INTRODUCTION

A critical phase of the population dynamics of marine invertebrates such as the blue crab *Callinectes sapidus* comprises settlement of postlarvae, recruitment of young juveniles, and post-settlement processes (i.e., dispersal, survival and growth) that determine the abundance and distribution of young juveniles (Caley et al. 1996). In this chapter, settlement is defined as the colonization of nursery habitats by postlarvae (= megalopae in the blue crab), whereas recruitment is defined as the influx of young juveniles into the population’s nursery habitats after metamorphosis to the 1st juvenile instar. Blue crab recruitment depends principally on four factors: (1) the size of the spawning stock (Lipcius and Stockhausen 2002); (2) larval and postlarval survival, which vary according to the vagaries of physical transport and biological processes in the water column (see Epifanio, Chapter 12); (3) postlarval settlement success and recruitment intensity of young juveniles in nursery habitats (van Montfrans et al. 1995; Heck et al. 2001); and (4) post-settlement dispersal, survival and growth (Etherington and Eggleston 2000, 2003; Heck et al. 2001). The last two factors are influenced significantly by the availability (quality and quantity) of nursery habitats such as seagrass beds and salt marshes (Heck et al. 2003; Minello et al. 2003) as well as food availability in those habitats (Seitz et al. 2005).

In this chapter, we address temporal and spatial patterns in settlement of megalopae and recruitment of young juveniles of the blue crab and the processes (i.e., dispersal, predation, food acquisition and habitat quality) that govern those patterns in nursery habitats throughout the range of the blue crab. Our emphasis is upon the initial benthic phase, which includes settling megalopae and young juveniles < 20 to 30 mm carapace width (CW). This delineation results from the current paradigm regarding blue crab settlement and recruitment, which posits that young juveniles > 20 to 30 mm CW emigrate from primary nurseries (e.g., seagrass beds) to secondary nurseries (e.g., salt-marsh-fringed mud coves—Pile et al. 1996). Although our emphasis is upon young juveniles, we periodically refer to studies with older juveniles when these provide either a clarifying
comparison or where the data for young juveniles is lacking. Chapter 14 by Hines extends our review for older juveniles, though that chapter is similarly redundant in places with our chapter when necessary to achieve clarity and comprehension.

Because various recent reviews of recruitment processes in marine and estuarine nursery habitats (Beck et al. 2001; Heck and Spitzer 2001; Gillanders et al. 2003; Heck et al. 2003; Minello et al. 2003) have appeared, all of which either emphasize or deal at length with the blue crab, we have written this chapter using a synthetic approach rather than the typical extensive review. We emphasize conceptual models of settlement, dispersal, and recruitment, rather than a listing of all published studies. The reader is directed to the previous reviews of recruitment processes, as well as the sections on juvenile ecology in Chapter 14 by Hines, and then to this chapter to fully understand the patterns and processes governing settlement and recruitment dynamics of blue crab postlarvae and young juveniles in nursery habitats.

In this chapter, we first portray the current conceptual model of blue crab settlement. Next, we discuss the evolutionary foundation of nursery habitat use for the blue crab and its congeners in the Caribbean, Gulf of Mexico and Western Atlantic. Subsequently, we address the patterns and processes of settlement and recruitment, with emphasis upon dispersal, predation including cannibalism, and feeding in nursery habitats of differing quality. Where appropriate, we emphasize the impact of these ecological factors upon blue crab population dynamics (see Fogarty and Lipcius, Chapter 16). Afterward, we synthesize the impacts of habitat fragmentation and degradation upon blue crab nurseries. Finally, we depict a revised conceptual model of blue crab settlement and recruitment, and indicate various gaps in our knowledge of settlement and recruitment that are in need of further research. In the final section, we also discuss conservation issues related to blue crab nurseries, such as habitat restoration and stock enhancement with juveniles. As such, this chapter follows upon the foundation established by Epifanio (Chapter 12) on larval ecology, and precedes biologically the discussions of the ecology of older juveniles and adults by Hines (Chapter 14) and population dynamics by Fogarty and Lipcius (Chapter 16).

**COLONIZATION AND SETTLEMENT IN NURSERY HABITATS**

The current paradigm of ontogenetic shifts in habitat use by the blue crab initially involves invasion of the estuary or coastal habitats by megalopae from the continental shelf (Fig. 1). Megalopae settle in seagrass or other structured habitats and metamorphose into the 1st benthic juvenile instar (J1), which is about 2.2-3.0 mm in carapace width (Pile et al. 1996). [Note: We use the convention of naming juveniles such that J1 = 1st benthic juvenile instar, J2 = 2nd benthic juvenile instar, etc. Both are used throughout the text.] Many of the J1 juveniles remain in seagrass beds until sometime after reaching the 9th instar at about 20 to 25 mm CW (see Smith and Chang [Chapter 6] for growth increments as a function of instar), due to the higher survival and growth conferred by the structure and food in seagrass beds (Morgan et al. 1996; Perkins-Visser et al. 1996; Pile et al. 1996; Moksnes et al. 1997; Eggleston et al. 1998; Pardieck et al. 1999; Heck and Spitzer 2001; Hovel and Lipcius 2001, 2002; Orth and van Montfrans 2002). In some cases, the youngest instars (J1-J5) emigrate from seagrass beds, apparently to avoid density-dependent cannibalism and predation, and to grow (Perkins-Visser et al. 1996; Pile et al. 1996; Etherington and Eggleston 2000; Blackmon and Eggleston 2001; Reyns and Eggleston 2004). The remaining larger juveniles (>25 mm CW) disperse from seagrass beds to other shallow-water habitats such as subtidal mud and sand flats, as they have seemingly reached a relative size refuge from predation and have outgrown the protection afforded to young juveniles by seagrass (and other structured habitats in different ecosystems). The larger juveniles are now presumably less vulnerable to predation outside of seagrass beds and thus able to use the ample prey occurring in unstruc-
tured shallow-water mud and sand flats, which harbor benthic infauna such as the Baltic macoma, *Macoma balthica* (Hines and Comtois 1985; Hines et al. 1990; Seitz and Lipcius 2001; Seitz et al. 2003, 2005).

In some cases, invading megalopae or dispersing young juveniles either do not encounter seagrass beds because they are advected past the beds (e.g., Stockhausen and Lipcius 2003) or seagrass beds are unavailable, such as in certain areas of Pamlico Sound, North Carolina (e.g., Etherington and Eggleston 2000, 2003) or estuaries of the Gulf of Mexico (e.g., Minello et al. 2003). In these instances, megalopae and young juveniles settle in alternative primary nurseries like oyster reefs, coarse woody debris, or salt marsh refugia. This conceptual model thus posits that young juveniles reside in structured habitats (e.g., seagrass beds, salt marshes, oyster reefs) safest from predation upon settlement and during early growth; unstructured habitats are generally viewed as unsafe at this stage in the life cycle (Heck and Spitzer 2001). As the juveniles grow (> 25 mm
CW) and become less susceptible to predation, they are able to leave the refuge of structured habitats and exploit the abundant prey in unstructured habitats. The corollary of this model is that structured habitats such as seagrass beds remain safe for larger juveniles, but that larger juveniles can maximize their growth by dispersing from the structured habitats in a density-dependent fashion; otherwise they would be subject to negative density-dependent growth (Perkins-Visser et al., 1996) and survival (Morgan et al. 1996; Pile et al. 1996; Heck et al. 2001). In addition, it has been suggested that risk of predation for juveniles in structured and unstructured habitats converges somewhere between 20 to 50 mm CW (Pile et al. 1996; Hovel and Lipcius 2001), such that young juveniles are able to use both structured and unstructured habitats at these sizes. Consequently, a major redistribution of juveniles into a broader range of habitats is expected at 20 to 50 mm CW. This concept is further amplified in the chapter on ecology of older juveniles and adults (see Hines, Chapter 14).

In the remainder of the chapter, we review the evolutionary foundation of nursery habitat use; settlement; dispersal; diet, feeding and growth; and, predator-prey interactions and survival in nursery habitats of blue crab megalopae and young juveniles, and refine the classic model of settlement and recruitment (Fig. 1) to incorporate recent findings that significantly alter our understanding of the patterns and processes of settlement and recruitment of the blue crab.

Evolvionary Foundation of Nursery Habitat Use

Crabs in the genus Callinectes characteristically inhabit diverse shallow marine and estuarine habitats where growth, development and mating occur (Williams 1984); the larval stages, however, need high oceanic salinities and warmer waters peaking at least to 20° C to develop (Norse 1977). Moreover, a subset of Callinectes species including C. sapidus requires estuarine waters (Norse 1977). These species (i.e., C. sapidus, C. bocourti, C. danae, and C. maracaiboensis) are large, catadromous, and generally found only near high islands of the Caribbean which have significant freshwater input to the surrounding coastal zone or in estuarine systems of the Gulf of Mexico and Western Atlantic (Norse 1977; Norse and Fox-Norse 1982). The significance of these two evolutionary characteristics is that (1) a specific stage (i.e., megalopa) is needed that returns to shallow estuarine nurseries from oceanic habitats where larvae develop, and that (2) this stage as well as young juveniles must further disperse throughout the extensive shallow nurseries in lagoons and estuaries where growth and development proceed.

The second item of significance related to the evolution of Callinectes deals with the question whether there is a single habitat type that is preferred by Callinectes (e.g., seagrass beds). A review of habitat use by Callinectes species most closely related to C. sapidus indicates that these species use a diverse suite of nursery habitats, including seagrass beds, mangroves, salt marshes, oyster reefs, rock rubble, algal patches, and various anthropogenic substrates, as well as unstructured mud and sand bottoms (Norse 1977; Norse and Fox-Norse 1982; Williams 1984). There is thus a general preference for heterogeneous substrates, with no specific habitat that is universally selected, though little is known about the ontogenetic shift in habitat use by juveniles for most species in the genus Callinectes.

Settlement

To understand settlement patterns and processes, it is essential to examine certain elements of the blue crab life history. Adult and juvenile blue crabs are estuarine-dependent (Williams 1984), whereas larvae require the high salinity of oceanic waters and are advected from the estuary in surface waters (Costlow and Bookhout 1959; Tankersley and Forward, Chapter 10). Blue crab larvae and megalopae are patchily distributed by physical processes in oceanic habitats while undergoing development. The duration of the megalopae stage under constant conditions of food availability, salinity, and temperature in laboratory studies varies among siblings and
is independent of larval duration (Sulkin and Van Heukelem 1986). Not surprisingly, different temperature and salinity regimes increase variability in megalopal duration. Such plasticity may be adaptive by enhancing the likelihood of on-shore transport under highly stochastic oceanic conditions enabling a successful encounter of an estuary where settlement occurs. Conversely, this plasticity will produce substantial variation in settlement patterns that differ temporally and spatially at various scales.

The megalopa stage is the phase in the life cycle responsible for reinvasion of estuarine or lagoonal nursery habitats, with ingress into estuaries accomplished via a combination of seasonal physical processes (Epifanio et al. 1984, 1989; Epifanio 1988a, b; Goodrich et al. 1989) and vertical migration behavior of megalopae (Mense and Wenner 1989; De Vries et al. 1994; Olmi 1994, 1995; Tankersley and Forward 1994; Forward et al. 1995, 2003; Tankersley et al. 1995). The magnitude of megalopal settlement within an estuary or lagoon initially determines population size, and is driven to a great extent by the spawning stock, as evident in significant stock-recruit relationships in blue crab populations (e.g., Lipcius and Stockhausen 2002; Eggleston et al. 2004), though there is no evidence of a significant stock-recruitment relationship in the Gulf of Mexico.

In Chesapeake Bay a major reduction in the spawning stock in 1992 was apparently due to poor recruitment (i.e., influx and settlement of megalopae) in the previous year despite high spawning stock and larval abundance that year (Lipcius and Stockhausen 2002). Since then, generally poor recruitment, in concert with high fishing and natural mortality, has maintained a depressed spawning stock that has not recovered in over a decade. The mechanism producing poor recruitment remains unidentified, though it likely involved alteration of environmental or biotic conditions necessary for successful larval survival and reinvasion of the Bay by megalopae from the continental shelf (Lipcius and Stockhausen 2002). This situation illustrates the likely influence of megalopal reinvasion and settlement on subsequent population abundance and fisheries production, and thus the need to understand pattern and process in settlement and recruitment.

Various factors influence the magnitude and success of megalopal ingress into an estuary and subsequent settlement behavior. After larval development and metamorphosis to the megalopal stage, active behavior during settlement can aid in assuring recruitment success. Metamorphosis is defined here as the embryologically or morphogenetically induced change accompanying settlement, and which constitutes the behaviorally mediated termination of a pelagic larval existence (sensu Scheltema 1974). Furthermore, habitat-specific responses by megalopae to chemical cues upon settlement may be important in ensuring that blue crabs, which have strong swimming capabilities of up to 12.6 cm s⁻¹ (Luckenbach and Orth 1992) and a highly developed sensory system, encounter preferred nursery habitats.

**Spatial Patterns**

Blue crab megalopae undergo complex changes in physiological state during their transition from an oceanic to an estuarine habitat. As megalopae move into an estuary, their physiological state progresses from intermolt in oceanic waters (Wolcott and DeVries 1994) to more advanced stages of pre-molt with increasing distance into estuaries or lagoons prior to metamorphosis (Lipcius et al. 1990; Metcalf and Lipcius 1992; Morgan et al. 1996). Those individuals in a more advanced physiological state are more likely to exhibit a response to chemical cues and therefore display habitat-selection behavior (Brumbaugh and McConaugha 1995; Welch et al. 1997). Since ingressing megalopae demonstrate proportional differences in molt stage, both spatially and temporally (Metcalf and Lipcius 1992; Morgan and Christy 1996; Hasek and Rabalais 2001), settlement patterns might also be influenced, in part, by such differences.

Cues associated with salinity reduction, marsh environments, various marine algae (Ulva spp., Bryopsis plumulosa, and Hypnea musciformis but not Sargassum natans, Scyphosiphon lomentaria, or Enteromorpha sp.) and seagrasses (SAV: Zostera marina, Halodule wrightii, and Ruppia maritima) reduce the time for
metamorphosis to the juvenile instars (McConaugha 1988; Forward et al. 1994, 1996, 1997; Wolcott and De Vries 1994; Brumbaugh and McConaugha 1995) or elicit selective settlement behavior. Active selection for *Z. marina* (Welch et al. 1997; van Montfrans et al. 2003) indicates that chemical components of seagrasses in estuaries directly and positively influence settlement behavior of megalopae, suggesting that such behavior during recruitment, combined with strong mobility, plays a key role in establishing initial densities of juvenile blue crabs in nursery habitats such as seagrass beds.

Some investigations have, however, provided conflicting evidence for the ability of megalopae to orient actively toward settlement sites. Diaz et al. (1999) suggested that chemical and visual cues function in predator avoidance rather than habitat selection by megalopae. Welch et al. (1997) found that blue crab megalopae were attracted to seagrass (*Z. marina* and *H. wrightii*) cues but avoided 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 three types of experimentally transplanted vegetation (*R. 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 for *S. alterniflora* when settlement was high indicated that additional investigation into such processes is warranted (Morgan et al. 1996).

Thus, the non-random pattern of blue crab distribution in nature may be deterministic, due in part to active habitat selection by recruiting stages (e.g., megalopae, young juvenile instars). Responses by blue crab megalopae to both estuarine- (Forward 1989; Forward et al. 1996, 2003) and habitat-specific (Welch et al. 1997; van Montfrans et al. 2003) cues operating at different spatial scales assure both the return of individuals to estuaries from the coastal ocean and their eventual distribution within estuarine nursery habitats. Such behavior may be an evolutionary response to two types of environmental factors: (1) general (*sensu* Forward et al. 1996) estuarine cues that, upon completion of larval development in optimal high salinity waters of the coastal ocean, initiate vertical migration behavior and effect the return of megalopae to estuarine habitats; and (2) specific responses to estuarine nursery habitat types (e.g., seagrass beds, algal habitats) and the avoidance of other less favorable habitats and predators, thereby assuring the greatest likelihood of recruitment success via maximal survival (Pile et al. 1996) and accelerated growth (Perkins-Visser et al. 1996).

Habitat-specific associations of blue crab megalopae and young juveniles occur throughout its range. Within Chesapeake Bay and North Carolina coastal areas, megalopae and the smallest juvenile crabs (1st to 7th instars) occur principally in seagrass meadows or shallow salt marsh detritus (e.g., *Z. marina* and *R. maritima*; Orth and van Montfrans 1987, 1990; Pile et al. 1996; Etherington and Eggleston 2000, 2003; Reyns and Eggleston 2004), whereas in the Gulf of Mexico they are often associated more exclusively with marsh habitats (Texas: Thomas et al. 1990; Rozas and Minello 1998; Minello 1999) and muddy substrates (Mississippi Sound: Rakocinski et al. 2003). In many instances, megalopal abundance predicts the availability of juvenile crabs in benthic habitats (Lipcius et al. 1990), though with substantial variability (Olmi et al. 1990).

In the north-central and western Gulf of Mexico, where tides are diurnal and very small, habitat associations differ significantly and are reflective of an important difference in the way Atlantic and Gulf coast marshes function for young blue crabs. The weaker tidal incursions in the Gulf of Mexico make use of salt marsh habitats easier for early settlers (megalopae and the first few instars), as they need only leave the marsh once a day, and many times during the summer when southerly winds prevail the marshes do not empty even at low tide. At some sites in coastal Alabama, widgeongrass (*Ruppia maritima*) grows interspersed with the *Spartina* salt marsh fringe (K. Heck, unpubl. obs.). Thus, marshes are likely to function differently and to be more important primary nurseries in the north central and western Gulf of Mexico than they are along the Atlantic
Temporal Patterns

Blue crab settlement across broad geographic scales has been examined using identical artificial settlement substrates to characterize daily and seasonal settlement patterns and magnitude. Statistical efficiency in such efforts can be attained by using only four (and sometimes three) substrates deployed at either the surface or bottom and sampled daily (Metcalf et al. 1995). Individual and coordinated studies of blue crab settlement throughout the Atlantic and Gulf coasts have revealed differences and similarities in settlement patterns. Overall, settlement throughout all areas occurs regularly during the recruitment season at low daily levels punctuated by extremely high episodic peaks (Fig. 2), which are either associated with various physical or astronomical influences (Fig. 3) or remain unexplained, and with substantially higher settlement along the Gulf of Mexico than the Atlantic coast (Fig. 4).

Atlantic Coast Patterns

Settlement by blue crab megalopae throughout the Atlantic coast is characterized by constant low levels of settlement punctuated by episodic peaks (Fig. 2a) that differ in timing geographically (van Montfrans et al. 1995). At northern latitudes (e.g., Delaware Bay, Chesapeake Bay, Pamlico Sound) recruitment generally occurs from August to November, whereas at more southern latitudes the settlement season becomes protracted, similar to that observed along the Gulf of Mexico and tropical locations (Fig. 2b). At the most northern site (Delaware Bay), patterns of settlement over four years (1989-1992) were unrelated to lunar phase and were influenced instead by the occurrence of southward, alongshore wind events (Jones and Epifanio 1995). It was postulated that the stochastic nature of the occurrence of southward winds coupled with the coincident availability of megalopal patches in near-shore waters could explain temporal variation in settlement of blue crab megalopae in Delaware Bay.

Lunar (van Montfrans et al. 1990) or semilunar (Metcalf et al. 1995; van Montfrans et al. 1995) periodicity in settlement patterns is evident from Chesapeake Bay, North Carolina (Forward et al. 2003, 2004) and South Carolina (Boylan and Wenner 1993) estuaries and lagoon systems (Fig. 3). Blue crab settlement in Chesapeake Bay (York River)
over multiple years was characterized largely by semilunar periodicity with settlement likely influenced by neap spring tidal cycles rather than direct linkage to lunar-associated behavior per se (Epifanio 1995; Metcalf et al. 1995; Olmi 1995).

In North Carolina (Newport River estuary), settlement over seven years (1993–1996; 1998; 2000; 2002) was unrelated to along- or cross-shore wind stress but indicated significant semi-lunar periodicity with neap tides during quarter phases of the moon (Fig. 3). Megalopae at two other geographical areas (one site at Wilmington and two in Pamlico Sound) over three years (1990–1993) also displayed a significant correlation but with new and full moon phases (Mense et al. 1995), as depicted in the summary of several Atlantic coast locations (Fig. 3). Conversely,
large-scale patterns of megalopal settlement over a decade (1996 to 2005) in Pamlico Sound were strongly influenced by the magnitude and track of tropical storms and hurricanes, as well as strong winds blowing towards the south and southwest, and were generally unrelated to lunar phase (Eggleston et al. 2005). Tidal amplitude as related to lunar period was most important to the advection of returning larvae and megalopae; significant variation in timing of settlement occurred annually with a 10-fold difference in the magnitude of overall settlement. Settlement also varied significantly as a function of location within the estuary.

Blue crab settlement in South Carolina from 1987 to 1988 occurred throughout the year with evidence of a semi-lunar pattern and with peak settlement occurring during waning phases of the quarter moon during apogee spring tides (Fig. 3 and Mense and Wenner 1989). Interestingly, the mean length of megalopae was significantly greater in spring than in the fall, and overall size distributions of ingressing megalopae also differed significantly. Similar seasonal differences in size were observed in the same South Carolina estuary by Boylan and Wenner (1993) and in the Gulf of Mexico by Stuck and Perry (1981). Size differences of megalopae in the Gulf of Mexico were also reflected in the size of newly metamorphosed juveniles. These differences were not attributed to temperature variation but instead, could have been caused by reduced food availability in spring, which could have caused starvation, suspension of the molt cycle in premolt (McConaugha 1985), or the metamorphosis into intermediate larval or postlarval stages, thereby resulting in a larger final size at metamorphosis (Stuck and Perry 1982). Though increased size might confer an advantage in predator-prey interactions, the exact benefit and geographical extent of size effects remain unresolved.

**Gulf Coast Patterns**

Patterns of megalopal settlement in the Gulf coast are similar to those for the Atlantic coast in that settlement often occurs at consistently low levels punctuated by episodic periods of extremely high settlement (Fig. 2). The magnitude of daily and annual settlement, however, is often one to two orders of magnitude greater in the Gulf of Mexico (Rabalais et al. 1995) than along the Atlantic coast (Fig. 4). Resulting abundances of juvenile crabs are often decoupled from settlement magnitude in the Gulf of Mexico, suggesting that density-dependent predation likely has a relatively greater effect on settling crabs in the Gulf of Mexico than Atlantic coast (Heck and Coen 1995; Heck and Spitzer 2001).

Blue crab settlement in Mississippi Sound (1991–1992) from May through November was decidedly episodic with highest overall settlement in the late summer and early fall (Perry et al. 1995). Remarkably high settlement was recorded, sometimes exceeding 10,000 megalopae per settlement substrate, which surpasses that typically found in Atlantic coast estuaries by at least one order of magnitude (Fig. 4). No significant correlations with various physical variables (temperature, salinity, astronomical tides, lunar periodicity, and average daily wind direction and speed) were evident, though spring tides coupled with onshore winds were associated with the majority of settlement events.

Along the Gulf coast of Alabama (Mobile Sound), settlement was more closely linked to tidal
amplitude than lunar cycle (Morgan et al. 1996). Settlement was highest with onshore winds and when tidal amplitude was minimal. Onshore winds apparently facilitated transport of megalopae into Gulf of Mexico estuaries episodically, though megalopae recruited regularly and abundantly during nocturnal flood tides of minimal amplitude, which is in contrast to Atlantic coast patterns whereby recruitment generally occurs at maximum-amplitude tides.

Overall, settlement throughout four Gulf coast estuaries was generally episodic and asynchronous across estuaries (Rabalais et al. 1995). The magnitude of settlement varied significantly by estuary and settlement was generally more protracted than in Atlantic coast estuaries (Fig. 2), most likely reflecting the extended spawning season in subtropical regions.

As noted previously, settlement on artificial substrates was 10 to 100 times higher in the Gulf of Mexico (Alabama, Mississippi, and Texas) than at Atlantic coast sites (Delaware, Virginia, North Carolina and South Carolina) (Fig. 4). Densities of young juvenile crabs were, however, similar along both coasts, suggesting that predation risk and mortality rates of megalopae and young juveniles were much higher in the Gulf than along the Atlantic coast (Heck and Coen 1995; Heck et al. 2001), particularly due to cannibalism (Moksnes et al. 1997; Hines and Ruiz 1995). The consistently low levels of settlement punctuated by episodic peaks over all sites throughout both the Atlantic and Gulf of Mexico coasts could confer the greatest option for recruitment success and population maintenance. Episodically high numbers of settling megalopae might overwhelm predators so that some survive ( predator swamping), whereas consistent low levels of settlement might allow continuous recruitment below density-dependent levels of prey detection throughout estuaries along both coastlines. At all sites examined where vegetation was present, settlement habitat preferences of megalopae were similar — vegetated or detrital habitats consistently harbored greater numbers of newly settled crabs than unvegetated habitats (Morgan et al. 1996; Heck et al. 2001).

### DISPERAL

As with other demographically open marine populations (Underwood and Fairweather 1989; Caley et al. 1996), the dispersal potential of the blue crab significantly influences population and metapopulation dynamics (Lipcius et al. 2005a), including that by oceanic larvae, colonizing postlarvae, and secondarily dispersing postlarvae and young juveniles (Palmer et al. 1996; Etherington and Eggleston 2000, 2003; Blackmon and Eggleston 2001; Etherington et al. 2003).

#### Primary Disperal

Megalopae are likely transported shoreward by wind-driven Ekman circulation and into estuaries by means of barotropic flow moving in from the shelf (reviewed by Epifanio and Garvine 2001; Epifanio, Chapter 12), which collectively determine dispersal patterns of megalopae and young juveniles into and among nursery habitats. Hence, the delineation of dispersal patterns and processes requires detailed information on environmental forcing functions. For instance, megalopal influx into Chesapeake Bay and Pamlico Sound, North Carolina was correlated with wind speed and direction (Goodrich et al. 1989; Mense et al. 1995; Eggleston et al. 2005), whereas megalopal influx in the Newport River near Beaufort Inlet, North Carolina was not correlated with cross-shelf or along-shore wind speed. Rather, settlement occurred at a semi-lunar periodicity with highest settlement at the times of neap tides during quarter phases of the moon (Forward et al. 2003, 2004). The proposed explanation for this relationship was that (1) megalopae underwent flood-tide transport for entrance into estuaries and up-estuary movement, and (2) the behavior underlying flood-tide transport was most effective when all of the nocturnal flood tide occurred in darkness (Forward et al. 2003, 2004). Megalopae may also use a combination of flood-tide currents and wind-driven currents in micro-tidal estuaries, such as Pamlico Sound, to reach shallow settlement habitats (Reyns et al., in press).

Once within the estuary, blue crabs settle in sub-
merged aquatic habitats (e.g., seagrass or other complex habitats) where they undergo metamorphosis to the first benthic instar (J1) (Heck and Thoman 1984; Orth and van Montfrans 1987; Etherington and Eggleston 2000), and from which secondary dispersal can occur (Reyns and Eggleston 2004). In the classic paradigm of settlement and dispersal, juveniles remained in these habitats until they reached the 5th to 7th instar (J5-J7) at about 20 mm CW, after which they emigrated into unvegetated habitats (Hines et al. 1987; Orth and van Montfrans 1987; Pile et al. 1996). Recent research on dispersal in Pamlico Sound, however, supports the hypothesis that recently settled young juveniles often exhibit pelagic emigration (Etherington and Eggleston 2000, 2003; Blackmon and Eggleston 2001; Reyns and Eggleston 2004), referred to as secondary dispersal.

**Secondary Dispersal**

Secondary dispersal derives from passive responses to environmental conditions (e.g., storm events), and active behavioral responses to physical (e.g., deteriorating habitat quality) or biotic (e.g., density-dependent emigration) conditions (Powers and Peterson 2000; Reyns and Eggleston 2004). Active secondary dispersal can also result from other biological processes, such as competition for food or shelter, and predator-mediated avoidance (Reyns and Eggleston 2004; Moksnes and Heck 2006).

Secondary dispersal of young juvenile blue crabs enhances the nursery capacity of estuarine systems by redistributing crabs from high-density settlement habitats to habitats that receive low megalopal supply (Etherington and Eggleston 2000, 2003). Secondary dispersal determines recruitment patterns on a regional scale, and can mask density-dependent relationships among early life stages (Etherington and Eggleston 2000, 2003). In Pamlico Sound, secondary dispersal by young juvenile blue crabs is most common in the first benthic instar stage (J1), with crabs distributed just off-bottom and at night (Reyns 2004; Fig. 5). Nighttime dispersal is a common behavioral strategy used by early life stages of many estuarine organisms to reduce predation by visual predators (Morgan 1995). Secondary dispersal from primary settlement habitats occurs during nighttime flood tides and average wind speeds (~ 5 m s⁻¹), although stronger winds (> 15 m s⁻¹) can induce passive secondary dispersal during daylight (Blackmon and Eggleston 2001; Reyns and Eggleston 2004). Moreover, the secondary dispersal of crabs can be density-dependent (Fig. 6) and regulated by intra-cohort (J1) crab density in seagrass (Reyns and Eggleston 2004). Field mark-recapture experiments determined that the probability of migration from seagrass by young juvenile blue crabs can be extremely high (0.29-0.72 in a 6 h⁻¹), and can exceed the probability of mortality (0.25-0.67 in a 6 h⁻¹ Etherington et al. (2003). Laboratory
experiments demonstrated that 1st to 5th instar crabs have a circadian rhythm in which crabs swim vertically during the time of night in the field; the time of peak vertical swimming did not correspond to the time of flood tide at collection sites, but consistently occurred at night between 0000 and 0300 h (Forward et al. 2004). While responses to environmental factors probably control the onset and end of vertical swimming by young juvenile blue crabs during flood tides in tidal areas, a circadian rhythm underlies secondary dispersal at night (Forward et al. 2004). A bio-physical field and computer modeling study found that secondary dispersal of J1 instars in wind-driven bottom current across Pamlico Sound to nursery habitats was only possible if tides were initially used to move crabs away from inlets and into the sound (Reyns 2004).

Reyns (2004) proposed a conceptual model of blue crab secondary dispersal in a predominantly wind-driven estuary such as Pamlico Sound, as follows. Initially, 1st instar blue crabs leave initial settlement habitats such as seagrass when intra-cohort densities become high or during high wind events. An endogenous swimming rhythm at night also places 1st instar crabs into the water column where they can take advantage of flood-tide transport up-estuary. As 1st instar crabs move away from the inlets, salinity signals and tidal currents weaken such that crabs no longer move into surface waters. Rather, 1st instar crabs continue to swim into the water column at night as a consequence of their circadian swimming rhythm and become entrained in near-bottom, wind-driven currents. Over several days, such saltatory movements result in across-sound secondary dispersal, after which crabs settle in shallow across-sound detrital habitats (Etherington and Eggleston 2000). Other studies reported collecting 1st instar blue crabs in the water column in Charleston Harbor, South Carolina (Mense and Wenner 1989) and Chesapeake Bay (Olmi et al. 1990). Thus, the tendency for young juvenile instars to undergo secondary dispersal may be more common than previously documented, and the patterns, mechanisms, and ecological consequences of such dispersal should be examined in a range of estuarine systems.

Secondary dispersal and colonization success is also strongly dependent on the interaction between hydrodynamic currents and habitat quality. For example, seagrass meadows provide key settlement habitat, food and refuge for megalopae and young juveniles (Etherington and Eggleston 2003 and references therein). In the York River, Chesapeake Bay, areal cover and distribution of seagrass beds has declined substantially from historic levels (R. J. Orth, VIMS, pers. comm.). Beds that existed 12 to 25 km upriver from the mouth have disappeared and have not recovered. A model for planktonic megalopal behavior, coupled with a 3-dimensional hydrodynamic transport model for the York River, Virginia was used to investigate potential effects of the decline in seagrass abundance, and hypothetical restoration, on blue crab settlement and recruitment to the benthos, both in seagrass and to unvegetated bottom (Stockhausen and Lepcius 2003). Effects of habitat loss were investigated in model simulations using two historic patterns of seagrass cover (ca. 1965 and ca. 1996), five patterns with intermediate loss of cover, and three settlement rates. Declines of crab settlement in seagrass (40%) and total settlement (25%) were not as great as the reduction in seagrass cover (70%). Although settlement was higher when seagrass cover was greater, a “settlement

\[ r^2 = 0.97, P < 0.0001 \]

Figure 6. Functional relationship between the pelagic concentration and benthic density of J1 (1st instar) blue crabs. Adapted from Reyns and Eggleston (2004).
shadow’’ created by seagrass near the river mouth reduced settlement in historic upstream seagrass beds and ameliorated effects associated with the loss of those beds. Increases in recruitment associated with restored seagrass beds differed significantly with restoration location, such that seagrass restoration in some locations enhanced recruitment substantially more than equivalent restoration in other locations, due to spatial variation in transport processes. Thus, landscape-level spatial patterns of existing and lost nursery habitat across the landscape interact with transport processes and megalopal behavior to determine settlement success and recruitment (Stockhausen and Lipcius 2003), and should be considered when evaluating population impacts of recruitment variation.

**DIET, FEEDING AND GROWTH**

The general food web of the blue crab is complex and involves a diverse set of predator–prey linkages (Fig. 7; also see Hines, Chapter 14). Juvenile blue crabs have a catholic diet consisting predominantly of benthic infauna and epifaunal invertebrates taken in proportion to their availability in the benthos; common prey include bivalves, fish remains, crabs, shrimp, amphipods, isopods, polychaetes, gastropods, and some plant and detrital matter (Tables 1, 2; Figs. 8, 9). In contrast to larger juvenile and adult crabs (Fig. 8), there is little evidence for cannibalism in young juvenile blue crabs < 40 mm CW (Fig. 9). The diet basically follows prey availability, which is dependent directly on habitat type. For instance, where gastropods were abundant in Gulf of Mexico seagrass beds, they comprised 45 % of the diet numerically, whereas they were virtually absent from the diet of juvenile blue crabs in seagrass beds that harbored few gastropods (Cote et al. 2001). Similarly, in upriver habitats where thin-shelled clams (i.e., Baltic macoma) were abundant, bivalves comprised about half of the diet numerically, but < 25 % in downriver habitats harboring substantially fewer bivalves (Mansour 1992). Besides the contrast in cannibalism rates, the other major difference between the diets of young juveniles and older,

![Figure 7. Food web of the blue crab in Chesapeake Bay, illustrating only those linkages with the blue crab as either predator or prey. Blue crab adults and juveniles are shown as separate compartments. Thicker lines indicate stronger connections, as determined from stomach contents studies. Derived from Lipcius (2005).](image-url)
Juvenile and Adult Stomach Contents

Figure 8. Composition of blue crab gut contents from four studies of adults and larger juveniles > 60 mm CW, and two studies of juveniles < 60 mm CW. The gut content studies are noted in Table 1. Note that all categories were not listed in each study, such that the “other” category may include polychaetes and other species.

Table 1. Blue crab gut contents from four studies of adults and larger juveniles > 60 mm CW, and two studies of juveniles < 60 mm CW. Four gut content studies include the following: (1) Mansour (1992) for adult and juvenile blue crabs in York and Rappahannock Rivers, Chesapeake Bay; (2) Laughlin (1982) for adults and juveniles in Apalachee Bay, Florida; (3) Hines et al. (1990) for adults and larger juveniles in the Rhode River, Chesapeake Bay; and (4) Tagatz (1968) for adults and larger juveniles in St. Johns River, Florida. (Note: not all categories were listed in each study so “other” category may include polychaetes for studies #2 and #4, for example.).

<table>
<thead>
<tr>
<th>Item</th>
<th>Adult Study Number</th>
<th>Juvenile Study Number</th>
<th>Adult Study 1</th>
<th>Adult Study 2</th>
<th>Adult Study 3</th>
<th>Adult Study 4</th>
<th>Summary Adult %</th>
<th>Summary Juvenile %</th>
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<tbody>
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<td>50</td>
<td>40</td>
<td>27</td>
<td>50</td>
<td>39</td>
<td>46</td>
<td>39</td>
</tr>
<tr>
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<td>5</td>
<td>11</td>
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<tr>
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<td>0</td>
<td>5</td>
<td>0</td>
<td>3</td>
<td>10</td>
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<tr>
<td>Others (including fish)</td>
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<td>11</td>
<td>11</td>
</tr>
<tr>
<td>Crustaceans (including shrimp, other crabs, amphipods)</td>
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<td>10</td>
<td>18</td>
<td>10</td>
<td>15</td>
<td>11</td>
<td>12</td>
<td>10</td>
</tr>
<tr>
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<td>0</td>
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<td>45</td>
<td>10</td>
<td>4</td>
<td>9</td>
<td>22</td>
</tr>
<tr>
<td>Gastropods</td>
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<td>10</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>5</td>
</tr>
</tbody>
</table>
Figure 9. Composition of blue crab gut contents from a recent study (Seitz et al., unpubl. obs.) of small juveniles (< 20 mm CW) and larger young juveniles (20 to 40 mm CW) collected in muddy coves fringed by salt marshes in the York River, Virginia (Chesapeake Bay).

Table 2. General gut contents of blue crabs from five descriptive studies of adults and larger juveniles > 60 mm CW, and mean of three studies of juveniles < 60 mm C. Four gut content studies include the following: (1) Rosas et al. (1994) for adults and larger juveniles in Gulf of Mexico subtropical lagoon and Halodule wrightii seagrass bed; (2) Cote et al. (2001) for juveniles in Gulf of Mexico Halodule wrightii seagrass beds; (3) Alexander (1986) for adults and juveniles in marshes and unvegetated soft bottoms of Gulf of Mexico; (4) Ryer (1987) for adults and larger juveniles in marshes and seagrass beds of York River, Chesapeake Bay; and (5) Stoner and Buchanan (1990) for adults and juveniles in a muddy tropical lagoon near Puerto Rico. None = none listed. Summary from an estimation of the mean from five studies.

<table>
<thead>
<tr>
<th>Item</th>
<th>Study Number</th>
<th>Adult #1</th>
<th>Juvenile #2</th>
<th>Adult #3</th>
<th>Juvenile #3</th>
<th>Adult #4</th>
<th>Adult #5</th>
<th>Juvenile #5</th>
<th>Summary Adults</th>
<th>Summary Juveniles</th>
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<td>Bivalves</td>
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<td>moderate</td>
<td>moderate</td>
<td>moderate</td>
<td>common</td>
<td>rare</td>
<td>common</td>
<td>rare</td>
</tr>
<tr>
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<td>moderate</td>
<td>moderate</td>
<td>moderate</td>
<td>moderate</td>
<td>common</td>
<td>rare</td>
<td>common</td>
<td>moderate</td>
</tr>
<tr>
<td>Polychaetes</td>
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<td>none</td>
<td>none</td>
<td>moderate</td>
<td>rare</td>
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<td>moderate</td>
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<tr>
<td>Others (including fish)</td>
<td></td>
<td>none</td>
<td>moderate</td>
<td>moderate</td>
<td>none</td>
<td>common</td>
<td>rare</td>
<td>moderate</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crustaceans (incl. shrimp, other crabs, amphipods)</td>
<td></td>
<td>moderate</td>
<td>none</td>
<td>moderate</td>
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<td>common</td>
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<tr>
<td>Detritus, plant matter</td>
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<td>common</td>
<td>moderate</td>
<td>common</td>
<td>moderate</td>
<td>rare</td>
<td>rare</td>
<td>rare</td>
<td>moderate</td>
</tr>
<tr>
<td>Gastropods</td>
<td></td>
<td>none</td>
<td>common</td>
<td>moderate</td>
<td>none</td>
<td>common</td>
<td>rare</td>
<td>rare</td>
<td>rare</td>
<td>moderate</td>
</tr>
</tbody>
</table>
larger crabs is that larger crabs usually had a larger proportion of their diet dominated by bivalves (Tables 1, 2; Figs. 8, 9).

For young juveniles, there is relatively little information on diet and food preferences (Laughlin 1982), though some studies indicate that the diet differs somewhat from that of older juveniles (Tables 1, 2; Figs. 8, 9). The diet of young juveniles typically has been inferred from studies of older juveniles larger than the 9th instar, usually 25 to 60 mm CW (Tables 1, 2; St. Johns River, Florida: Tagatz 1968; Apalachicola Bay, Florida: Laughlin 1982; Rhode River, Chesapeake Bay: Hines et al. 1990; York and Rappahannock Rivers, Chesapeake Bay: Ryer 1987; Mansour 1992; Caribbean: Stoner and Buchanan 1990; Gulf of Mexico: Alexander 1986; Rozas et al. 1994; Cote et al. 2001). In a recent gut content study (Seitz et al., unpubl. obs.), the percentage of the various prey items in guts of the smallest juvenile crabs differed from that in larger juveniles and adults. Juvenile crabs < 20 mm CW in unvegetated habitats of the York River, Chesapeake Bay, consumed a majority of amphipods, polychaetes, and plant matter, with no conspecifics in guts of crabs < 40 mm in CW (Fig. 9). Cannibalism begins to become apparent at sizes > 40 mm CW (compare Fig. 8 [published literature] with Fig. 9 [Seitz et al., unpubl. obs.]). Thus the smallest juvenile crabs feed on smaller prey items, as would be expected from limitations of their small feeding appendages.

The role of nursery food availability in enhancing blue crab recruitment is unresolved, but recent studies have demonstrated that blue crab abundance correlates with that of its principal prey (Fig. 10), such as the Baltic clam (Seitz et al. 2003, 2005), so that prey abundance must be measured to define the carrying capacity of nursery habitats. In addition to crab abundance correlating with clam abundance, growth of juvenile blue crabs can be substantially higher in upriver unvegetated habitats (where clam densities are high) than in seagrass or in downriver unvegetated habitats (Fig. 11; Seitz et al. 2003, 2005). However, juvenile crab growth in seagrass is often higher than that in downriver unvegetated habitats (with lower clam densities). Thus, upriver unvegetated mud and sand habitats serve as valuable, alter-native nursery habitats for juvenile blue crabs due to food availability and prospects for growth.

Some studies have suggested that unvegetated habitats are important for later juvenile stages of the blue crab (Mense and Wenner 1989; Rakocinski et al. 2003; Lipcius et al. 2005b). There is likely an ontogenetic shift from structured habitats such as seagrass to unvegetated habitats sometime in the juvenile phase (at approximately the 9th instar), but the mechanism is not merely that juveniles reach a
size at which they are able to survive and feed outside of the vegetated habitats. Instead, older juveniles can enhance their growth by utilizing the high prey densities in unvegetated sand and mud flats, such as those in highly productive upriver areas of estuaries. For instance, these highly productive regions in the York River and similar subestuaries can be associated with extensive marsh systems or with the estuarine turbidity maximum (Seitz et al. 2003, 2005).

Habitats such as coarse woody debris (Everett and Ruiz 1993), shallow water (Dittel et al. 1995; Hines and Ruiz 1995), marsh edge (Etherington and Eggleston 2000; Minello et al. 2003), and shallow marsh-fringed coves (Seitz et al. 2005) serve as alternative nurseries that enhance feeding and growth for juvenile crabs. Shallow subtidal marsh systems of Chesapeake Bay subestuaries are supplied with rich allochthonous organic carbon and have high densities of deposit-feeding bivalve prey for blue crabs (Seitz et al. 2005). Moreover, in Delaware Bay and low-salinity portions of other estuaries that lack extensive vegetated nurseries, the expansive subtidal sand and mud flats, particularly those bordering salt marshes, apparently serve as critical nurseries for the blue crab (King et al. 2005). Secondary production of young juvenile blue crabs in nursery habitats is therefore dependent not only on the likelihood that megalopae and young juveniles will be transported to those habitats, but also on the quality and carrying capacity of nursery habitats. A severe deficiency in our understanding of the importance of nursery habitats for growth of young juveniles is the lack of quantitative information that directly links secondary production of juveniles with food availability in nursery habitats, as well as the impact of habitat loss and degradation on secondary production of the juvenile blue crabs.

**PREDATOR-PREY INTERACTIONS AND SURVIVAL**

Post-settlement survival is determined by predation intensity and by nursery habitat quality, which jointly govern the secondary production potential of natural and restored habitats, and which ultimately determine the value of these habitats in fostering production of exploited species such as the blue crab (Peterson and Lipcius 2003). Nursery habitat quality includes the influence of prey availability and refuge potential from predation, which determines post-settlement mortality of young juveniles.

**Predator-Prey Interactions**

Blue crabs are thought to suffer high mortality by pelagic predators during their larval development, although direct measures of such interactions have not been quantified. Morgan (1989) demonstrated that estuarine-dependent species with life-history characteristics requiring exportation form an estuary during the larval (zoeal) phase, such as the blue crab, are more vulnerable to predation because their zoeae have significantly shorter spines than those of species that complete larval development within an estuary. Such morphological constraints broaden the suite of gape-limited predators that consume planktonic crab larvae.

After metamorphosis into the megalopa and while being transported from oceanic environments toward nursery habitats within an estuary, ingressing megalopae exhibit elaborate daily vertical migration rhythms which are thought to limit daytime mortality by visual predators during transport to suitable nursery habitats (Olmi and Lipcius 1991). Mesocosm experiments demonstrated that sand shrimp *Crangon septemspinosa* are voracious predators on megalopae, and grass shrimp *Palaemonetes pugio* also have the capacity to consume megalopae (Olmi and Lipcius 1991). Predation by the mummichog *Fundulus heteroclitus* on megalopae and three sizes of juvenile crabs was also intense in experimental mesocosms but was moderated by habitat structure, life-history stage and juvenile crab size (Orth and van Montfrans 2002).

Inter-cohort cannibalism can be a major source of mortality in megalopae and young juveniles (Moksnes et al. 1997), though there is little field evidence that crabs < 40 to 60 mm CW prey on conspecifics. In mesocosm experiments, cannibalism among megalopae during settlement was dependent
upon molt stage and occurred on sand substrates, but not in *Zostera marina* when megalopae metamorphosed to the first juvenile instar in mesocosm experiments (Moksnes et al. 1997). Furthermore, when megalopae were exposed to juvenile crab predators, mortality via inter-cohort cannibalism was significant, though moderated by habitat type (seagrass < sand) and by crab density (low < high) for crabs smaller than J5. Juvenile crab predators exhibited an inversely density dependent (type II) functional response in sand, causing high mortality at low prey (i.e., megalopal) densities (Moksnes et al. 1997). In contrast, juvenile crab predators in *Zostera marina* displayed a weak density-dependent (type III) functional response causing significantly lower mortalities at low prey densities. Thus, intra-cohort cannibalism by larger juveniles upon recent settlers (megalopae and smaller juveniles) can be a major source of mortality among newly settled crabs, especially in sandy habitats, and up to the J5 stage in seagrass habitats after which crabs no longer maintain a refuge in size from conspecific predators (Moksnes et al. 1997). Though the field evidence is lacking, these findings illustrate the potential for cannibalism to be significant within recruiting cohorts of young juveniles.

Numerous fish species consume juvenile blue crabs. In the Gulf of Mexico, a broad suite of approximately 67 species are predators on blue crabs, with other species listed as potential crab predators (Appendix 2 in Guillory and Elliot 2001). Among these, red drum *Sciaenops ocellatus* was ranked as the top piscine predator with a 33% frequency of occurrence of blue crabs in the diet, followed by sea catfish *Arius felis* (23% frequency) and several others (black drum *Pogonias cromis*, sheepshead *Anchostargus probatocephalus*, and spotted seatrout *Cynoscion nebulosus*: Appendix 2 in Guillory and Elliot 2001). Additionally, Guillory and Elliot (2001) listed 12 known or potential invertebrate predators (including conspecifics), as well as 3 species of reptiles, 11 birds, and 3 of mammals as predators on blue crabs.

The suite of predators on blue crabs varies with numerous factors including the size and species of predator, life-history stage, feeding habits, residency within an estuary and a host of environmental characteristics (Van Engel 1987). For example, many species known to consume blue crabs in the Gulf of Mexico have distributional ranges that extend throughout the Atlantic coast of North America although their densities may differ regionally. The abundant and highest ranking predatory fish on blue crabs in the Gulf of Mexico, red drum, occurs northward along the Atlantic coast to New Jersey but is rare near its northern limits (Murdy et al. 1997). Because this species is intolerant of low water temperatures and it occurs sporadically at temperate latitudes, its effect on blue crabs in colder parts of the range is weaker than that throughout the Gulf of Mexico.

Blue crabs in temperate zones (i.e., Chesapeake Bay) recruit as megalopae during fall as water temperatures decline (van Montfrans et al. 1990) and most predatory fish (except striped bass) depart the shallows. Movements of striped bass, a cold-tolerant species, contrast with those of all other fish predators in that they enter the shallows (including blue crab seagrass nursery habitats) during fall to feed. Studies that quantified the presence of small crabs in SAV habitats coincident with elevated striped bass predator densities demonstrated that striped bass were the top predatory fish on blue crabs in Chesapeake Bay (van Montfrans et al., unpubl. obs.). Few scientific investigations have quantified the impact of pelagic predators on blue crabs in temperate areas (Hollis 1952; Manooch 1973; Boynton et al. 1981; Hartman and Brant 1995; Walter and Austin 2003). Other important fish predators (van Montfrans et al. unpublished) on juvenile crabs include Atlantic croaker *Micropogonias undulatus*, weakfish *Cynoscion regalis*, spot *Leiostomus xanthurus*, and northern puffer *Sphoeroides maculatus*.

Evidence is mounting that cannibalism is a major force accounting for a great percentage of juvenile blue crab mortality in nature (see Heck and Coen 1995; Heck et al. 2001; Heck and Spitzer 2001). Mortality due to predation in Mobile Bay, Alabama was estimated to be as high as 95% daily, although vegetated habitats often dampened these effects. Blue crab mortality due to predation therefore depends on the abundance and activity of finfish predator populations and density-dependent
cannibalism, which lower natural survival of juvenile crabs in nurseries and thereby ultimately affect spawning stock size. Furthermore, factors that reduce the availability of protective habitats for juvenile crabs (e.g., habitat degradation) can potentially increase predation-induced mortality of juvenile stages in the blue crab life cycle.

**Survival and Nursery Habitat Quality**

**Value of Structured Nursery Habitats**

Structured shallow-water habitats such as seagrass beds, salt marshes and mangrove forests are considered the most valuable nurseries for marine and estuarine fish and invertebrates with complex life cycles because they enhance survival, movement and feeding rates relative to nearby unstructured (e.g., unvegetated) habitats (Heck and Thoman 1984; Beck et al. 2001; Heck et al. 2003; Minello et al. 2003). For the blue crab, several field and laboratory investigations have demonstrated that juveniles survive at substantially higher rates in seagrass or other structured habitats than in unvegetated subtidal habitats (Everett and Ruiz 1993; Perkins-Visser et al. 1996; Ryer et al. 1997; Heck and Spitzer 2001; Hovel and Lipcius 2001, 2002). Consequently, there is currently a paradigm that the critical nurseries for marine and estuarine species including the blue crab are structurally complex habitats such as seagrass beds and salt marshes (Heck et al. 2003; Minello et al. 2003).

Seagrass provides young juvenile crabs a refuge from visual-searching predators (Heck and Thoman 1984; Ruiz et al. 1993; Moksnes et al. 1997; Ryer et al. 1997; Heck and Spitzer 2001; Hovel and Lipcius 2001, 2002). Consequently, there is currently a paradigm that the critical nurseries for marine and estuarine species including the blue crab are structurally complex habitats such as seagrass beds and salt marshes (Heck et al. 2003; Minello et al. 2003). The recent findings that some unvegetated habitats serve as good nursery habitats are applicable to moderately sized juveniles (~25 to 50 mm CW), but megalopae and the youngest juveniles <20 mm CW are apparently better suited for unvegetated habitats such as seagrass beds and salt marshes (Heck and Thoman 1984; Orth and van Montfrans 1990; Pile et al. 1996).

That a large fraction of the youngest juvenile blue crabs reside and survive well in seagrass beds, salt marshes and mangroves (where those occur) is consistent with the classic paradigm that structured shallow-water habitats are valuable nurseries for marine and estuarine fish and invertebrates in general (Beck et al. 2001; Heck et al. 2003; Minello et al. 2003) and for the blue crab in particular (Orth and van Montfrans 1987; Perkins-Visser et al. 1996; Pile et al. 1996; Eggleston et al. 1998; Pardieck et al. 1999; Hovel and Lipcius 2001, 2002). Survival of these juveniles is often higher in seagrass than in adjacent unvegetated (sand) flats, as observed in many earlier studies (Pile et al. 1996; Hovel and Lipcius 2001, 2002). But, at broader spatial scales (i.e., upriver versus mouth habitats) and in different habitat types (i.e., mud) survival of juveniles does not fit the pattern of higher survival in structured habitats, as we describe below.

**Value of Unstructured Nursery Habitats**

Investigations comparing survival, growth and abundance in vegetated and unvegetated habitats have typically been conducted at sites that are in close proximity, usually within a few 100 m (Fig. 12). A few studies have indicated that abundance of blue crab juveniles may be relatively high in unvegetated, structurally simple habitats (e.g., subtidal mud flats) distant from the characteristic seagrass nurseries (Figs. 13, 14; Mense and Wenner 1989; Lipcius and Van Engel 1990; Heck and Spitzer 2001; Rakocinski et al. 2003; Lipcius et al. 2005b; Posey et al. 2005; Seitz et al. 2005), and survival of small juvenile blue crabs may be enhanced in such habitats, particularly in the extremely shallow zone (Ruiz et al. 1993;
Figure 12. Representation of a field layout of tethering experiments in nursery habitats of the York River, Virginia. Each triangle indicates the location of an individual tethered crab or a set of tethered crabs that represent independent replicates. Adapted from Lipcius et al. (2005b).

Figure 13. Abundance of young juvenile blue crabs < 13 mm CW in the Cape Fear River estuary of North Carolina in the summer of 2002. Areas of low salinity are characteristically unstructured mud and sand subtidal habitats. From Posey et al. (2005).

Figure 14. Density of blue crab juveniles in Mouth, Downriver and Upriver locations in the York River, Virginia, Chesapeake Bay. Habitats were Subtidal Mud, Subtidal Sand, and Deep-Water Mud at all locations, whereas SAV (seagrass) habitats only occurred at the Mouth location. Adapted from Lipcius et al. (2005b).
Dittel et al. 1995; Hines and Ruiz 1995; Heck and Spitzer 2001; Lipcius et al. 2005b; Posey et al. 2005). For example, in estuaries of the Atlantic coast a substantial fraction of each population’s juveniles (~ 40 % or more) inhabit shallow unstructured mud and sand habitats, which are characteristically in the subtidal zone fringing salt marshes in the upriver segments of tributaries (Mense and Wenner 1989; Ruiz et al. 1993; Hines and Ruiz 1995; Rakocinski et al. 2003; Lipcius et al. 2005b; Posey et al. 2005). Most of the remaining juveniles reside in SAV beds near the mouths of tributaries, while a small fraction inhabits deep mud channels and the remaining shallow portions of the tributaries.

Recent manipulative tethering experiments on survival of young juveniles 15 to 55 mm CW (25 to 55 mm CW — Lipcius et al. 2005; 15 to 30 mm CW — Posey et al. 2005) indicate that an absence of considerable structure in shallow-water habitats does not preclude high survival of juveniles in those habitats (Figs. 15, 16). These juvenile crabs survived at much higher rates in unstructured upriver habitats than in SAV or unstructured sand and mud habitats near the mouths of tributaries in North Carolina (Fig. 15; Posey et al. 2005) and Chesapeake Bay (Fig. 16; Lipcius et al. 2005b); in some cases the difference was considerable — about four-fold. Similarly, survival of juveniles 5 to 20 mm CW in salt marshes and sand flats was often not substantially different from that in seagrass beds in the Gulf of Mexico (Fig. 17; Heck and Spitzer 2001). Hence, other factors besides habitat structure, such as predator and alternative prey abundance, must strongly influence the likelihood of predation in those habitats. In addition, seagrass is not present in low-salinity areas throughout a large fraction of the estuarine and lagoonal habitats of the blue crab, and overall areal coverage of unvegetated habitats is high compared to vegetated habitats such as seagrass (Stockhausen and Lipcius 2003).

The reduction in blue crab populations during the 1990s and into the present (Lipcius and Stockhausen 2002; Eggleston et al. 2004) implies that predation pressure on juveniles from cannibalism in Chesapeake Bay and North Carolina sounds has been reduced over the past decade. This could

![Figure 15](image1.png)

Figure 15. Survival of tethered juveniles 15 to 30 mm CW in the Cape Fear River system of North Carolina. Areas of moderate salinity were typically unstructured subtidal mud and sand habitats where survival could be as high as that near seagrass beds at the mouth of the estuary. Adapted from Posey et al. (2005).

![Figure 16](image2.png)

Figure 16. Survival of tethered juveniles 25 to 55 mm CW in various habitats of the York River, Virginia in Chesapeake Bay. Mouth and Upriver habitats are unstructured mud and sand subtidal habitats. The habitats spanned a 40-km stretch of the York River, and individual crabs were tethered no less than 50 m apart, but usually more than 100 m apart to foster independence among replicate crabs. Adapted from Lipcius et al. (2005b).
explain why predation rates on juvenile crabs have been low in recent experiments conducted in Chesapeake Bay and North Carolina, though in some cases the experiments have contrasted vegetated and unstructured habitats with similar results (Lipcius et al. 2005b). Densities of potential cannibals have been generally low in unvegetated habitats during the recent two decades, often 0.1 to 1 m⁻², which would serve as a mechanism that reduces cannibalism rates and promotes high survival in unstructured habitats (Lipcius et al. 2005b; Posey et al. 2005).

Collectively, the findings indicate that particular unstructured shallow-water habitats (e.g., marsh-fringed mud coves) should be viewed as vital nurseries, complementary to structured nurseries such as seagrass beds and salt marshes (Beck et al. 2001; Heck et al. 2003; Minello et al. 2003). In hindsight, the work of Minello, Rozas and colleagues foreshadowed the recent findings on the value of alternative nursery habitats, other than seagrass beds, particularly salt marshes and associated habitats (see review in Minello et al. 2003).

**Size, Season and Survival**

In temperate locations such as Delaware Bay and Chesapeake Bay, survival follows a seasonal pattern with lowest survival in summer when predators are most active (Fig. 18). In more southerly locations such as the Gulf of Mexico, there is reduced seasonality in survival due to the nearly year-round foraging activity of finfish and invertebrate predators (Heck and Spitzer 2001), which may be the major reason for the substantial reduction in abundance of young-of-the-year juveniles in these subtropical locations.

Field studies that examined mortality of a range of juvenile crab sizes (J2 and J3 instars measuring 3.1 to 5.9 mm CW; J7 to J9 instars measuring 10.7 to 16.1 mm CW; and larger crabs 11.7 to 34.8 mm CW) and in which individuals were tethered among simulated seagrass plots spanning the natural range of ambient shoot densities, indicated a range of interactions between crab size and shoot density (Schulman 1996). Greatest survival for the smallest crabs occurred at low shoot densities, whereas J7 to J9 instars and larger crabs exhibited increasing survival with increasing shoot density. Experimental survival correlated with patterns of crab density associated with shoot density in natural seagrass. Intercohort cannibalism was evoked to explain the observed patterns in that smallest juveniles avoided...
the higher seagrass densities that contained the highest densities of larger conspecifics, whereas larger individuals occupied more densely vegetated plots that provided them protection from larger predators. A similar increase in survival of young juveniles across a range in crab size from 10 to 70 mm CW has been observed in seagrass beds (Pile et al. 1996), in unvegetated habitats of the York River, Chesapeake Bay (Fig. 19), and along an estuarine gradient in the Neuse River (Posey et al. 2005). Survival generally increases with size up to about 50 mm CW, when it apparently reaches an asymptote, at least in nursery habitats (Fig. 19).

CONCEPTUAL MODEL OF RECRUITMENT PROCESSES IN NURSERY HABITATS

Given recent findings on survival and abundance of young and moderately-sized juveniles (<55 mm CW), the conceptual paradigm on habitat use by blue crab juveniles requires modification (Fig. 1). As noted in the classic paradigm, megalopae reinvade estuarine or coastal nursery habitats from the continental shelves of oceanic environments, and settle in seagrass or other structured habitats where they metamorphose into the 1st benthic juvenile instar. These are considered the primary nurseries as they provide apparently optimal settlement substrate for megalopae and safe, food-rich habitat for the youngest juveniles < 20 mm CW (Fig. 20). Megalopae may also be advected and bypass seagrass beds for upriver structured habitats such as salt marshes, which can serve as the primary nursery (Fig. 20). Many of the 1st instar juveniles remain in seagrass beds until sometime after reaching the 9th instar at about 20 to 25 mm CW, due to the size-specific survival (Fig. 19) and higher survival and growth conferred by the structure and food in seagrass beds (Morgan et al. 1996; Perkins-Visser et al. 1996; Pile et al. 1996; Eggleston et al. 1998; Pardieck et al. 1999; Heck and Spitzer 2001; Hovel and Lipcius 2001, 2002; Orth and van Montfrans 2002). If densities are too high in the seagrass beds, the youngest instars (1st to 3rd) emigrate from seagrass beds to avoid density-dependent cannibalism (Etherington and Eggleston 2000; Blackmon and Eggleston 2001; Reyns and Eggleston 2004) and growth (Perkins-Visser et al. 1996), and migrate to other seagrass beds or alternative primary nursery habitats upstream, such as mangroves, salt marshes, oyster reefs and coarse woody debris. The remaining larger juveniles (>25 mm CW) disperse from seagrass beds, where they have outgrown the refuge afforded by seagrass, to other shallow-water habitats that serve as secondary nurseries, such as subtidal mud and sand flats or salt marshes, where they obtain plentiful prey and a spatial refuge from the predators utilizing seagrass beds (Fig. 20). The larger juveniles are now more vulnerable to predation in the seagrass beds and must emigrate to the unstructured shallow-water mud and sand flats or salt marshes serving as secondary nurseries, which harbor benthic infauna such as the Baltic macoma and which have fewer and less diverse predators, particularly at times other than the intense summer predation period.

This refined conceptual model (Fig. 20) thus posits that megalopae and the youngest juveniles reside in structured primary nursery habitats (e.g., seagrass beds, salt marshes, oyster reefs) safest from predation upon settlement and early growth, although some of the youngest juveniles disperse at

Figure 19. Size-specific survival of juvenile blue crabs tethered in various habitats of the York River, Chesapeake Bay. Data derived from Moody (2001) and subsequently analyzed with logistic regression.
an early stage (1st to 3rd instars) to other structured or unstructured nurseries due to density–dependent emigration resulting from reduced survival and growth at higher conspecific densities. As the juveniles grow (> 25 mm CW), they become more susceptible to predation in seagrass beds because they outgrow the size-specific protection of seagrass structure, and become less susceptible to predation by gape-limited predators in salt marsh and alternative nursery habitats due to their bigger size. Consequently, these larger young juveniles depart the settlement and primary nursery habitats to exploit the refuge and abundant prey of secondary nursery habitats, both structured and unstructured (Fig. 20). Structured habitats such as seagrass beds may once again become a relative refuge from predation and source of abundant food when the juveniles grow to over 60 mm CW, as evidenced by the abundance of larger crabs feeding, molting, and mating in seagrass beds. Specifically, we posit that larger juveniles (> 25 mm CW) emigrate from seagrass beds and other structured primary nursery habitats to unstructured mud and sand flats and salt marshes serving as secondary nurseries, not only to reduce density-dependent growth and mortality, but also because survival and food availability are substantially higher in many
unstructured shallow-water habitats. In particular, mud and sandy mud coves or shores fringed by salt marshes in the upriver portions of riverine systems appear to be valuable secondary nurseries for blue crab juveniles, even when there are seagrass beds in the system.

These findings are consistent with those of field investigations in systems that lack seagrass beds (e.g., Delaware Bay, Cape Fear River system, upper Chesapeake Bay), wherein abundance and survival of young juvenile crabs is substantially higher in shallow subtidal mud and sand flats than in deeper or downriver habitats (Ruiz et al. 1993; Dittel et al. 1995; Hines and Ruiz 1995; Lipcius et al. 2005b; Posey et al. 2005). In these and other systems abundance of blue crab juveniles may be relatively high in unvegetated, structurally simple habitats (South Carolina: Mense and Wenner 1980; Chesapeake Bay: Lipcius et al. 2005; North Carolina: Posey et al. 2005; Mississippi: Rakocinski et al. 2003; Rakocinski and McCall 2005). These collective findings demonstrate that abundance and survival of larger juvenile blue crabs may be high in shallow unstructured habitats, whether in systems with or without seagrass beds, and that these habitats should therefore be viewed as essential nursery habitats.

The enhanced survival of larger juveniles in the shallow unstructured subtidal habitats relative to seagrass beds and other structured or deeper habitats is likely due to a combination of factors including positive density-dependent survival, a reduction in the diversity and abundance of piscine and invertebrate predators, and lower cannibalism rates (Hines et al. 1990; Ruiz et al. 1993; Dittel et al. 1995; Hines and Ruiz 1995; Moksnes et al. 1997; Lipcius et al. 2005b; Posey et al. 2005), as potential cannibals can feed on abundant alternative prey (e.g., Baltic macoma; Hines and Comtois 1985; Mansour and Lipcius 1991; Clark et al. 1999a, b; Seitz et al. 2003, 2005).

The major implications of these findings are that the abundance and survival of juveniles in shallow-water habitats of the same type (e.g., mud coves) can differ radically depending on the location of those habitats, and that a lack of structure per se (e.g., SAV) in potential nursery habitats does not prevent habitation by juveniles. In addition, given the recent findings that a combination of seagrass beds near the river mouths and upriver subtidal mud and sand flats encompass a relatively small fraction (20 % for instance, in lower Chesapeake Bay) of all nursery habitats, and that most (e.g., ~90 % in lower Chesapeake Bay) of the population’s juveniles reside in those habitats, then a relatively small fraction of potential nursery habitats comprises the functional nursery grounds of the blue crab in such systems.

The evidence on young juvenile blue crabs indicates that unstructured shallow-water nursery habitats, particularly subtidal mud and sand flats fringing salt marshes, should be accorded protection from habitat degradation and that they be designated as essential blue crab nursery habitats for conservation and restoration (e.g., in spatial management and protected areas; Lipcius et al., 2003, 2005a; Stockhausen and Lipcius, 2003), in the same manner as seagrass beds and other structured habitats (Beck et al. 2001; Heck and Spitzer 2001; Heck et al. 2003; Minello et al. 2003). The production potential of blue crabs that use salt marshes, seagrass beds and alternative nursery habitats fringing developed shorelines has likely been severely reduced due not only to direct habitat destruction but also due to indirect degradation of subtidal mud and sand flats fringing salt marshes, mangroves and seagrass beds (Hovel and Lipcius 2001; Seitz et al., in press). Such changes may be playing a major role in the continuing decline of the blue crab along the Atlantic and Gulf of Mexico coasts.

REFERENCES


Etherington, L.L. and D.B. Eggleston. 2003. Spatial dynamics of large-scale, multi-stage crab (*Callinectes
**sapidus** dispersal: Determinants and consequences for recruitment. Canadian Journal of Fisheries and Aquatic Sciences 60:873-887.


Hines, A.H., R.N. Lipcius and A.H. Haddon. 1987. Population dynamics and habitat partitioning by size, sex, and molt stage of blue crabs *Callinectes sapidus* in a
subestuary of central Chesapeake Bay. Marine Ecology Progress Series 36:55-64.


Minello, T.J. 1999. Nekton densities in shallow estuarine
habitats of Texas and Louisiana and the identification of essential fish habitat. Pages 43-75 in L.R. Benaka (ed.). Fish Habitat: Essential Fish Habitat and Rehabilitation. American Fisheries Society Symposium 22. Bethesda, Maryland.


Reyns et al. In press.


in Mississippi coastal waters. Gulf Research Reports 7:93-95.


