenile mortality and distribution have been performed on older juveniles long after settlement (discussed by Keough &Downes 1982, Connell 1985, Hunt &Scheibling 1997) it remains unclear if differential predation is the proximate cause of the non-random distribution, or if habitat selection by postlarvae or juveniles, possibly in response to predation, are responsible.

Active habitat selection at settlement has been demonstrated in the laboratory for an increasing number decapod species with large and strong swimming postlarvae (Botero &Atema, 1982; Herrnkind &Butler, 1986; Fernandez et al. 1993, Liu &Loneragan 1997, Hedvall et al. 1998, Stevens &Kitaka 1998, van Montfrans et al. 2003). Settling stages of many decapods respond to various chemical and physical cues, including chemical cues from adult conspecifics (Jensen 1989, O'Connor 1991), various habitats (Forward et al. 1994, Wolcott & De Vries 1994, Brumbaugh & McConaugha 1995, Welch et al. 1997) and predators (Welch et al. 1997, Diaz et al. 1999), as well as light characteristics (Boudreau et al. 1990), and structural cues (Botero & Atema 1982, Fernandez et al. 1993, Hedvall et al. 1998). These studies suggest that many decapods have highly selective behavior during settlement, and that habitat selection by postlarvae may be responsible for the non-random distribution of juvenile stages. However, most studies have been performed in small containers with still water, and less is known about settlement behavior under natural flow conditions in the field (but see Eggleston &Armstrong 1995, Feldman et al. 1997, Moksnes 2002).

Post-settlement dispersal has recently received attention as an important process for juvenile distribution and local population dynamics (Palmer et al. 1996). Juveniles of many fish and invertebrate species are highly motile and redistribute between habitats after settlement with large effects on the juvenile distribution on both local (Frederick 1997, Moksnes 2002) and regional scales (Beukema & de Vlas 1989, Etherington & Eggleston 2000). Still, the effect of juvenile dispersal on abundance and distribution of benthic organisms is often ignored or minimized in experiments addressing mortality and recruitment in motile organisms (see Palmer et al. 1996 for discussion). Few attempts have been made to assess habitat selection at settlement, early post-settlement predation and habitat selection by juveniles concurrently in the field, and there is a general lack of understanding on how these processes interact, and of their relative importance for settlement and post-settlement distribution of young recruits.

In the present study we assess the relative role of (1) selection of habitats at settlement, (2) habitat selection by dispersing young juveniles, and (3) habitat-specific predation rates as they affect the distribution of young juvenile blue crabs among 4 different microhabitats within a shallow nursery area. These processes were assessed concurrently over 2 to 3 days using cage techniques. The aim of the study was (1) to test the proximate effect of these 3 processes on the juvenile distribution within nursery areas, (2) to investigate whether blue crab megalopae select one specific habitat based on particular cues, or whether any structurally complex habitat is selected for settlement, and (3) to assess the nursery value of live oyster habitats in terms of settlement densities and refuge from predation for young juvenile blue crabs.

Study system

The blue crab *Callinectes sapidus* Rathbun is a large, epibenthic omnivore that inhabits soft-bottom coastal areas from Canada to Brazil (Williams 1984), and is one of the most ecologically (e.g. Hines et al. 1990) and commercially important species (e.g. NMFS, 1988) in estuaries of the Western Atlantic and Gulf of Mexico. Blue crabs have a complex life cycle in which planktonic larvae are advected from estuaries and undergoes development in coastal waters. In the Gulf of Mexico, ovigerous females migrate from oligohaline areas to the mouths of estuaries and release larvae from February to October (Daugherty 1952, Perry 1975, Milliken &Williams 1984). After 5 to 10 weeks offshore (Costlow & Brookhout 1959) the postlarvae (megalopae) reinvade the estuaries from March to November, with a peak settlement occurring in August -September (Stuck & Perry 1981, Rabalais et al. 1995, Morgan et al. 1996) when high densities of young juvenile crabs are found in shallow water habitats (Heck et al. 2001, Spitzer et al. 2003).

Young juvenile blue crabs (< 20 mm spine to spine carapace width; CW) are concentrated in structurally complex habitats and as many as 90% of the juveniles in a given area may occur in seagrass or submerged marshes (Perry 1975, Heck & Orth 1980, Weinstein & Brooks 1983, Heck & Thoman 1984, Orth & van Montfrans 1987). In the Chesapeake Bay, the settlement and juvenile habitat for blue crabs is primarily seagrass (i.e. *Z. marina* and *Ruppia maritima*; Heck & Thoman 1981, Orth & van Montfrans 1987, Pardieck et al. 1999), whereas in the Gulf of Mexico high densities of young juvenile crabs are also found marsh habitats (Thomas et al. 1990, Wilson et al. 1990a, Heck et al. 2001, Spitzer et al. 2003, review by Zimmerman et al. 2000). In contrast to the Atlantic coast, marshes in the northeast gulf coast are partly flooded more or less continuously during summer and fall due to increased monthly sea levels coupled with southerly winds (Stout 1984), which likely explains the higher abundance of juveniles in gulf coast marshes. Recent studies have found high densities of young juvenile blue crabs also in macroalgae (Wilson et al. 1990, **Epifanio et al. 2003**), milfoil *Myriophyllum spicatum* and shallow detrital habitats (Etherington & Eggleston 2000), and coarse woody debris (Everett & Ruiz 1993), **demonstrating that blue crabs can settle and survive in a many different habitats, and** indicating that these habitats may provide important alternative nursery habitats for blue crabs in estuarine systems lacking extensive seagrass beds or **flooded** marsh habitats. **In the southern part of Mobile Bay area, Alabama, where salinities are high enough to allow blue crab settlement (Morgan et al. 1996), the dominant habitats for juvenile blue crabs are salt marshes and submerged aquatic vegetation, which cover approximately 3291 ha and 1861 ha, respectively (Stout 1990).** Both habitats harbor similarly high densities of young juveniles (yearly average range from 36 to 76 crabs m^{-2}; Heck et al. 2001, Spitzer et al. 2003). Oyster reefs are also an abundant shallow water habitat in **the southern part of Mobile Bay (approximately 1210 ha; Stout 1990)** that represent a potential nursery habitat for juvenile blue crabs. However, little is presently known regarding settlement rates, juvenile densities and survival rates in oyster habitats (but see van Montfrans et al. 2003).

Laboratory and field tethering experiments have demonstrated that predation mortality in juvenile blue crabs is lower in seagrass and algal habitats than on unstructured sand and mud habitats (Wilson et al. 1987, 1990, Pile et al. 1996, Moksnes et al. 1997), suggesting that predation may be the proximate process for the juvenile distribution within shallow nursery areas. However, recent laboratory experiments have demonstrated that blue crab megalopae actively select seagrass over other available habitats (van Montfrans et al. 2003) suggesting that habitat selection at settlement may be responsible for juvenile patterns in the field. Moreover, the distribution of young juvenile crabs among two seagrass species in Chesapeake Bay differed between size classes (Pardieck et al. 1999), suggesting either an ontogenetic change in habitat preference and redistribution of juvenile crabs, or habitat specific predation rates. No study to date has concurrently assessed habitat selection of megalopae and juveniles, and predation in natural field conditions, and little is known regarding their relative importance for the distribution of juvenile blue crabs.

MATERIAL AND METHODS

The study area

The cage experiment was carried out at Point aux Pins, the eastern tip of a shallow (< 2m) soft sediment embayment of the Mississippi Sound, Alabama (Lat. 30° 22´28´´Long 88° 15´22´´**Fig. 1**). This relatively pristine area is affected by a fresh water outflow from Mobile Bay estuary and mean summer salinity normally range from 20 to 27 ppt (Morgan et al. 1996). Summer temperatures in the shallow bay are stable around 30 °C (Stutes 1996). The tides are diurnal, with semidiurnal tides occurring every 2 weeks during minimum tidal amplitudes, and with a mean tidal amplitude of approximately 40 cm. The site is protected from wave exposure and current speeds are low (1.3-4.3 cm/s; Morgan et al. 1996). The shore is lined with marshes, mostly black needlerush *Juncus roemerianus,* and lesser amounts of smooth cordgrass *Spartina alterniflora*. In the shallow water (<0.3 m MWL) outside the march, scattered patches of oysters (*Crassostrea virginia*) are found, which are replaced by a more or less continuous seagrass bed in deeper water. In the spring, widgeon grass *Ruppia maritima* dominates, butis replaced by shoal grass *Halodule wrightii* in August. Shoal grass is an unbranched Cymodocean with fine, short leaves (<3 mm in width). At Point aux Pins, average leaf length and density in August and September are around 14 cm and 5000 leaves m^{-2} (Stutes 1996). Because of high turbidity, seagrass rarely grow deeper than 1 m.

Preliminary studies of cage artifacts

We were concerned that the mesh used in the cage experiment could constitute a settlement substrate for blue crab megalopae and function as a filter that either artificially increased or decreased the number of settlers in caged versus uncaged habitats. To study how the behavior of blue crab megalopae and young juvenile crabs was affected by the cage structure, and to test if it affected the colonization rates of habitats inside cages, we performed preliminary laboratory and field experiments.

A laboratory experiment was carried out at Dauphin Island Sea Lab in August 2002 to observe how megalopae and juvenile crabs behaved when encountering the cage and to test if the cage affected colonization rates. The experiment was performed in two large tanks (2.4 x 0.45 m; l x w) made of transparent acrylic sheets. The bottom of the tanks was covered with a 2 cm layer of sieved (750 µm) dry beach sand, and filled to 30 cm depth with natural sea water (total volume 336 l). A slow, flow-through current (**3** l $min.^{-1}$) was generated along the tanks by pumping water in at one end of the tank, and letting it overflow at the opposite end. A patch of artificial seagrass from the field experiment (see below for details) was placed in the center of each tank. In one randomly chosen tank, two sheets (0.45 x 0.45 m) of the same 3 mm mesh net used in the cage experiment were placed on each side of the patch, approximately 1.4 m apart, covering the cross section of the tank. At the beginning of an experimental trial, approximately 20 blue crab megalopae and 20 second juvenile instar (J2) crabs were introduced at the upstream end of the tank and left for approximately 16 h over night. Observations of crab behaviors were made during the first 30 min and at the end of each trial. Upon termination of a trial, 2 PVC-partitions were pushed into the sediment on each side of the patch to separate the seagrass patch from the cage mesh. Crabs were collected with hand nets in each of the 3 resulting sections of the tank. Recovered crabs were enumerated alive. Four replicate trials with and without cage mesh were assessed. The proportion of recovered megalopae and J2 crabs found in the seagrass patches were separately tested as dependent variables in a one factor ANOVA models using cage mesh (absent or present) as the independent variable.

A field experiment was carried out to assess if settlement of blue crabs inside experimental cages reflected estimates of settlement on "standardized" artificial settlement collectors. The collectors consisted of ‘hogs-hair’ air-conditioner filter material wrapped around a PVC-pipe that floated at the surface (see van Montfrans et al. 1995 for details on the method). We used 3 experimental cages with a 3 mm mesh that allowed blue crab megalopae and first instar juveniles (J1 crabs) to pass through. The cages were placed 30 m apart at 0.7 m depth on unvegetated mud bottom and carefully emptied on epifauna prior to the start of each trial (se below for details). A collector was placed inside and next to each cage, and retrieved after 24 h. Four trials were performed from August 8 to September 30. The number of blue crab settlers (megalopae + J1 crabs) was analyzed both in a two factor mixed model ANOVA using treatment (caged and open; fixed factor) and date (random factor) as the independent variables, and in a simple linear regression analysis between paired caged and open collectors.

Because the uncaged collectors were floating at the surface at 1 m depth, above open mud bottom, we assumed that predation on these collectors would be reduced, and a significant correlation between caged and open collectors would indicate that the cage artifact did not seriously affect settlement in the cages. This experiment would also provide an estimate of predation on settlement collectors.

Cage experiment - settlement, predation and post-settlement movements

To assess the relative importance of habitat selection by postlarvae and juveniles, and of predation on the abundance and distribution of juvenile blue crabs, a cage experiment was performed in August and September 2002. The experimental setup consisted of small habitat patches placed in a shallow nursery area either with or without cages. The mesh of the cages allowed settling megalopae and the smallest juvenile crabs to enter, but prevented most predators from entering. We assessed 4 types of habitat treatments: natural shoal grass, artificial **sea**grass, oysters and mud, and 2 types of cage treatments: plots with and without predator-exclusion cage. The experimental setup was repeated 2 times using three and four replicates of each cage-habitat combination in the first and second trials, respectively.

The cages were 1.41 m x 1.41 m x 1.25 m (l x w x h) with no top or bottom, were made of polyethylene non-woven fibers with 3 mm mesh, and were supported by a 9.5 cm reinforcement bar frame. This mesh allowed blue crab megalopae and juveniles up to 5.5 mm spine to spine carapace width (CW) to pass through the mesh, but excluded most potential predators on blue crab megalopae and larger juveniles. The lower 15 cm of the cages were buried into the sediment, and the upper parts remained above the water surface at all times. The habitats were placed in the center of each cage in a circular patch of approx. 0.17 m^2. Thus the experimental habitats were separated by at least 1 m from the cage walls. The habitats consisted of: (1) live shoal grass *H. wrightii* (approx. 4000 shoots m^{-2}, of 15-20 cm length, equivalent to natural densities in the study area; Stutes 1996), that was transplanted with intact sediment from natural grass beds next to the cages, and whose epifauna was removed by carefully lifting the grass above the water and shaking the shoots in the water; (2) artificial seagrass mats made from green polypropylene plastic ribbons tied to a plastic mesh at 200 shoots per mat (4 blades per shoot of approximately 6 mm width and 45 cm lengths, equivalent of approximately 1150 shoots m^{-2}); (3) oyster clumps of live oysters and oyster shells (approximately 40 live and dead oysters, respectively), collected in the area and soaked in freshwater for 30 min, shaken under water and visually inspected to remove epifauna, and placed in a natural upright position, in a tightly packed patch that reached approximately 10-15 cm above the sediment; and (4) bare mud from which structured substrates (e.g. oyster shell and drift algae) were removed as necessary. The artificial grass was used to simulate a wide-leafed seagrass habitat at high natural density (i.e. turtle grass, a dominant nursery habitat for juvenile blue crabs in other areas), and to assess the importance of physical structure vs. chemical cues of the habitat in blue crab settlement. Cages and uncaged plots were placed in a single row along shore, approximately 5-10 m apart. At the start of an experimental trial, cages were carefully emptied of animals using hand held dip nets and a suction sampler (c.f. Orth &van Montfrans 1987) driven by a gasoline-powered pump (Honda WB 20X). Experimental treatments were randomly allocated to the plots. Uncaged natural seagrass and mud plots consisted of natural habitat patches of similar size that were emptied of epifauna at the start of an trial by hand.

At the end of a trial, the experimental plots were sampled by placing a 1 m tall plastic sampling cylinder with a bottom area of 0.20 m^2 over the habitat and into the sediment. The cylinder was subsequently emptied, including the top 2 cm of the sediment, into a 500 µm sieve using the suction sampler. Thus, only the 0.20 m^2 plot in the center of the cages was sampled to avoid including animals on the cage structure. The samples were immediately put on ice and later frozen before analysis in the laboratory. The cages were subsequently sampled by dip nets to assess if any unwanted predators were present. All epibenthic animals were identified under stereo microscops, measured and enumerated. *Callinectes sapidus* megalopae and juvenile crabs were distinguished from *C. similis* using the criteria established by Stuck & Perry (1982). In the first trial, the experiment was run for 2 d (August 13-15) and the habitat plots were placed at approximately 0.7 m depth (MWL), about 50 m from the marsh edge. Because of problems with low settlement rates and flooding of the cages (see results), the second trial was run for 3 d (September 16 to 18), in a shallower location (0.4 m depth MWL), approximately 10 to 20 m from the marsh edge. An independent estimate of blue crab settlement was obtained using standardized artificial settlement collectors, to determine whether settlement in the caged habitats reflected larval supply at the study site. Three replicate collectors were sampled concurrently with each cage trial. Each were immersed for 24 h, floated at the surface next to cages, and was collected during daylight.

The number of blue crab settlers (megalopae and J1 crabs), the proportion J1 crabs (no. J1 crabs/no. settlers). the number of second and third juvenile instars (J2-3 crabs; 4.1-6.0 mm CW), and the number of potential predators on blue crab megalopae and J1-3 crabs (cannibalistic juvenile blue crabs >6.0 mm CW, shrimp >7 mm carapace length, fish > 15 mm total length; Olmi & Lipcius 1991, Moksnes et al. 1997) were tested separately as dependent variables in a 2-factor ANOVA using habitat (seagrass, artificial grass oyster, and mud), cage (predator-exclusion, and uncaged plots) as the independent variables. If habitat specific predation changed the distribution of juvenile crabs, the interaction effects between cage and habitat should have been significant. The number of larger juvenile crabs (>6.0 mm CW) in open habitat plots were analyzed in a one factor ANOVA using habitat as the independent variable. Each trial was analyzed separately because of problems with excluding predators in trial 1 (see results) and because different exposure times and replicates were used in the two trials. Before analyses were performed, all data were tested for homoscedasticity with Cochran's C-test (Sokal &Rohlf 1981), and log(x+1)-transformed to homogenize variances. A posteriori multiple comparison tests were carried out with the Student-Newman-Keuls (SNK) procedure.

RESULTS

Pilot studies - Cage artifacts

In the laboratory study, recovery rate of megalopae and J2 crabs were 87% and 99% on average, respectively. Losses of megalopae were likely due to cannibalism from J2 crabs since recovery rates of megalopae in tanks without larger conspecifics were 100% (n=10; Moksnes unpubl. data). Direct observations of megalopae at the beginning of each laboratory trial showed that many postlarvae swam straight through the 3 mm mesh, but that most, after encountering the net, either landed on and clung to the mesh, or turned around and swam away from it. Many J2 crabs also hesitated upon encountering the net, and dug into the sediment next to it. At the end of the trials only a few megalopae or J2 crabs were seen on the nets (<10% on average).

The proportion of the recovered megalopae found in the artificial seagrass patch was not significantly affected by the presence of a cage ($F = 1.92$, $df = 1, 6$, $p = 0.21$), although a trend of lower settlement in the grass was observed in treatments with a cage mesh (43% on average) in comparison with those without (62%). A similar, non-significant, trend was observed for J2 crabs where 39% and 63% of the crabs were found in the seagrass patch in treatments with and without cage mesh, respectively ($F = 3.25$, $df = 1, 6$, $p = 0.11$). Settlement was on average 31% and 38% lower in caged seagrass patches in comparison with uncaged treatments for megalopae and J2 crabs, respectively. These results indicate that the cage artifact should not seriously affect settlement rates in caged habitats, and most importantly, that the direction of this artifact is to decrease settlement inside cages in comparisons to habitats without cages. Thus, comparisons between open and caged habitats should produce a conservative estimate of predation mortality on juvenile crabs.

In the field experiment with artificial collectors, larval supply varied significantly between 14 and 49 settlers collector^{-1} 24 h^{-1} during the 4 experimental trials, and the number of settlers was significantly higher on caged than uncaged collectors in all trials (**Table 1**). The losses on uncaged collectors varied between 6 and 34%. The number of settlers on uncaged and caged collectors correlated significantly and showed a good fit (Linear regression analysis; $F = 29.3$, $df = 1, 10$, $p = 0.001$, $r^2 = 0.75$; **Fig. 2**). These preliminary results suggest that the mesh tended to decrease settlement inside the experimental cages, but that this artifact is small and constant so that settlement in caged habitats still represented larval supply to the site. These results also indicate that predation on uncaged collectors in shallow water can be significant (on average 20%), but that it did not obscure the temporal settlement pattern in this experiment. **This study is the first to assess the effect of predation on blue crab settlement on artificial collectors and the results indicate that this common method to estimate larval supply may not be seriously affected by variable predation rates, consistent with the results from a similar study of *Carcinus maenas* megalopa (Moksnes & Wennhage 2001).**

Cage experiment - settlement, predation and post-settlement movements

The cage experiment indicated that active habitat selection by both megalopae and juvenile crabs affected the distribution of juvenile crabs within the nursery area. Predation was variable and at times high in both open mud bottom and structurally complex habitats, but had little effect on the distribution of settlers and juvenile crabs.

In the first trial in August, high water levels flooded the cages the last night of the experiment, allowing some potential predators on juvenile crabs to enter the cages (mainly juvenile blue crabs and adult grass shrimp), and, therefore, the number of predators did not differ significantly between caged and open habitats, although the average density of predators on open plots was more than twice as high (**Fig. 3; Table 2**). Overall, significantly more predators were collected in artificial seagrass and oyster habitats than in natural seagrass and mud habitat (SNK-test at $p < 0.05$). The number of predators was low and similar between habitats in caged habitat plots (1 and 5 predators plot^{-1}), whereas in open plots densities of predators appeared higher in artificial grass and oysters (18 and 10 predators plot^{-1}, respectively) than in natural grass and mud (1 predator plot^{-1}). However, the interaction effect was not significant ($p = 0.06$).

Low numbers of settlers (megalopae + J1 crabs) were collected on the artificial settlement collectors during the 2 day trial (on average 2.6 d^{-1}). The numbers of settlers were also low in the experimental habitat plots, but densities still differed significantly between habitats in both caged and open treatments; no effect of cage treatments were seen (**Fig. 4; Table 2**). Densities of settlers were significantly higher in artificial grass (7.8 settlers plot^{-1}) compared to oysters and mud habitats (1.7 and 1.0 settlers plot^{-1}, respectively), while densities in natural seagrass (4.8 settlers plot^{-1}) did not differ from the other habitats (SNK-test at $p < 0.05$). Most settlers were J1 crabs (84%) at the end of the trial. The low number of settlers in the sample precluded a test of the proportion of J1 crabs. Low numbers of J2-3 blue crabs colonized all habitat plots and densities appeared higher in natural grass (on average 2.2 crabs plot^{-1}) compared to mud habitats (0.8 crabs plot^{-1}), and consistently lower in uncaged compared to caged habitats (on average 43% lower). However, no significant treatment effects were found (**Fig. 5; Table 2**). Larger juveniles (6.1-20.0 mm CW; approximately J4-10 crabs) colonized the open habitat plots in low numbers (0-2.7 crabs plot^{-1}) but no significant habitat effects were found (**Fig. 6; Table 3**).

High settlement of a small **panopeid crab (Xanthoidea: Panopeidae;** megalopae and J1 crabs 0.7 and 1.2 mm CW, respectively; c.f. ***Eurypanopeus* sp.**) occurred during the experiment, and almost exclusively in the oyster habitat (on average 77 settlers plot^{-1}), which differed significantly from all other habitats (<2 settlers plot^{-1}). No significant effects of cage treatments were found although settlement densities were on average 36% lower in uncaged oyster habitats than in caged treatments; no losses occurred in the other habitats (**Fig. 7; Table 4**; SNK-test at $p < 0.05$).

In the second trial in September, significantly higher densities of predators were found in the open plots in all habitats (**Fig. 3; Table 2**). The differences were most pronounced in the artificial seagrass habitat, in which, on average, 5 x higher density of predators were collected in the uncaged habitat (mainly grass shrimp and juvenile blue crabs). Densities of predators also differed between habitats, and significantly higher densities of predators were collected in artificial grass and oyster habitats (9.0 and 5.1 predators plot^{-1}, respectively) compared to the mud habitat (1.4 predators plot^{-1}); densities in natural seagrass (2.9 predators plot^{-1}) did not differ from the other habitats (**Fig. 3; Table 2**; SNK-test at $p < 0.05$). Juvenile blue crabs, grass shrimp **(*Palaemonetes* spp.)** and gobiid fish, and to a lesser extent juvenile penaeid shrimp dominated the predator assemblage in the open habitat plots in both trials.

The settlement collectors demonstrated high larval supply of blue crabs during the 3 d trial (on average 67.9 settlers d^{-1}), which was reflected in high settlement densities in the habitat plots. Densities of settlers were significantly lower in mud (on average 6.9 settlers plot^{-1}) compared to the 3 structurally complex habitats (20.3 to 35.1 settlers plot^{-1}), which did not differ from each other, and there was no significant effect of cages (**Fig. 4; Table 2**; SNK-test at $p < 0.05$). The number of settlers in the structurally complex habitats was more similar in the caged treatments (25.3 to 26.8 settlers plot^{-1}), compared to the open habitats (13.7 to 44.5 settlers plot^{-1}), but the cage x habitat interaction effect was not significant ($p = 0.16$). The proportion of J1 crabs (no. J1 crabs/no settlers) was similar between caged and uncaged treatments (85% and 84 %, respectively), and between the different habitats (74% to 92%), and did not differ significantly between treatments (**Table 2**).

High numbers of J2-3 blue crabs also colonized the habitat plots (up to 43 crabs plot^{-1}), and both the cage and habitat treatments had significant effects on juvenile densities (**Fig. 5; Table 2**). Significantly higher densities of J2-3 crabs were found in all the caged habitats compared to the uncaged plots. The proportional difference between caged and open habitatss appeared to be largest in natural grass (72%) and smallest in mud (16%), but this difference did cause a significant cage x habitat interaction effect ($p = 0.13$). Significantly higher densities of J2-3 crabs were found in the natural grass habitat (26.8 crabs plot^{-1}) compared to mud (3.6 crabs plot^{-1}), in both caged and open plots. Densities in artificial grass and oysters habitats (9.9 and 9.4 crabs plot^{-1}, respectively) did not differ significantly from the other habitats (SNK-test at $p < 0.05$). The distribution of larger juvenile blue crabs (6.1-20.0 mm CW) in open habitat plots differed from J2-3 crab distribution, and significantly higher densities were collected in the artificial seagrass habitat (9.0 crabs plot^{-1}) compared to the other habitats (1-2.3 crabs plot^{-1}), which did not differ significantly from each other (**Fig. 6; Table 3**; SNK-test at $p < 0.05$)

High settlement of **the panopeid megalopae** occurred also in the second trial and, similar to the first, significantly higher densities were found in the oyster habitat (on average 67 settlers plot^{-1}) compared to the other habitats (< 4 settlers plot^{-1}). No significant effects of cage treatments were found although settlement densities were on average 50% lower in uncaged oyster habitats than in caged treatments (**Fig. 7; Table 4**; SNK-test at $p < 0.05$). Salinity and temperature varied between 20 and 24 psu, and 29 and 30.5° C, respectively during the experimental periods.

DISCUSSION

Habitat selection

Seagrass beds and marshes are thought to provide a nursery function for blue crabs and many other invertebrate and fish species by increasing survival and growth and subsequent export of individuals to the adult population, in comparison to other juvenile habitats (see Heck et al. 2003, Beck et al. 2003 for review). **However, for small, vulnerable blue crab settlers the risk of predation may be extremely high in these shallow habitats due to the high density of juvenile fish, shrimp and cannibalistic conspecifics that also aggregate there**, as well as high densities of resident small fish (e.g. *Fundulus* spp) and grass shrimp (*Palaemonetes* spp.), most which can cause high predation mortality on blue crabs settlers (Olmi & Lipcius 1991, Moksnes et al. 1997, Orth & van Montfrans 2002). This is supported by field experiments where predation mortality on tethered young juvenile blue crabs in seagrass and marsh habitats often exceed 90% 24 h^{-1} in the study area (Heck et al. 2001, Spitzer et al. 2003) and 70% 24 h^{-1} in Chesapeake Bay (Pile et al. 1996). Thus, although shallow nursery areas provide favorable temperatures and resources for juvenile growth, refuge rather than growth should be the main concern during settlement and the early benthic stages. Blue crab megalopae that are carried into shallow water habitats should therefore avoid unstructured mud and sand habitats where predation mortality can be even higher (Pile et al. 1996, Moksnes et al. 1997, Heck et al. 2001), and select the first refuge providing habitat they encounter. Because juvenile blue crabs are good swimmers, they could redistribute to more optimal habitats after settlement and metamorphosis. **This conceptual settlement model was supported in the present study where blue crab megalopae indiscriminately selected all structurally complex habitats for settlement over unstructured mud, and where young benthic crabs quickly redistributed within the nursery area resulting in a size-specific distribution between habitats.**

Blue crab settlers. Blue crab settlement in predator exclusion cages was similarly high in artificial seagrass, live shoal grass, and live oyster habitats (on average 69-89 settlers m^{-2}), but significantly lower in mud (on average 26 settlers m^{-2}). **This pattern was clearest in the September trial when larval supply was high, and the exclusion of predators was more successful. Because this settlement pattern occurred in caged habitat where predation was substantially reduced, the result suggests that megalopae actively selected all the structurally complex habitats over mud. The settlement distribution between habitats did not change in the uncaged treatments despite high densities of potential predators (on average 33 predators m^{-2}; mainly grass shrimp and larger juvenile cannibals**), suggesting that habitat selection at settlement was the **dominant** process affecting the initial distribution of juvenile blue crabs, and that predation **may have little direct effect** on settlement patterns. Settlement in live oyster clumps varied between trials, but was significantly higher than mud in September when the highest settlement of all habitat treatments occurred in the uncaged oyster habitat (on average 223 settlers m^{-2}). This result demonstrates that blue crab megalopae can use live oyster habitats as initial settlement sites, and that survival during settlement and metamorphosis in oysters can be high despite high numbers of potential predators, suggesting that oyster beds may constitute important nursery habitats for juvenile blue crabs.

These results suggest that blue crab megalopae are opportunistic rather than habitat specific in their choice of a settlement habitat. Moreover, the high settlement in artificial seagrass that were clean from epiphytes and epifauna suggest that physical structure was more important than a habitat specific chemical cue in the habitat choice, and indicate that a settlement habitat is selected for refuge rather than for food. That blue crabs are opportunistic in their choice of a settlement habitat is supported by most studies that have assessed the distribution of blue crab settlers concurrently in several structurally complex habitats. In the study area, densities of blue crab settlers are often similarly high in both seagrass (*H. wrighthii*, *R. maritima*) and marsh habitats (Heck et al. 2001). In a field experiment **with uncaged habitats**, settlement densities were always very low on open mud, **but high and similar in both** live seagrass *R. maritima* and live marsh grass *S. alterniflora* and *J. roemerianus* (Morgan et al. 1996), as in this study. **In a similar study,** Eggleston et al. (1998) **found high settlement in both** artificial seagrass and oyster shell habitats in North Carolina, USA. In Chesapeake Bay, blue crab settlers were found principally in seagrass, and less in marsh habitats (Orth & van Montfrans 1987, 1990), but densities were similar in different seagrass species (e.g. *Z. marina* and *R. maritima*; Pardieck et al. 1999). Moreover, the fact that blue crabs settle and metamorphose in high numbers on artificial settlement collectors in many areas in both the Atlantic and in the Gulf of Mexico, even when they are located next to large seagrass beds (van Montfrans et al. 1995, Rabalais et al. 1995, Morgan et al. 1996, this study) supports the hypothesis that **premolt** megalopae select the first refuge habitat they encounter **in the nursery area**. The only contrasting result is from a field experiment in Chesapeake Bay where settlement densities were significantly higher in live *Z. marina* than in live oysters and mud (van Montfrans et al. 2003). However, because predators had access to the habitats it is not clear whether this pattern was due to habitat selection or habitat specific predation rates. Selection for a non-specific structurally complex habitat has also been demonstrated for green crab megalopae *Carcinus maenas* (Hedvall et al. 1998, Moksnes 2002) and may be common in highly mobile decapods such as portunid crabs that can easily redistribute after settlement.

These results are not consistent with suggestions that habitat-specific chemical cues play a dominant role when blue crab megalopae select a settlement habitat. Metamorphosis in blue crab megalopae is accelerated by chemical cues from both eelgrass *Z. marina* and salt marsh vegetation (Forward et al. 1994, Wolcott & De Vries 1994, Forward et al. 1996) and it has been proposed that megalopae **use chemical cues to select between settlement habitats** (Welch et al. 1997, **Forward et al. 2003**, van Montfrans et al. 2003). **Although evidence is mounting that the behavior of premolt megalopae is strongly affected by various chemical cues, their role in the selection between microhabitats is less clear. Forward et al. (2003) demonstrated in an elegant laboratory flume study that premolt megalopae swam upstream in response to decreasing turbulence (simulating the end of an nocturnal flood-tide) only when odors from *Z. marina* or *S. alterniflora* were present in the water, suggesting that megalopae use chemical cues from aquatic vegetation to swim towards a settlement site. In support of this result,** megalopae in still-water laboratory experiments preferred live *Z. marina* over artificial seagrass with similar dimensions (van Montfrans et al. 2003). **However, these results were not supported in laboratory choice experiments in which premolt megalopae did not responded to cues from *Z. marina*** (Welch et al. 1997, Diaz et al. 1999), **possibly because these studies were performed in still water conditions (Forward et al. 2003). In a field study,** chemical cues from *S. alterniflora*, *Z. marina* and *H. wrightii* had no effects on overall blue crab settlement densities on artificial collectors, but odors from the latter two increased the proportion of premolt megalopae (Welch et al. 1997). **Negative chemical cues appear to generate a stronger effect on megalopal behaviors, and odors from various predators (e.g *Paleamonetes pugio, Uca* spp., *Panopeus herbstii*) and live oysters (*C. virginia*) decreased settlement on artificial collectors (Welch et al. 1997). Chemical cues prom predators also stimulated a flight response in megalopae (Diaz et al. 1999) and decreased the positive response to cues from aquatic vegetation (Forward et al. 2003).**

In contrast to these studies, our results do not support that chemical cues play a major role in the selection of a settlement habitat in natural field conditions. We found the highest settlement in live oyster patches, and similar high settlement in artificial seagrass and live *H. wrightii*, although the former lacked positive chemical cues, and harbored >25x higher densities of *Palaemonetes* spp. (on average 52 m^{-2}) than did *H. wrightii* in uncaged treatments. Although the canopy height and total surface area were larger for the artificial seagrass than for the shoal grass patch, which could have confounded an effect of chemical cues, these variables appeared less important since the highest settlement occurred in the oyster habitat with the smallest vertical profile and surface area. Moreover, the artificial grass **and oyster habitats** were not selected due to a lack of alternative habitats since the experimental plots were surrounded by natural grass beds. Neither were **they** selected as a transient habitats by megalopae not competent to settle (c.f. Morgan et al. 1996) since over 84% of all settlers were J1 crabs when the habitats were sampled after 2 to 3 days, **and the proportion J1 crabs did not differ between habitats**. **Thus, the present results indicate that flow patterns generated by the habitat and/or tactile cues from the physical structure are more important than chemical cues when selecting a settlement habitat.** Positive cues from seagrass and marsh habitats may play an important role in accelerating megalopae into premolt so that metamorphosis can occur quickly once a structurally complex shallow water habitat is encountered, **and be important also in the large scale selection of a settlement area, as indicated by Forward et al. (2003). However, once in a shallow nursery area, the abundance of various positive and negative chemical cues may cancel each other out, making physical cues more important in the selection of microhabitats. Further studies assessing how various chemical cues in different concentrations interact with each other and with physical stimuli in a flow environment are necessary to understand the complex process of habitat selection in blue crab megalopae.**

Juvenile blue crabs. High numbers of J2-3 blue crabs colonized the predator exclusion cages in September resulting in similarly high densities in the structurally complex habitats (on average 28 to 75 crabs m^{-2}) and **significantly** lower densities on mud (on average 13 crabs m^{-2}) **compared to natural shoal grass**. This result demonstrates that young juvenile crabs are highly mobile within nursery habitats and redistribute soon after metamorphosis. Because a megalopa cannot molt into a J2 crabs during the 2 to 3 d period of the experiment (Milliken & Williams 1984), the distribution of J2-3 crab was not a result of settlement and subsequent growth. **However, because blue crab settlers and J2-3 crabs demonstrated similar habitat preferences, the movements by J2-3 crabs did not cause a significant change of the initial settlement distribution, although a preference for natural shoal grass was indicated for J2-3 crabs.** The distribution of J2-3 crabs did not change **significantly** in the presence of local predators, although significant losses occurred in all uncaged habitats (on average 44% 3 d^{-1}), demonstrating that habitat selection was the dominant process responsible for the distribution of J2-3 blue crabs. **In highly mobile benthic species such as portunid crabs, post-settlement movement may exercise a larger affect on local distribution than does predation. Similar to the present results, habitat selection by dispersing J2-3 green crabs was more important than habitat-specific predation rates in explaining the distribution of young juveniles within nursery areas in Sweden (Moksnes 2002).**

This study demonstrates that size- and habitat-specific predation rates do not restrict the smallest blue crabs to stay within patches of refuge habitats. Instead juveniles appear to constantly migrate between patches of various habitats, regularly crossing areas of unstructured mud (experimental habitats were separated by on average 5-10 m of unstructured mud from natural refuge habitats), resulting in a very dynamic distribution of juveniles within nursery areas. Moreover, recent demonstration of planktonic dispersal of J1-5 blue crabs suggest that young juveniles may regularly redistribute also on a regional scale (Etherington & Eggleston 2000, Blackmon & Egglestone 2001). This is also supported by the regular presence of young juvenile blue crabs on collectors that are fished several meters above the bottom, 100's of meters away

from the closest nursery area (Moksnes unpubl. data). These results are in accordance with the conclusion by Sogard (1989), from a field study assessing colonization of artificial seagrass patches, that post-settlement redistribution by decapods and fish can be as important as larval supply in structuring local seagrass communities. Thus, it's important not to view the distribution of young juvenile blue crabs as static, and any attempts to follow juvenile cohorts over time in a local area to assess, for example, density-dependent losses of juveniles (c.f. Pile et al. 1996), must also assess juvenile dispersal rates to ensure that the same cohort is measured over time.

The distribution of J4-10 blue crabs differed from the distribution of settlers and J2-3 crabs in the September trial by having low **and similar** densities in mud, oyster and natural shoal grass (on average 8.3 crabs m^{-2}), and significantly higher densities in the artificial seagrass (on average 45 crabs m^{-2}). Because this distribution was only assessed in uncaged habitats, both habitat selection and predation could have caused this non-random distribution. However, considering that predation did not have a significant effect on the distribution of smaller blue crabs, which are thought to be more vulnerable to predation (Pile et al. 1996, Moksnes et al. 1997), habitat selection by colonizing crabs appears to be the most plausible explanation. **This suggestion is supported by laboratory studies in which juvenile blue crabs selected high seagrass over unvegetated sediment; the presense of predators increased the selection of vegetated habitats, but had no direct effect on the distribution (Williams et al. 1990).** The different habitat selection by J4-10 crabs and smaller juveniles is consistent with a shift in habitat use by juvenile crabs in Chesapeake Bay where the distribution of settlers and J2-3 crabs did not differ between seagrass species whereas larger juveniles were significantly more abundant in *R. maritima* than in *Z. marina* (Pardieck et al.

1999). An increased size refuge from predation and cannibalism, and increased difficulty in burying between seagrass rhizomes have been proposed to cause an ontogenetic shift in habitat use for crabs >7 mm CW from seagrass habitats to adjacent marsh and mud habitats in Chesapeake Bay (Pile et al. 1996, Moksnes et al. 1997). Although the present study indicates that an ontogenetic shift in habitat use may occur **also** at a similar juvenile size in the Gulf of Mexico, there is little evidence from tethering studies in Alabama that larger juveniles receive a size refuge from predation (Heck et al. 2001, Spitzer et al. 2003). The more specific selection exercised by the larger juveniles may instead indicate that the requirements of shelter change for crabs >6 mm CW, and that the artificial seagrass habitat was selected because it provides a better refuge from predation for larger juveniles than do the other habitats. The higher canopy, broader blades and larger space between the shoots appeared to be better scaled to shelter the larger juveniles than the thin blades of shoal grass (<3 mm width) with very high shoot density. **Consistent with these suggestions, juvenile blue crabs >5 mm CW were associated with lower density shoal grass than was smaller juveniles in a similar nursery area in Alabama (Williams et al. 1990).**

Panopeid *settlers.* In contrast to the opportunistic settlement in several structured habitat demonstrated by blue crab megalopae, settlement of **the panopeid megalopae (c.f. *Eurypanopeus* sp.)** in the predator exclusion cages occurred almost exclusively in the oyster habitat where densities were on average 160x higher than in the other habitats. These results demonstrate that the **panopeid** megalopae **could** efficiently select live oyster habitats for settlement over a scale of 10s of meters, and suggest that active habitat selection and not predation is the proximate process responsible for the initial benthic distribution of this

panopeid crab. Because of the relatively small size and possibly weak swimming ability of this postlarva, differences in hydrodynamics between habitats (c.f. Fonseca et al. 1982) may play a larger role for its settlement than for blue crab megalopae with swimming capabilities up to 13 cm s^{-1} (Luckenbach & Orth 1992). However, passive deposition of larvae (c.f. Eckman 1983, Hannan 1984, Butman 1987) probably had little effect on the **panopeid** settlers considering the low current speeds in the area (1-4 cm/s; Morgan et al. 1996) and taking into account that 93% of all settlers were found in the habitat with the smallest surface area and vertical profile. Moreover, the presence of the cage should decrease the hydrodynamic differences between habitats; i.e. the hydrodynamic baffling cage artifact should make test between habitats conservative. The strong response to one specific habitat indicate that a chemical cue from the oysters may be involved in the selection process. **Although little is known regarding the effect of chemical cues on settlement behavior in *Eurypanopeus* species, chemical cues from adult habitats induced metamorphosis in other panopeid crabs (e.g. Panopeus herbstii; Weber & Epifanio 1996). The interstices within oyster bars constitute the adult habitat for several *Eurypanopeus* species (Williams 1984 (?), Meyer 1994). The specific selection of the adult habitat in the panopeid megalopae may reflect a limited ability to redistribute after settlement. *Eurypanopeus* crabs are small and poor swimmers and much less capable in locating a specific habitat as juveniles in comparison to portunid crabs.**

Predation and distribution of juvenile blue crabs

The effect of predation on blue crab settlers and young juveniles was variable between trials and size classes, and was surprisingly low for settlers and significant only for J2-3 crabs. However, in no case did the losses from uncaged patches differ significantly between habitats, suggesting little **direct** effect of predation on the distribution of crabs. This result is surprising considering that habitat specific predation rates (e.g. higher predation mortality in unstructured mud and sand habitats) are thought to be a major ultimate process influencing the selection of structurally complex habitats at settlement (Moksnes et al. 1998 **Others?**). **However, an aggregation of predators in nursery habitats, and a refuge at low prey numbers in unstructured habitats can decrease the effect of habitat-specific predation rates on the settlement distribution (Moksnes 2002). Correspondingly we propose that habitat selection and the functional response of small predators increased their abundance and capture rates in nursery habitats, and decreased the proximate effect of predation on the distribution juvenile blue crabs.**

Settlers. The effect of predation on settlers in the present study was variable between trials and habitats, but was, in general, small and never significant. This result was surprising considering the significant predation effect on the artificial settlement collectors in the pilot study, and because similar experiments using the same cages demonstrated high and significant effects of predation on blue crabs settlers in artificial grass (up to 70% $3d^{-1}$; Moksnes & Heck unpubl. data). A trend was seen of consistently higher losses in the mud habitat where settlement densities were on average 52% lower in uncaged than caged treatments; in the 3 structurally complex habitats this loss varied between 0 and 46%. However, this effect was never strong enough to cause a significant change of the settlement pattern. The small overall effect of predation on settlers may partly be explained by the cage artifact that may have reduced settlement in caged treatment with about 30%**. Differences between caged and uncaged treatments may have been further reduced by low rates of predation occurring in caged habitats.** Low numbers of small gobid fish, grass shrimp and juvenile blue crabs, that could potentially eat blue crab settlers, remained in many cages despite our efforts to remove them at the start of the experiment, and J3 crabs, which can cannibalize megalopae (Moksnes et al. 1997), entered most cages in significant numbers. **However, the cage treatments still reduced the overall abundance of small potential predators with over 50% in both trials, and they** were efficient in keeping out larger shrimp and crabs, and in particular transient fish predators (e.g. *Fundulus* spp, juvenile *Sciaenids*) that are common in the nursery area, but that were never found inside the cages.

J2-3 blue crabs. The cages were efficient in excluding larger predators and very few potentially predator on J2-3 crabs were found inside the cages. The loss of J2-3 crabs from uncaged treatments was high in all habitats in both trials (on average 44% 3 d^{-1}) and significant in the last trial when crab densities were high. Both predation and emigration in response to the presence of predators may explain the loss of J2-3 crabs in the uncaged habitats. However, the latter suggestion is not supported by behavioral studies of young juvenile blue crabs, in which emigration rates from artificial seagrass patches were not affected by densities of larger cannibalistic crabs, the dominant potential predator found in the uncaged habitats (Moksnes & Heck unpubl. data). Predation mortality is therefore the most plausible explanation for the losses of J2-3 crabs, and the loss rates correspond well with predation rates from cannibalistic juvenile crabs in laboratory and cage enclosure experiment

(Moksnes & Heck unpubl. data). Because the preliminary laboratory experiment with J2 crabs suggested that the cage structure will decrease colonization of caged habitats by 38%, the average loss rate of J2-3 crabs should constitute a conservative estimate of predation mortality for this size-class.

Although the effect of predation was strong, it did not change the distribution of J2-3 crabs between habitats that were proportionally similar in caged and uncaged treatments. In fact, predation rates appeared higher in the structurally complex habitats (on average 44 to 55% loss) than on mud (24% loss). The high losses in the complex habitats may be explained by the fact that larger juvenile cannibals, grass shrimp, and small fish predators selected and aggregated in the same habitats as did young juvenile blue crabs, resulting in on average 5 times higher densities of small predators in the structurally complex habitats compared to open mud. Although the sampling method may have underestimated the densities of fast swimming fish on open mud, this may not have been severe due to the low visibility that allowed fish and shrimp to be regularly caught. Small predators are themselves vulnerable to predation from larger fish and crabs, and J4-10 blue crabs, shrimp and small fish probably selected the structurally complex habitats to reduce predation mortality. **That the number of predators may affect the survival of juvenile crabs is supported by** several recent field studies that have demonstrated a negative correlation between the number or survival of young juvenile crabs and the abundance of small invertebrate predators (**e.g. J1 blue crabs vs. *Palaemonetes* spp., Eggleston et al. 1998; survival of tethered J5-12 blue crabs vs. juvenile crabs, Hovel & Lipcius 2002; survival of blue crab settlers and J2-3 crabs vs. juvenile cannibals, Moksnes & Heck unpubl. data; survival of green crab settlers vs.**

juvenile cannibals, Moksnes *in press*) suggesting that habitat specific abundance of predators must be taken into account when assessing prey survival in different habitats.

In addition, prey densities may also affect predation rates due to the behavioral response of the predators. Recent studies have demonstrated that juvenile crab predators and shrimp can display a type III functional response to prey densities **(c.f. Holling 1959)** in both structurally complex habitats and open sand (Moksnes et al. 1997, Wennhage 2002, Moksnes *in press*) resulting in a refuge in low prey numbers and proportionally higher predation mortality at high prey densities. Such behavioral responses may explain why predation mortality of J2-3 blue crabs appeared to be highest in natural shoal grass, the habitat with the highest densities of J2-3 prey crabs, and lowest in the mud habitat where very few prey crabs were found in the caged treatments. Density-dependent predation may also explain why predation on xanthid settlers appeared highest in the oyster habitat. The effect of prey densities on predator behavior may explain the apparent paradox of why postlarvae select to settle in structurally complex habitats when predation mortality may not be lower there. If postlarvae settled randomly among habitats, the resulting increased prey abundance on mud would increase the predators' foraging activity on postlarvae, and, subsequently, increase the proportional settlement mortality in mud above that in the structurally complex habitats due to the lack of refuges in mud. **Many** laboratory studies on decapods have demonstrated that when prey densities (and predator densities) are kept equal between habitats, predation mortality on postlarvae and young juveniles are substantially lower in structurally complex habitats than in unstructured mud or sand (Johns & Mann 1987, Isaksson et al. 1993, Dittel et al. 1996, Barshaw & Lavalli 1988, Moksnes et al. 1997, 1998, Fernadez 1999). Thus, if many postlarvae settled randomly in shallow nursery areas, postlarvae with a behavior to settle preferentially in refuge habitats would have a selective advantage, retaining the behavior in the most individuals of the population.

These results demonstrate the importance of taking into account the habitat-specific distribution of both prey and predators when assessing the effects of predation on juvenile distributions, and indicate that habitat-specific predation rates may have a smaller proximate effect on juvenile distribution in motile species than generally thought. Density-dependent predation rates and an aggregation of small predators and young juvenile blue crabs in the same habitats may explain the fact that predation rates on tethered blue crabs can be as high in seagrass and marsh habitats as in adjacent unstructured mud or sand habitats (Pile et al. 1996, Heck et al. 2001, Spitzer et al. 2003), and explain the often reported lack of correlation between juvenile blue crab densities and **the structural complexity of the habitats** (Etherington & Eggleston 2000, Hovel 2003)**, and the negative correlation between survival of tethered juveniles and seagrass shoot density (Schulman 1996, Hovel & Lipcius 2002)**. The few studies that have assessed habitat selection at settlement and predation concurrently in cage experiments found strong effects of habitat selection on settlement patterns, but little effect of predation (Eggleston &Armstrong 1995, Feldman et al. 1997, Moksnes 2002), consistent with the present study.

In summary, our results suggest that habitat selection by both settlers and young juveniles are responsible for the distribution of juvenile blue crabs within shallow nursery areas. Although predation caused significant mortality on juvenile crabs, it had little direct effect on juvenile distribution, probably because the habitat selection and functional response of small predators increased their abundance and capture rates in the nursery habitats. The behavioral plasticity of blue crab megalopae that allowed them to successfully settle and metamorphose in several different structurally complex habitats, makes this species well adapted to survive in many different coastal environments, and probably less sensitive to variation in abundance of any specific nursery habitat. The high settlement and survival in oyster habitats indicates that the nursery value of this and other little studied habitats with high structural complexity may be underestimated. A better understanding of how these habitats contribute to the recruitment of adult blue crabs may be critical for an efficient management of coastal habitats and blue crab fisheries.

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Table 1. *Field experiment - Artificial settlement collectors.* Two-factor ANOVA models testing the number of blue crab settlers (megalopae and J1 crabs) as a function of cage treatment and year class.

Source of variation	*df*	Error term	SS	*F*
Cage treatment (A)	1	AxB	192.7	10.3*
Date (B)	3	Residual	1497.8	14.9****
A x B	3	Residual	18.8	0.2 (ns)
Residual	16	Residual	100.8	

* $p < 0.05$, **** $p < 0.0001$, (ns) $p > 0.05$

Table 2. *Cage experiment - Habitat selection and predation.* Two-factor ANOVA models testing the number of potential predators on juvenile blue crabs, the number of blue crab settlers, the proportion J1 crabs (no. J1 crabs/no. settlers) and the number of J2-3 blue crabs as a function of cage treatment and habitat in trial 1 and 2. All numbers were log(x+1)-transformed and the proportion was angular transformed.

		No. predators		No. settlers		Prop. J1 crabs		No. J2-3 crabs	
Source of variation	*df*	SS	*F*	SS	*F*	SS	*F*	SS	*F*
Trial 1									
Cage treatment (A)	1	0.01	0.09 (ns)	0.00	0.02 (ns)			0.04	0.47 (ns)
Habitat (B)	3	1.53	6.57**	1.73	5.66**			0.15	0.60 (ns)
A x B	3	0.72	3.09 (ns)	0.05	0.15 (ns)			0.05	0.21 (ns)
Residual	15	1.17		1.53				1.22	
Trial 2									
Cage treatment (A)	1	0.53	5.15*	0.02	0.45	0.00	0.08 (ns)	1.06	9.67**
Habitat (B)	3	1.32	4.30*	1.80	11.3****	0.18	3.25 (ns)	1.47	4.50*
A x B	3	0.25	0.82 (ns)	0.30	1.87	0.07	1.32 (ns)	0.69	2.11 (ns)
Residual	23	2.35		1.22		0.43		2.51	

* $p < 0.05$, ** $p < 0.01$, **** $p < 0.0001$, (ns) $p > 0.05$

Table 3. *Cage experiment - Habitat selection and predation.* One-factor ANOVA models testing the number of juvenile blue crabs (6 to 20 mm CW; log(x+1)-transformed) that colonized open habitat plots as a function of habitat treatments in trial 1 and 2.

		Trial 1		Trial 2	
Source of variation	*df*	SS	*F*	SS	*F*
Habitat	3	0.39	1.42 (ns)	1.06	6.57**
Residual	11	0.73		0.59	

Table 4. *Cage experiment - Habitat selection and predation.* Two-factor ANOVA models testing the number of mud crab settlers (log(x+1)-transformed) as a function of cage treatment and habitat in trial 1 and 2.

		Trial 1(1)		Trial 2	
Source of variation	*df*	SS	*F*	SS	*F*
Trial 1					
Cage treatment (A)	1	0.004	1.51 (ns)	0.31	2.12 (ns)
Habitat (B)	3	0.06	7.37**	12.2	27.43****
A x B	3	0.002	0.20 (ns)	0.18	0.41 (ns)
Residual	15	0.04		3.41	

** p < 0.01, **** p < 0.0001, (ns) p > 0.05

(1) No. of settlers was log(log(x+1)+1)-transformed in trial 1

FIGURE CAPTIONS

Figure 1. Study area in coastal Alabama, USA.

Figure 2. *Callinectes sapidus.* Relationship between the number of blue crabs settlers (megalopae and J1 crabs) on artificial collectors provided with predator exclusion cages, and the number of settlers on uncaged collectors.

Figure 3. *Cage experiment -predators.* Mean number of predators (+SE) in 4 different experimental habitat patches (artificial seagrass, live shoal grass, live oyster and mud) with or without predator exclusion cages sampled after 48 h (August) and 72 h (September). Different letters above bars indicate significantly different means at $P < 0.05$ SNK-test.

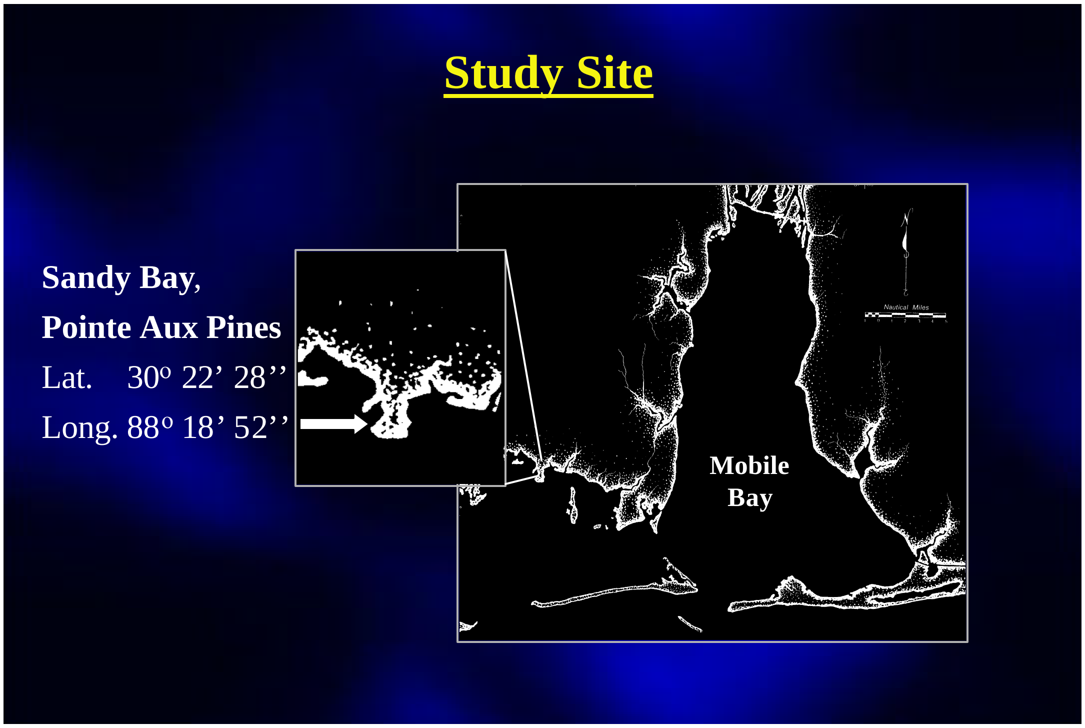
Figure 4. *Callinectes sapidus - settlers.* Mean number of blue crab settlers (+SE) in 4 different experimental habitat patches with or without predator exclusion cages in August and September. Different letters above bars indicate significantly different means at $P < 0.05$ SNK-test.

Figure 5. *Callinectes sapidus - J2-3 crabs.* Mean number of J2-3 crabs (+SE) in 4 different experimental habitat patches with or without predator exclusion cages in August and September. Different letters above bars indicate significantly different means at $P < 0.05$ SNK-test.

Figure 6. *Callinectes sapidus - J4-10 crabs.* Mean number of J4-10 crabs (+SE) in 4 different experimental habitat patches with or without predator exclusion cages in August and September. Different letters above bars indicate significantly different means at $P < 0.05$ SNK-test.

Figure 7. *Panopeid crab.* Mean number of panopeid settlers (+SE) in 4 different experimental habitat patches with or without predator exclusion cages in August and September. Different letters above bars indicate significantly different means at $P < 0.05$ SNK-test.

Fig. 1



Study Site

Sandy Bay,

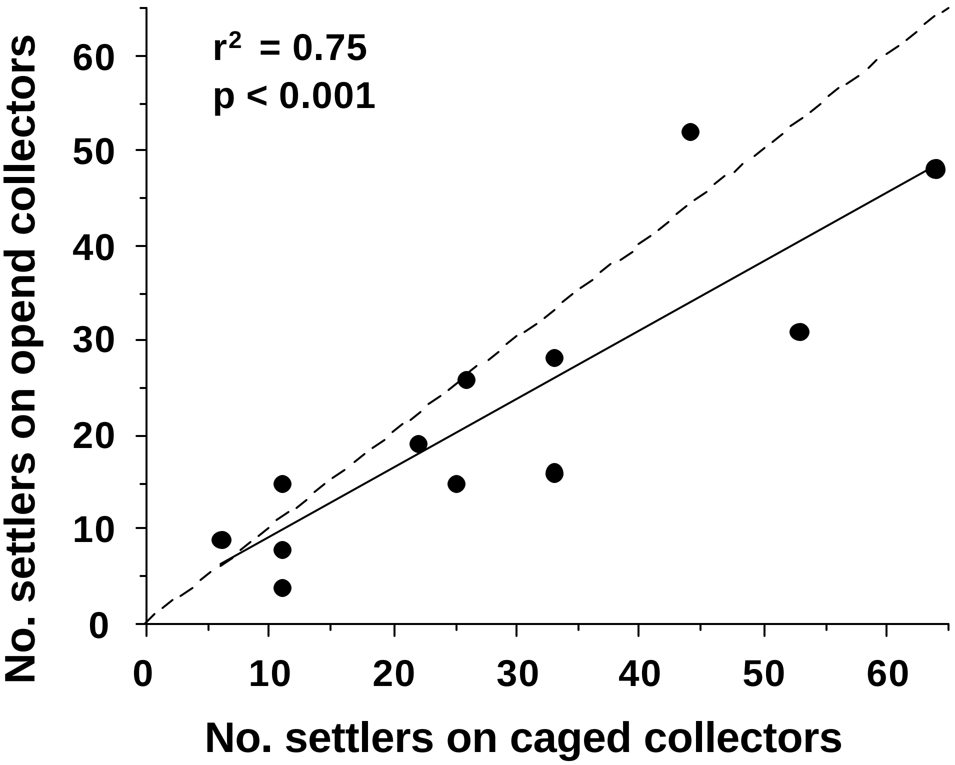
Pointe Aux Pines

Lat.   30º 22’ 28’’

Long. 88º 18’ 52’’

Map of Mississippi Sound

Fig. 2



r2 = 0.75
p < 0.001
60
50
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30
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10
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No. settlers on opend collectors
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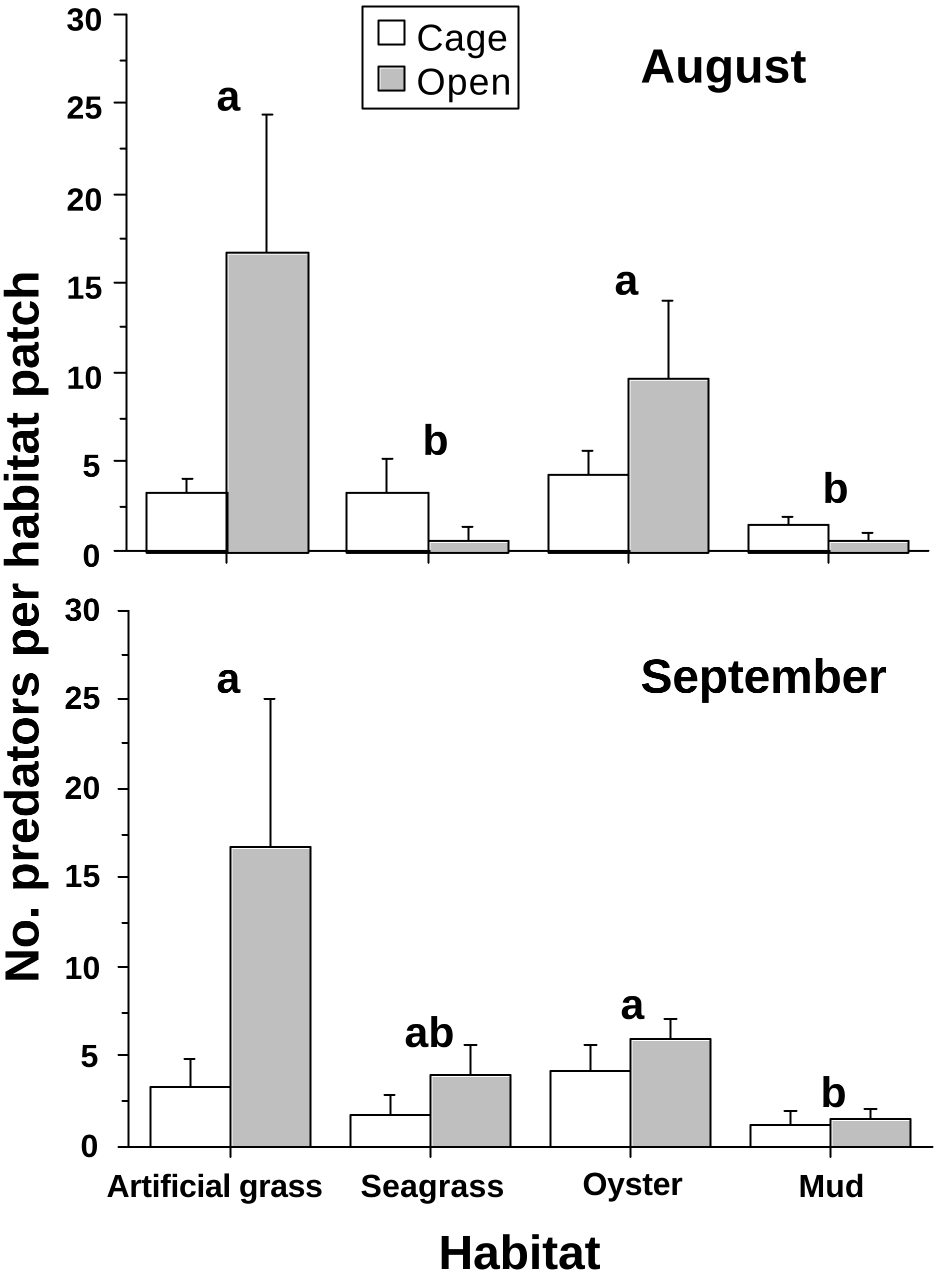
60
No. settlers on caged collectors

Fig. 3



☐ Cage
▨ Open
August
September
a
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b
a
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b
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25
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15
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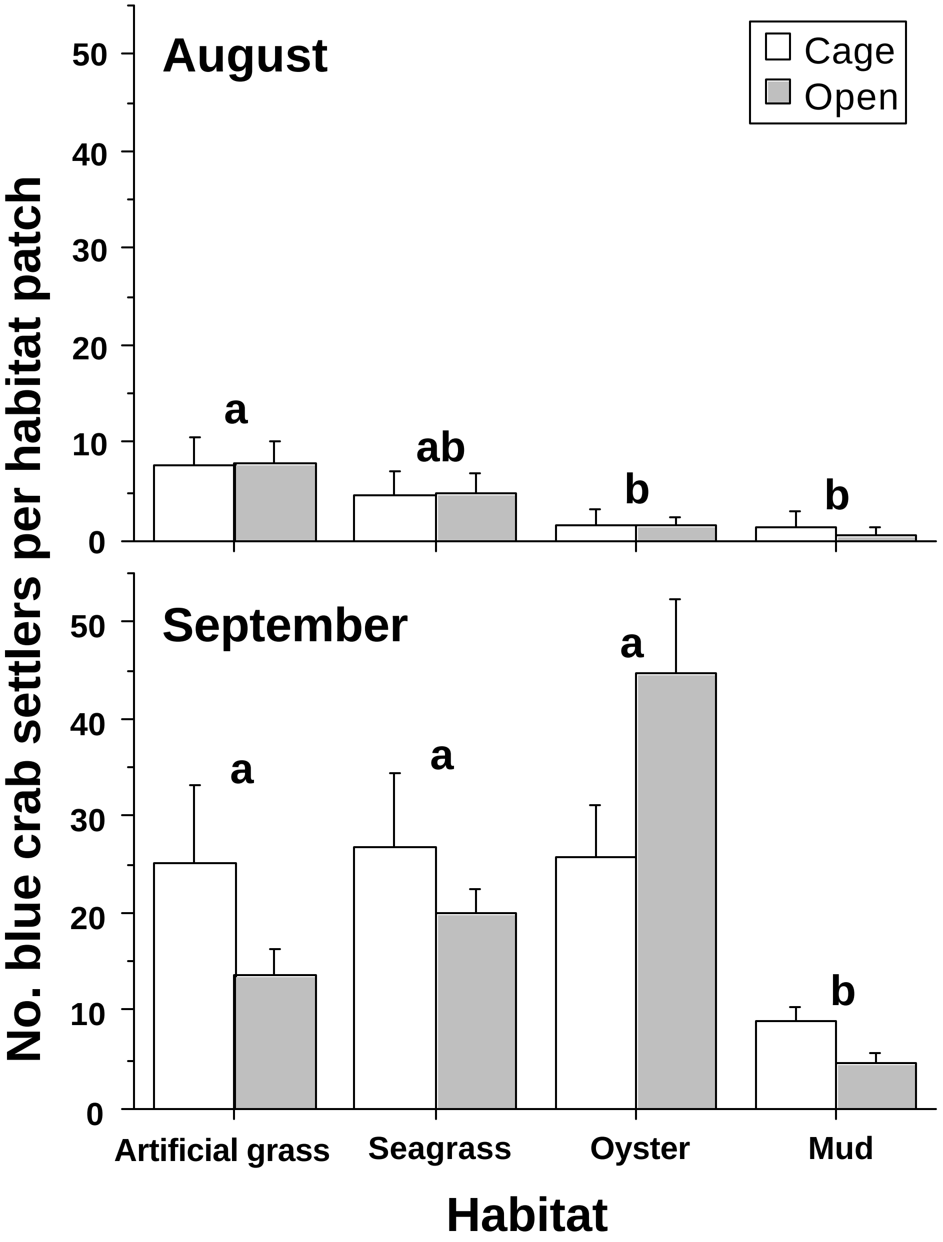
5
0
No. predators per habitat patch
Artificial grass
Seagrass
Oyster
Mud
Habitat

Fig. 4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☐ Cage
▨ Open
No. blue crab settlers per habitat patch
0
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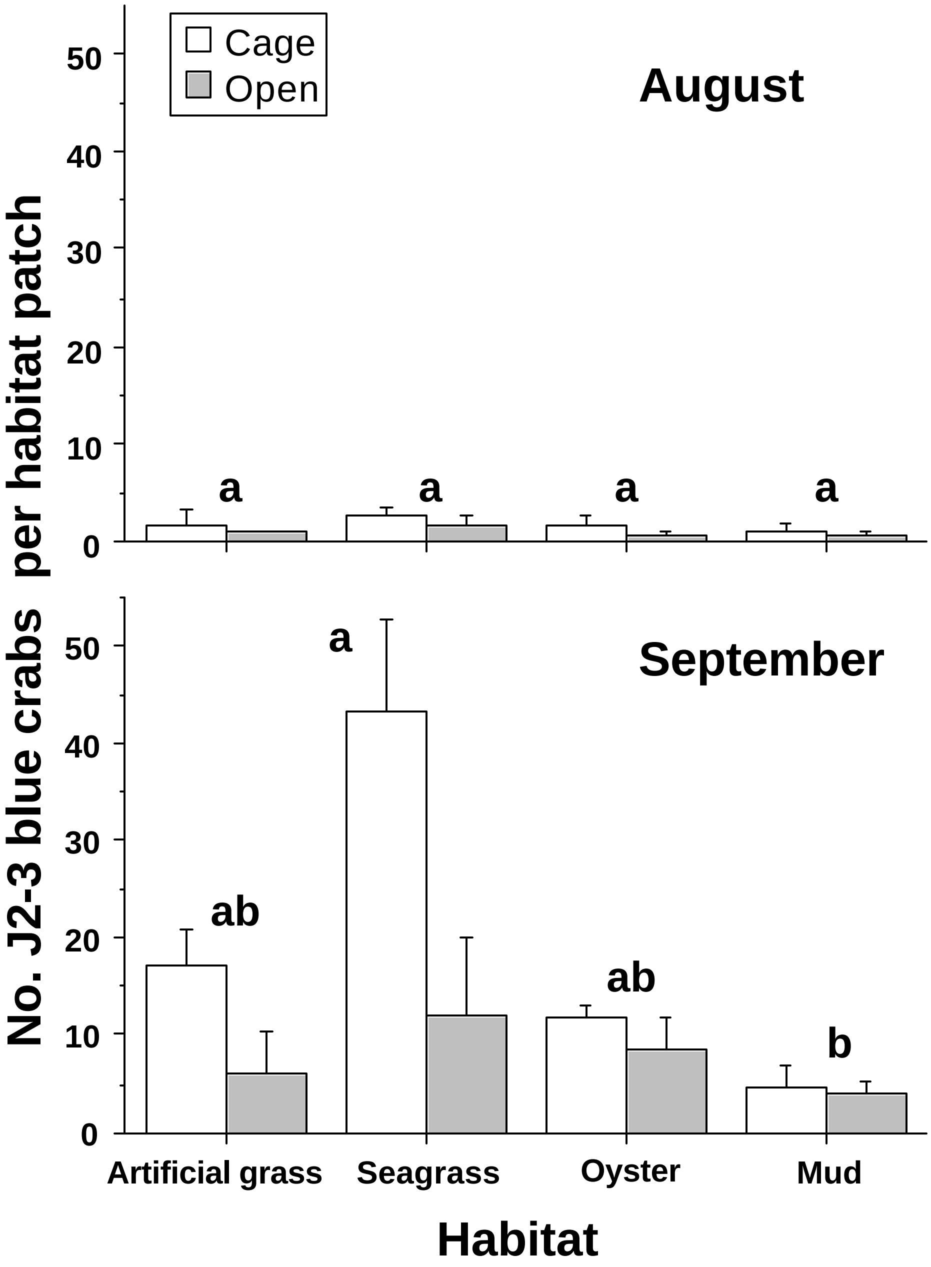
Artificial grass
Seagrass
Oyster
Mud
Habitat

Fig. 5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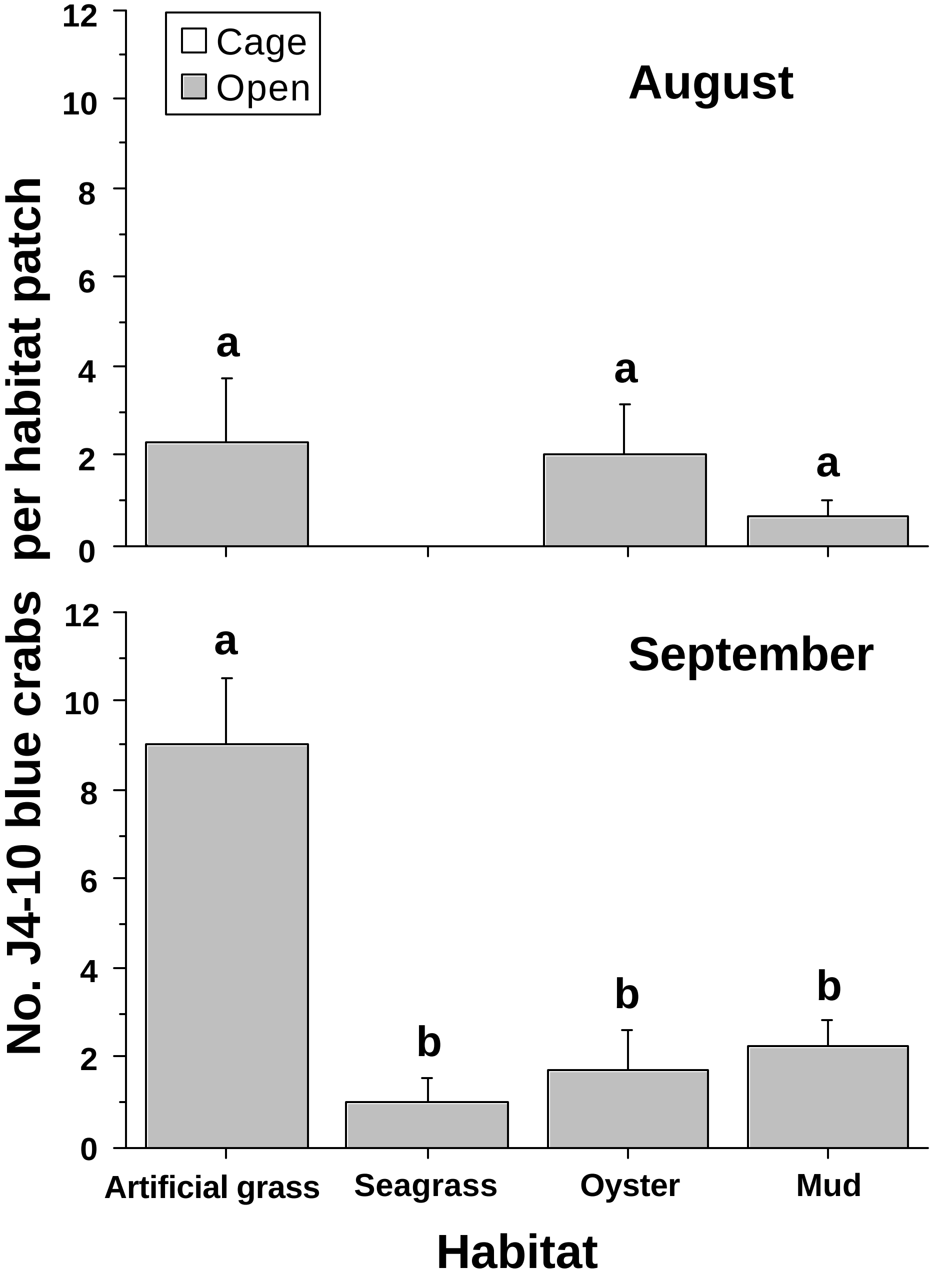
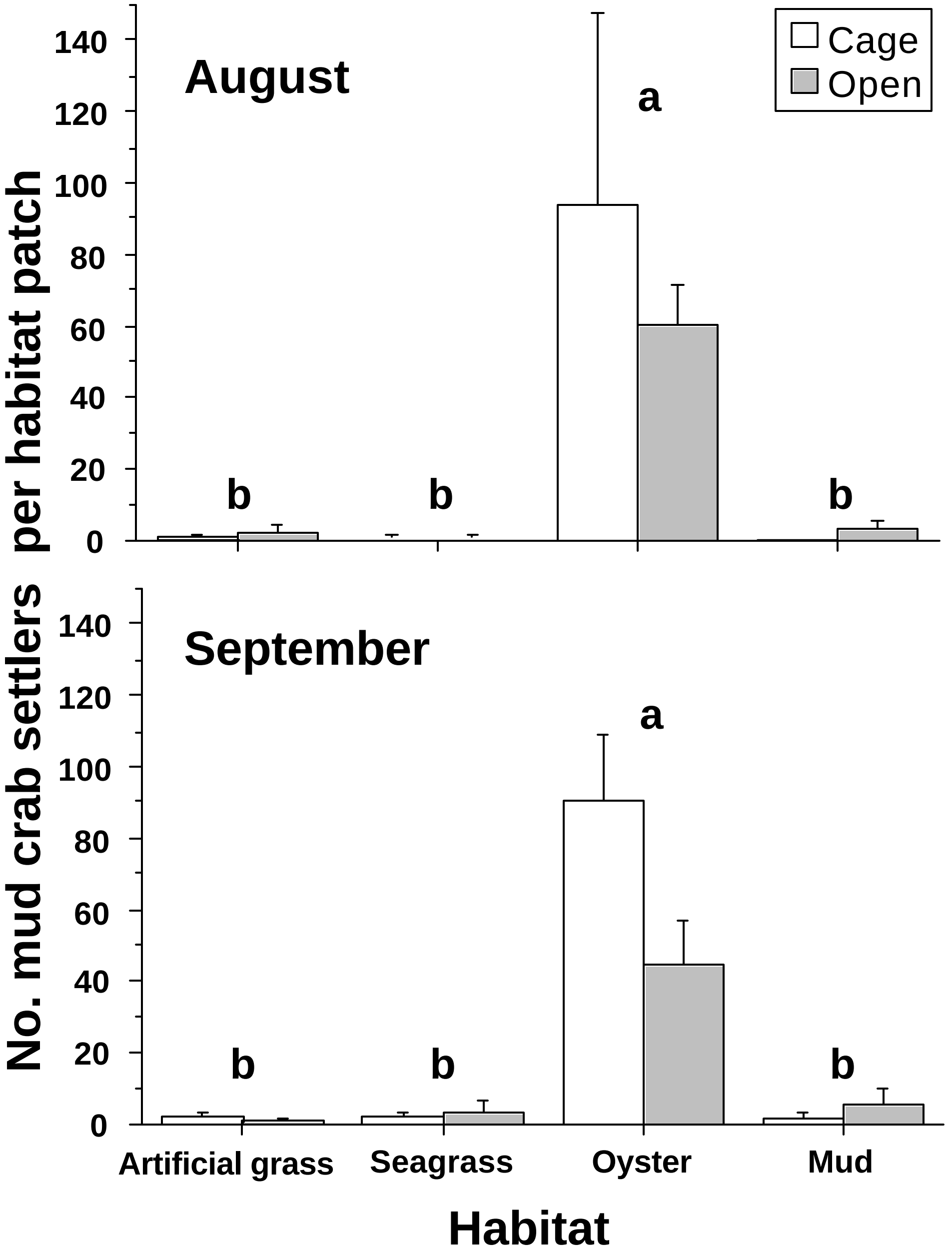
No. J2-3 blue crabs per habitat patch
Artificial grass
Seagrass
Oyster
Mud
Habitat

Fig. 6



□ Cage
▨ Open
August
September
No. J4-10 blue crabs per habitat patch
0
2
4
6
8
10
12
a
a
a
a
b
b
b
Artificial grass
Seagrass
Oyster
Mud
Habitat

Fig. 7


August
September
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120
140
0
20
40
60
80
100
120
140
No. mud crab settlers per habitat patch
Artificial grass
Seagrass
Oyster
Mud
Habitat