THE BLUE CRAB

Callinectes sapidus

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and

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Chapter 13

Ecology of Postlarval and Young Juvenile Blue Crabs

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INTRODUCTION

A critical period of the life histories 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). We define settlement as the colonization of nursery habitats by postlarvae (= megalopae in the blue crab) and recruitment 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 are lacking. Chapter 14 by Hines extends our review for older juveniles, though there is some unavoidable repetition.

Because various recent reviews of recruitment processes in marine and estuarine nursery habitats have appeared (Beck et al. 2001; Heck and Spitzer 2001; Gillanders et al. 2003; Heck et al. 2003; Minello et al. 2003), 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 recruitment. 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 influence of these ecological factors upon blue crab population dynamics (also see Fogarty and Lipcius, Chapter 16) and note the effects of habitat fragmentation and degradation upon blue crab nurseries. We then 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 discuss conservation issues related to blue crab nurseries, such as habitat restoration and enhancement with juveniles. 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).

SETTLEMENT AND RECRUITMENT IN NURSERY HABITATS

The classic 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). As we will argue, this paradigm needs to be revised as a result of recent research that has been refining our knowledge of habitat use by different juvenile stages. According to the classic model, megalopae settle in seagrass or other structured habitats and metamorphose into the 1st benthic juvenile instar (J1), which is about 2.2 to 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 forms are used throughout the text.] Many of the J1 juveniles remain in seagrass beds until sometime after reaching the 7th instar at about 20 to 30 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, predation, and food limitation (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 (>20 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 a need for 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 unstructured shallow-water mud and sand flats,

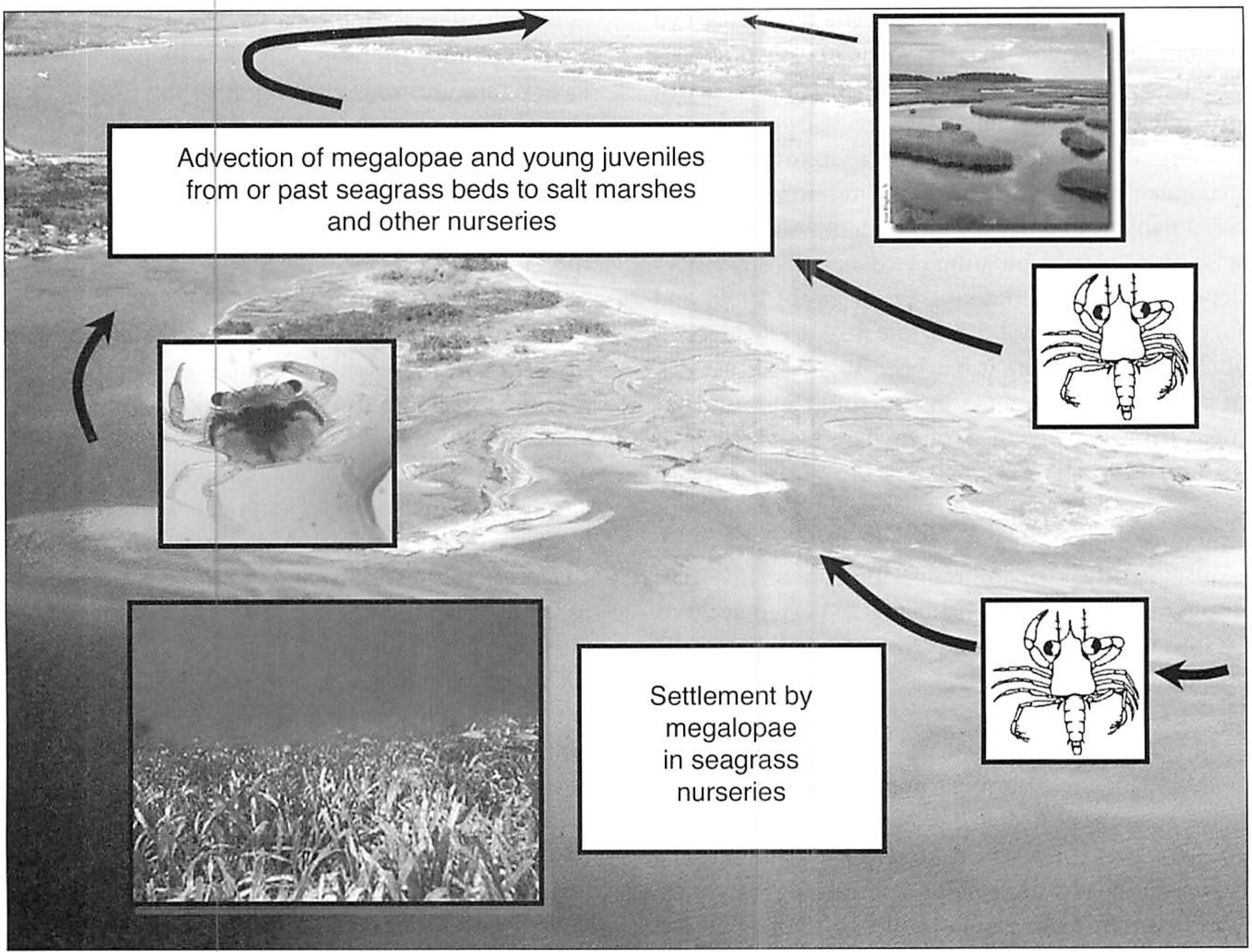

Figure 1. Classic conceptual model of colonization of nursery habitats by megalopae, and recruitment into alternative nursery habitats by megalopae and young juveniles. In the model, megalopae either colonize and settle in preferred primary nursery habitats such as seagrass beds, or when these are unavailable, they settle in coarse woody debris, the intertidal or subtidal zone of salt marshes, oyster reefs, or other structured habitats. Megalopae may not settle in seagrass beds if hydrodynamic currents advect the megalopae past the seagrass. Aerial photo by Marcel M. Montane.

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 southeast estuaries and 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 (>20 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. We then refine the classic model of settlement and recruitment (Fig. 1) to incorporate recent findings that have significantly altered our understanding of the patterns and processes of settlement and recruitment of the blue crab.

EVOLUTIONARY 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 and catadromous. Populations are found in the Caribbean only near high islands that 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.

Also of significance in the evolution of *Callinectes* is whether this species prefers a single type of habitat, 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). Thus, *C. sapidus* exhibits no preference for a specific habitat type, 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; also see 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 megalopal 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 onshore transport under highly stochastic oceanic conditions, thereby 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 life cycle phase responsible for reinvasion of estuarine or lagoonal nursery habitats, with ingress into estuaries accomplished by 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) the previous year, despite high spawning stock and larval abundance (Lipcius and Stockhausen 2002). Since then, a combination of generally poor recruitment, heavy fishing, and natural mortality has depressed spawning stocks, which have still not recovered. The causes of poor recruitment remain unidentified, though they likely involve 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 to chemical cues upon settlement may be important in ensuring that megalopae, 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). Because ingressing megalopae demonstrate variation 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 variability.

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 DeVries 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 these nursery habitats.

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 promote the return of megalopae to estuarine habitats; and (2) specific responses to estuarine nursery habitat types (e.g., seagrass beds, algal habitats), including avoidance of other less favorable habitats and predators, which enhance the likelihood of recruitment success via maximal survival (Pile et al. 1996) and accelerated growth (Perkins-Visser et al. 1996).

Habitat-specific utilization by blue crab megalopae and young juveniles occurs throughout their range. Within Chesapeake Bay and North Carolina coastal areas, megalopae and the smallest juvenile crabs (1st-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 more often associated with marsh habitats (Texas: Thomas et al. 1990; Rozas and Minello 1998; Minello 1999) and muddy substrates (Mississippi Sound: Rakocinski et al. 2003). In some 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 facilitate use of salt marsh habitats by early settlers (megalopae and the first few instars), as they need only leave the marsh once a day. 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* sp. salt marsh fringe (K. Heck, unpubl. data). 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 coast (Thomas et al. 1990; Zimmerman et al. 2000; Minello et al. 2003).

Temporal Patterns

Blue crab settlement across broad geographic scales has been examined using identical artificial settlement substrates to characterize daily and seasonal settlement patterns. 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). These authors 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).

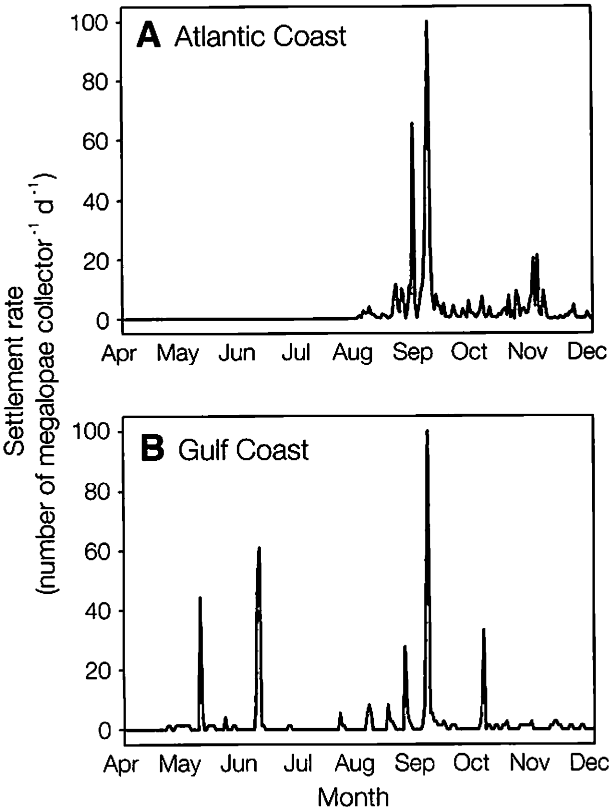

Figure 2. Representative settlement patterns of megalopae on artificial settlement substrates (= collectors) in (A) Atlantic coast estuaries and (B) Gulf of Mexico coastal habitats. Note the highly episodic nature of both time series, and the protracted annual settlement season in the subtropical Gulf of Mexico region. The data were adapted from settlement time series selected from (A) the York River, Virginia (van Montfrans et al. 1995) and (B) Terrebonne Bay, Louisiana (Rabalais et al. 1995). Settlement rates (mean number of megalopae collector^{-1} d^{-1}) were standardized by setting the peak for each region to 100.

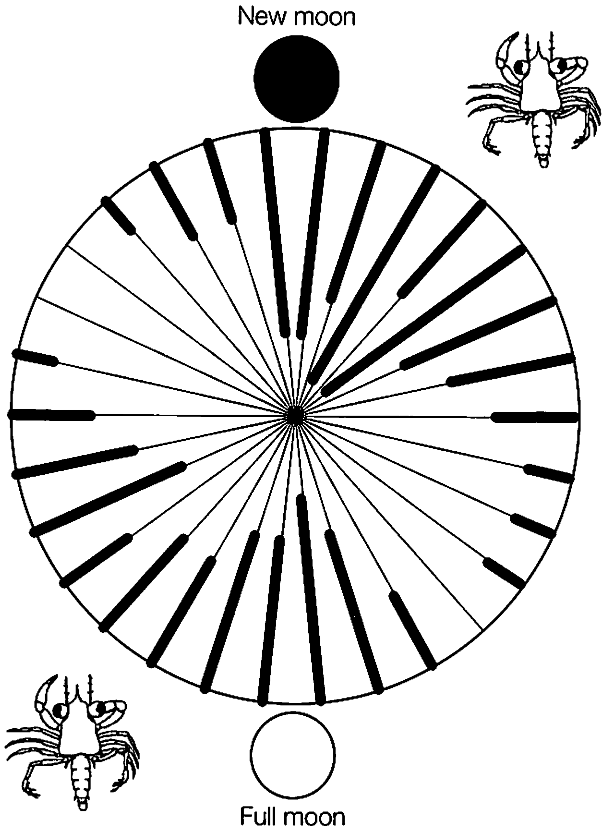

Figure 3. Semi-lunar periodicity in settlement of blue crab megalopae in Atlantic coast estuaries. The lengths of the solid bars represent the cumulative number of peaks (range 0 to 6) in megalopal settlement at each stage of the lunar cycle and are derived from settlement time series from Delaware Bay, Tangier Sound (Virginia), York River (Virginia), North Carolina, and Charleston Harbor (South Carolina) (van Montfrans et al. 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 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 (1996-2005) 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

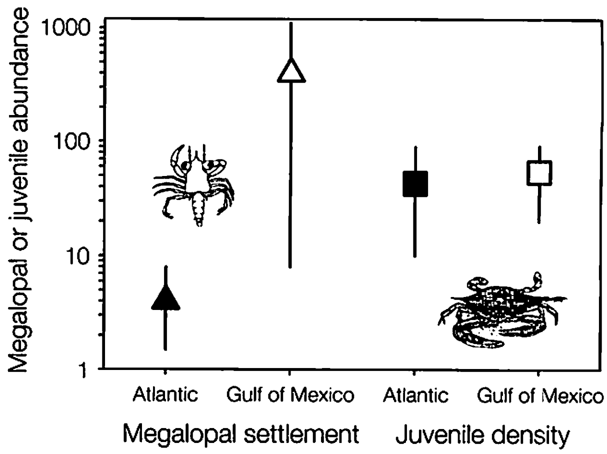

Figure 4. Comparison of the magnitude of megalopal settlement and juvenile density in Atlantic and Gulf of Mexico estuaries. Note the order of magnitude higher mean settlement in the Gulf of Mexico than along the Atlantic coast. Adapted from Rabalais et al. (1995).

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, leading to starvation, suspension of the molt cycle in premolt (McConaugha 1985), or the metamorphosis into intermediate larval or postlarval stages, thereby prolonging larval duration and 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 variation 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 greater in the Gulf of Mexico (Rabalais et al. 1995) than along the Atlantic coast (Fig. 4). Resulting abundances of juvenile crabs, however, are often decoupled from settlement abundances 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 on the 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 contrasts with 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 (Hines and Ruiz 1995; Moksnes et al. 1997). 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 larvae 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).

DISPERSAL

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 Dispersal

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; also see 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 is that (1) megalopae undergo flood-tide transport for entrance into estuaries and up-estuary movement, and (2) the behavior underlying flood-tide transport is most effective when all of the nocturnal flood tide occurs 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 submerged 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 remain in these habitats until they reach the 5th to 7th instar (J5-J7) at about 20 mm CW, after which they emigrate 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 by Etherington et al. (2003) determined that the probability of emigration from seagrass by young juvenile blue crabs can be extremely high (0.29-0.72 in a 6-h period), and can exceed the probability of mortality (0.25-0.67 in a 6-h period). 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

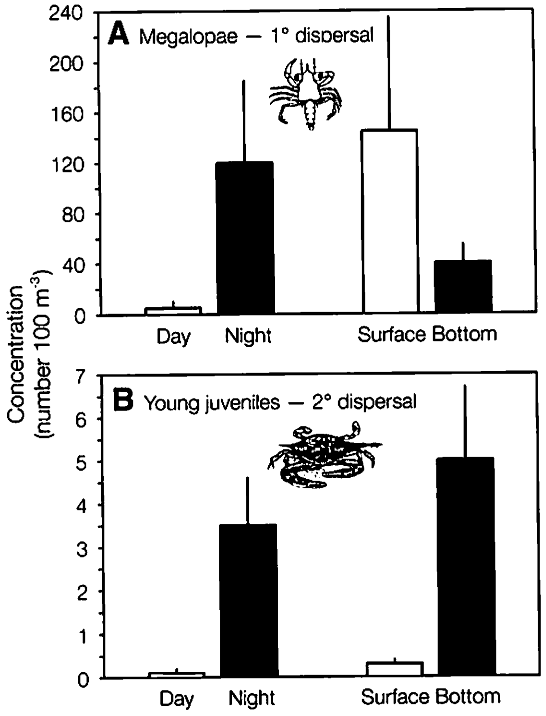

Figure 5. Vertical and diurnal distribution of (A) megalopal and (B) young juvenile blue crabs collected with a towed plankton net and benthic sled during a synoptic plankton cruise sampling within Pamlico Sound in 2000 and 2001. Vertical bar = standard error. Adapted from Reyns (2004).

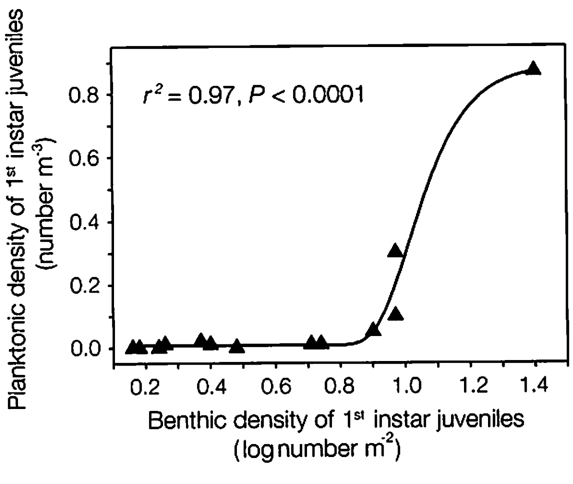

Figure 6. Density-dependent (sigmoid) relationship between the pelagic and benthic densities of J1 (1st instar) juvenile blue crabs. For reference, planktonic density increased significantly when benthic density approximated 10 crabs m^{-2}. Adapted from Reyns and Eggleston (2004).

found that secondary dispersal of J1 instars in wind-driven bottom currents 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 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 Lipcius 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 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 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; Fig. 8). In contrast to larger juvenile and adult crabs (Table 1), there is little evidence for cannibalism in young juvenile blue crabs <40 mm CW (Fig.

8). The diet basically follows prey availability, which is dependent directly on habitat type. For instance, when 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). In addition to the contrast in cannibalism rates, the other major difference between the diets of young juveniles and older, larger crabs is that the latter usually had a larger proportion of their diet dominated by bivalves (Tables 1, 2; Fig. 8).

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; Fig. 8). 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. data), the percentages of different prey in the smallest juvenile crabs differed from those in larger juveniles and adults. Juvenile crabs <20 mm CW in unvegetated marsh-fringed coves of the York River, Chesapeake Bay, consumed mostly amphipods, polychaetes, and plant matter, with no conspecifics in guts of crabs <40 mm in CW (Fig. 8). Cannibalism begins to become apparent at sizes >40 mm CW (compare Table 1 [published data] with Fig. 8 [Seitz et al., unpubl. data.]). 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

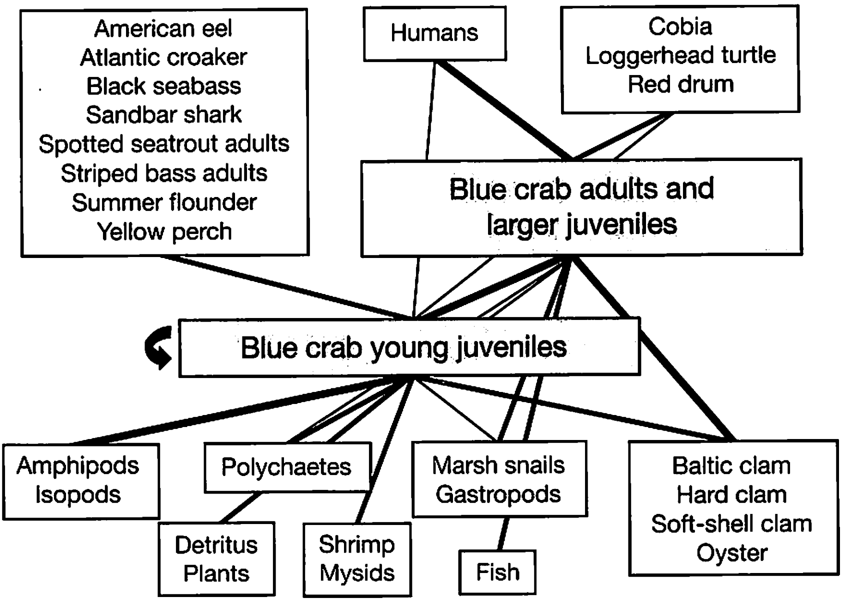

Figure 7. Food web of the blue crab in Chesapeake Bay, illustrating only those linkages with the blue crab as either predator or prey, and with emphasis on young juveniles. The compartment for blue crab young juveniles is specific to juveniles <40 mm CW. Thicker lines indicate stronger connections, as determined from stomach content studies depicted in Fig. 8. Modified from Lipcius and Latour (in press).

Table 1. Blue crab gut contents (percentages) from studies of adults and larger juveniles >60 mm CW and studies of juveniles <60 mm CW. 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 Apalachicola 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 "Others" category may include polychaetes for studies #2 and #4, for example.

Item	Juvenile	Adult	Juvenile	Adult	Adult	Adult	Average Percentage	
	#1	#1	#2	#2	#3	#4	Juvenile	Adult
Bivalves	50	55	27	40	50	39	39	46
Blue crabs	5	30	1	11	15	8	3	16
Polychaetes	20	5	0	0	5	0	10	3
Others (including fish)	15	5	7	14	5	20	11	11
Crustaceans (including shrimp, other crabs, amphipods)	10	5	10	18	15	11	10	12
Detritus, plant matter	0	0	45	5	10	4	22	5
Gastropods	0	0	10	12	0	0	5	3

studies have demonstrated that blue crab abundance correlates with that of the crab's principal prey (Fig. 9), such as the Baltic macoma 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. 10; Seitz et al. 2003, 2005). However, juvenile crab growth in seagrass is often higher than in downriver unvegetated habitats (with lower clam densities). Thus, upriver unvegetated mud and sand habitats serve as valuable, alternative 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

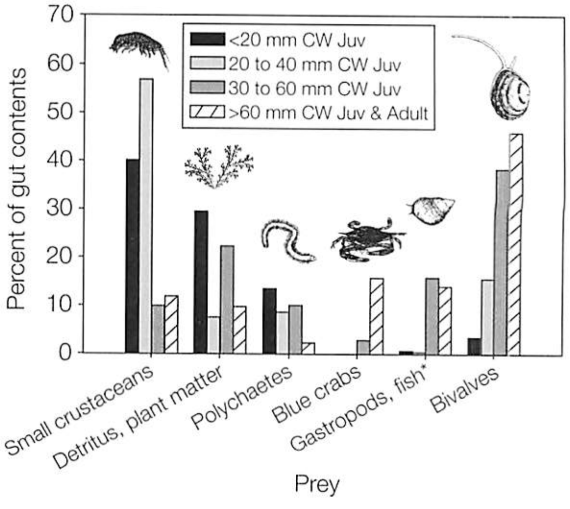

Figure 8. Comparison of blue crab gut contents from a recent study (Seitz et al., unpubl. obs.) of small juveniles (<20 mm CW) and larger young juveniles (20-40 mm CW) with those of larger juveniles and adults (Table 1). * miscellaneous prey.

Table 2. General gut contents of blue crabs from four descriptive studies of adults and larger juveniles >60 mm CW and three of juveniles <60 mm CW. Studies include the following: #1 Rosas et al. (1994) for adults and larger juveniles in a 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 the 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 is an estimation of the mean from the relevant studies.

Item	Adult	Juvenile	Adult	Juvenile	Adult	Adult	Juvenile	Summary	
	#1	#2	#3	#3	#4	#5	#5	Adults	Juveniles
Bivalves	common	none	moderate	moderate	moderate	common	rare	common	rare
Blue crabs	common	moderate	moderate	moderate	moderate	common	rare	common	moderate
Polychaetes	none	none	none	none	moderate	rare	common	rare	moderate
Others (including fish)	none	none	moderate	moderate	none	common	rare	moderate	rare
Crustaceans (incl. shrimp, other crabs, amphipods)	moderate	none	moderate	moderate	moderate	common	common	common	moderate
Detritus, plant matter	none	common	moderate	common	moderate	rare	rare	rare	moderate
Gastropods	none	common	moderate	moderate	none	common	rare	rare	moderate

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 7th-9th instar), though the mechanism is not merely that juveniles reach a size at which they are able to survive and feed outside of the vegetated habitats; rather, 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 blue crab nurseries (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 defi-

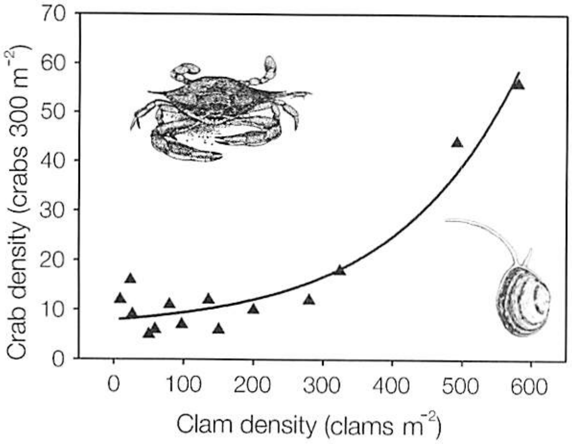

Figure 9. Relationship between blue crab and Baltic macoma densities in the York River, Chesapeake Bay. Adapted from Seitz et al. (2003).

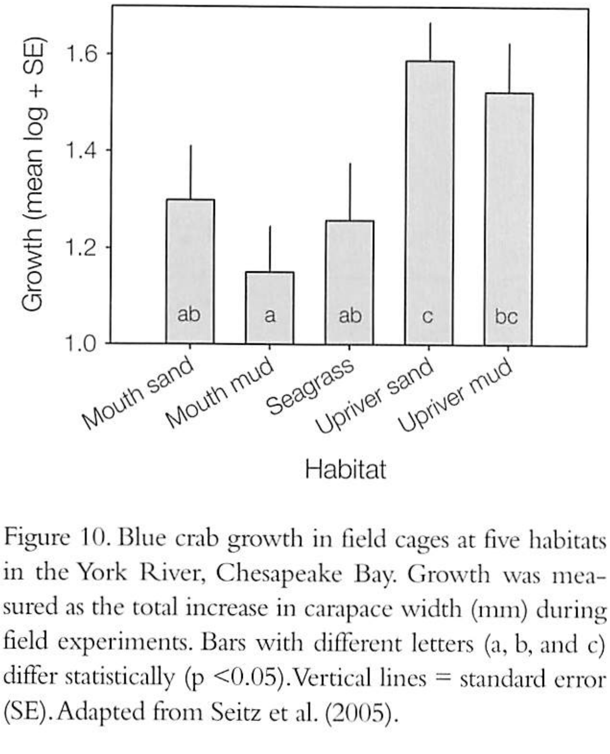

Figure 10. Blue crab growth in field cages at five habitats in the York River, Chesapeake Bay. Growth was measured as the total increase in carapace width (mm) during field experiments. Bars with different letters (a, b, and c) differ statistically ($p < 0.05$). Vertical lines = standard error (SE). Adapted from Seitz et al. (2005).

ciency 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 effect of habitat loss and degradation on secondary production of these juveniles.

PREDATOR-PREY INTERACTIONS AND SURVIVAL

Post-settlement survival is related to predation intensity and nursery habitat quality, which jointly govern the secondary production potential of natural and restored habitats, and thus 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 affects 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 from 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). 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 (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). Recent mesocosm experiments indicate that very small juveniles are capable of high levels of cannibalism, and the efficiency of a cannibal appears not to be related to absolute size, but rather to the relative size ratio between cannibal and prey (Moksnes and Heck 2006). 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 prey 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 *Archosargus 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 of 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 occurs sporadically at temperate latitudes, its effect on blue crabs in colder parts of the range is weaker than in the Gulf of Mexico.

Blue crabs in temperate zones (e.g., Chesapeake Bay) recruit as megalopae during fall as water temperatures decline (van Montfrans et al. 1990) and most predatory fish (except striped bass *Morone saxatilis*) 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 densities demonstrated that striped bass were the top predatory fish on blue crabs in Chesapeake Bay SAV beds (van Montfrans et al., unpubl. data). Few scientific investigations have quantified the effect 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 on juvenile crabs include Atlantic croaker *Micropogonias undulatus*, weakfish *Cynoscion regalis*, spot *Leiostomus xanthurus*, and northern puffer *Sphoeroides maculatus* (van Montfrans et al., unpubl. data).

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). Several field and laboratory investigations have demonstrated that blue crab 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; Pile et al. 1996; Moksnes et al. 1997; Ryer et al. 1997; Heck and Spitzer 2001; Hovel and Lipcius 2001, 2002). Such findings have led to the 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; Orth and van Montfrans 2002) and enhances growth rates (Perkins-Visser et al. 1996). Therefore, seagrass is commonly considered an ideal nursery habitat for the blue crab (Heck and Thoman 1984; Orth and van Montfrans 1990; Pile et al. 1996). While megalopae and young juvenile crabs (<J9 instar) are afforded increased survival in seagrass compared to unvegetated habitats, this difference vanishes in later juvenile stages (>J9 instar; Pile et al. 1996). The recent findings that some unvegetated habitats serve as good nursery habitats are applicable to moderately sized juveniles (~20-50 mm CW), but megalopae and the youngest juveniles <20 mm CW are apparently better suited for vegetated habitats such as seagrass beds and salt marshes (Heck and Thoman 1984; Orth and van Montfrans 1990; Pile et al. 1996; Hovel and Lipcius 2001, 2002).

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 hundred meters (Fig. 11). 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. 12, 13; Mense and Wenner 1989; Lipcius and Van Engel 1990; Heck and Spitzer 2001; Rakocinski et al. 2003; Lipcius et al. 2005b;

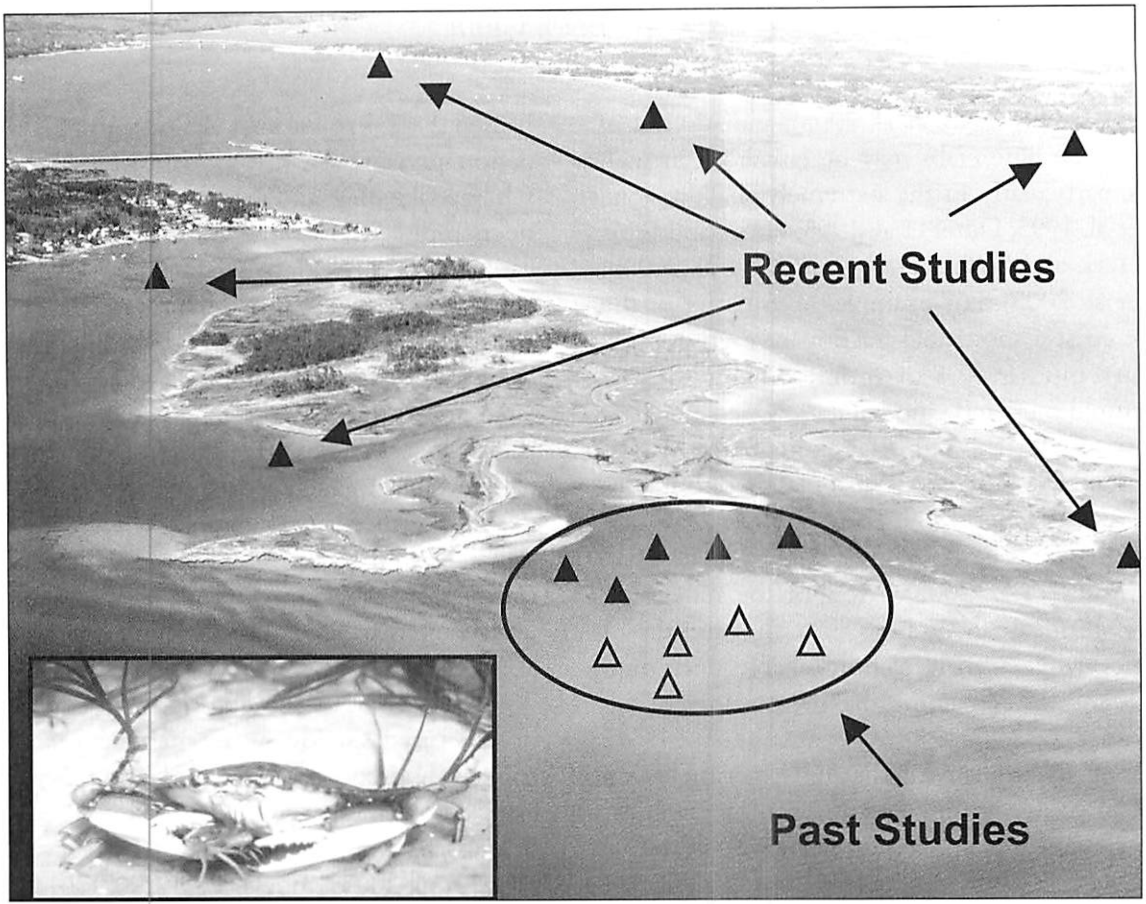

Figure 11. Representation of a field layout of tethering experiments in nursery habitats of the York River, Virginia. Each triangle indicates the location of an individual tethered crab or a set of tethered crabs that represent independent replicates. Adapted from Lipcius et al. (2005b).

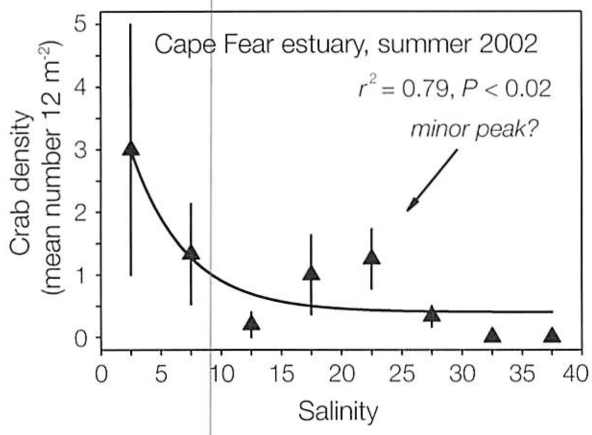

Figure 12. Abundance of young juveniles <13 mm CW. A negative exponential curve was fit to the mean densities as a function of the salinity interval midpoint. Salinity is presented as a pure ratio with no dimensions or units according to the Practical Salinity Scale (UNESCO 1985). Vertical lines = standard error. Adapted from Posey et al. (2005).

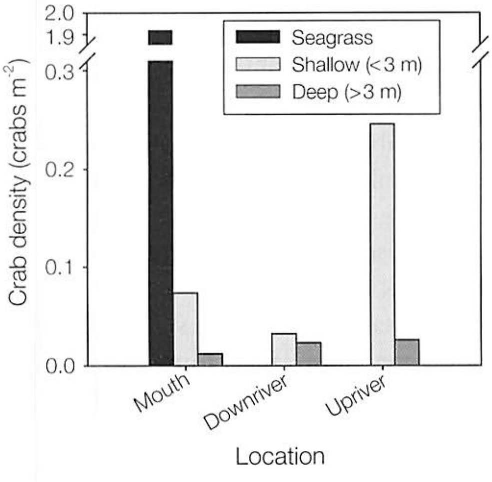

Figure 13. Density of blue crab juveniles in mouth, downriver, and upriver locations in the York River, Virginia, Chesapeake Bay. Habitats were shallow subtidal (mud or sand) and deep-water (mud) at all locations, whereas SAV (seagrass) habitats only occurred at the mouth location. Adapted from Lipcius 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; 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 (25-55 mm CW — Lipcius et al. 2005b; 15-30 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. 14, 15). These juvenile crabs survived at much higher rates in unstructured upriver habitats than in SAV or in unstructured sand and mud habitats near the mouths of tributaries in North Carolina (Fig. 14; Posey et al. 2005) and Chesapeake Bay (Fig. 15; 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. 16; 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 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 Habitat Features

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. 17). 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 tethering experiments on survival of three juvenile crab sizes (3-6, 11-16, and 20-35 mm CW) in simulated seagrass plots of natural shoot densities indicated strong interactive effects between crab size and shoot density (Schulman 1996). Smallest crabs

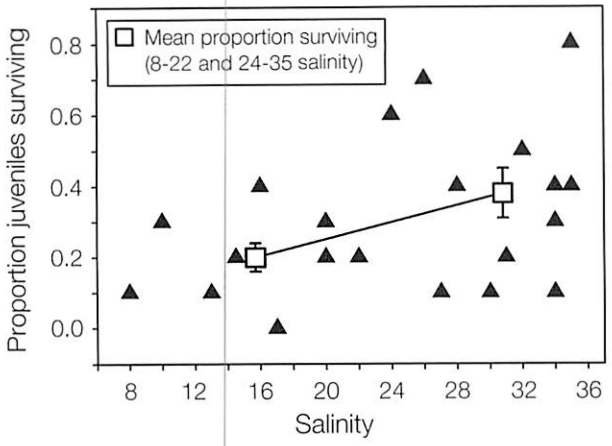

Figure 14. Survival of tethered juveniles 15 to 30 mm CW in the Cape Fear River system of North Carolina. Proportion juveniles surviving = fraction of 10 crabs alive after 2 h. Areas of moderate salinity were typically unstructured subtidal mud and sand habitats where survival could be as high as that near seagrass beds at the mouth of the estuary. Vertical bar = SE. Adapted from Posey et al. (2005).

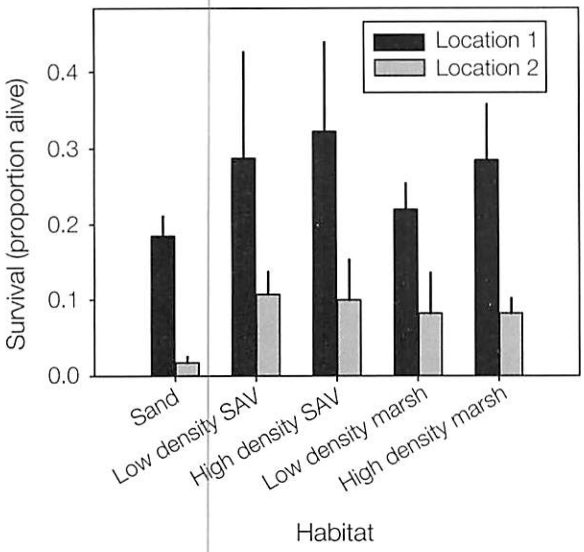

Figure 16. Survival of tethered juveniles 5 to 20 mm CW in various habitats near Mobile Bay, Alabama, in the Gulf of Mexico. Survival (proportion alive) = mean fraction of 10 crabs alive after 24 h. Each value is the mean of four sets of experiments conducted in September 1990, 1991, 1997, and 1998. There was no significant effect of habitat type, and most of the habitats were in relatively close proximity, as opposed to those in Figures 14 and 15. Location 1 = Point aux Pins; location 2 = Mobile Delta. Vertical lines = standard error. Data derived from Heck and Spitzer (2001).

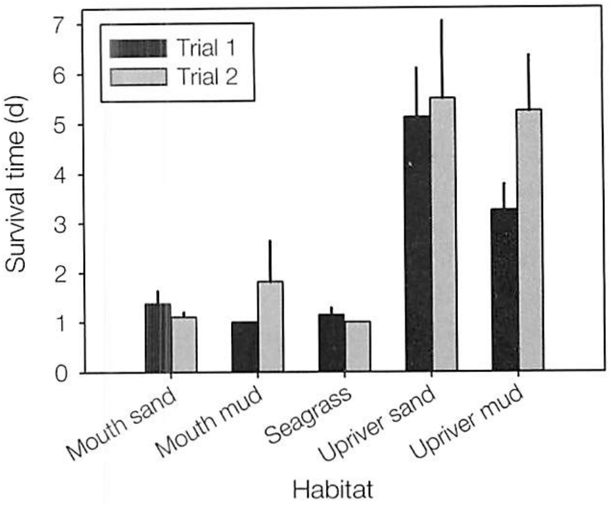

Figure 15. Survival of tethered juveniles 25 to 55 mm CW in various habitats of the York River, Virginia, in Chesapeake Bay. Mouth and Upriver habitats were unstructured mud and sand subtidal habitats. The habitats spanned a 40-km stretch of the York River, and individual crabs were tethered no less than 50 m apart, but usually more than 100 m apart to foster independence among replicate crabs. Vertical lines = standard error. Crabs in Upriver sand and Upriver mud had significantly higher survival times than crabs in Mouth sand, Mouth mud, and Seagrass. Adapted from Lipcius et al. (2005b).

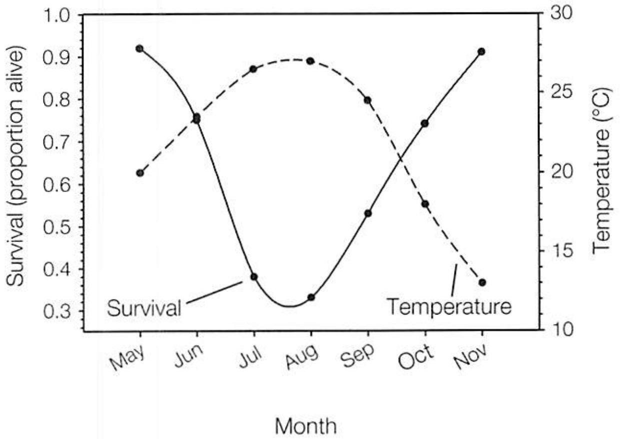

Figure 17. Seasonal pattern in temperature and survival of juvenile blue crabs tethered in various habitats of the York River, Chesapeake Bay. Survival (proportion alive) = mean fraction of 10 crabs alive after 24 h from a series of experiments. Data derived from Moody (2001).

survived best at low shoot densities, whereas survival of larger juveniles increased at higher shoot densities. Smallest juveniles likely avoid high seagrass densities, which harbor larger crabs and fish apt to prey upon the smallest juveniles, whereas larger juveniles find refuge in dense seagrass. Similar patterns in size-specific survival of young juveniles 10 to 70 mm CW occurred in other seagrass beds (Pile et al. 1996) and in unvegetated marsh-fringed habitats (Fig. 18; Posey et al. 2005). Survival in nursery habitats generally increases with size up to about 50 mm CW, where it approaches an asymptote (Fig. 18). The features of nursery habitats can also alter juvenile survival (Hovel and Lipcius 2001, 2002). In natural seagrass fragments, survival was directly related to a combination of patch size and seagrass shoot density. Juvenile survival was highest in smaller patches, likely due to the prevalence of predators in larger patches, which have high shoot densities (Hovel and Lipcius 2001, 2002). Consequently, fragmentation and alteration of nursery habitats have potentially dramatic effects on the survival of young juvenile blue crabs.

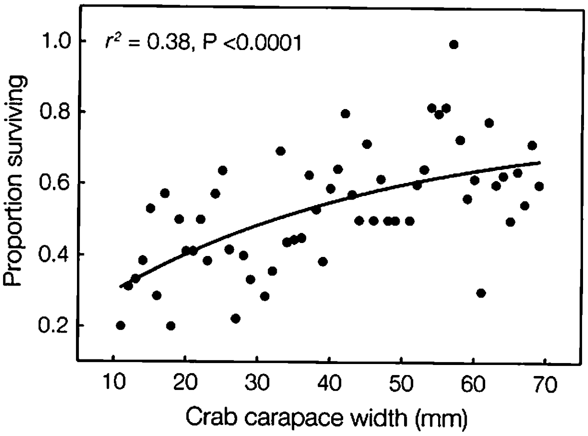

Figure 18. Size-specific survival of juvenile blue crabs tethered in various habitats of the York River, Chesapeake Bay. Proportion surviving = mean fraction of 10 crabs alive after 24 h from a series of experiments. Data derived from Moody (2001) and subsequently analyzed with non-linear regression of a power function.

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 classic paradigm on habitat use by blue crab juveniles (Fig. 1) requires modification. According to this 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 appear to provide optimal settlement substrate for megalopae and safe, food-rich habitat for the youngest juveniles <20 mm CW (Fig. 19). However, megalopae may also bypass seagrass beds and be advected to upriver structured habitats such as salt marshes, which can serve as the primary nursery (Fig. 19). Many of the 1st instar juveniles remain in seagrass beds until sometime after reaching the 7th instar at about 20 to 30 mm CW, due to the size-specific survival (Fig. 18) 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-3rd) emigrate from seagrass beds to avoid density-dependent cannibalism (Etherington and Eggleston 2000; Blackmon and Eggleston 2001; Reyns and Eggleston 2004) and reduced 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 (>20 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 generally obtain plentiful prey and have a spatial refuge from predators in seagrass beds (Fig. 19). 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

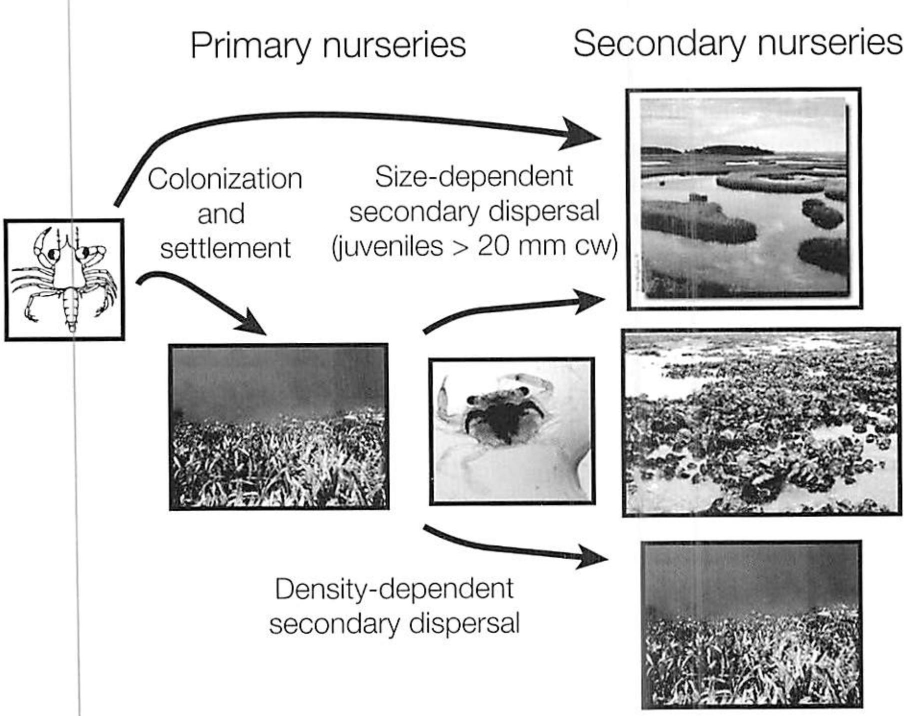

Figure 19. Revised conceptual model of recruitment in nursery habitats by megalopae and young juveniles, using the Chesapeake Bay and other systems with seagrass beds as a model. Colonization and settlement are as described in the conceptual model of Figure 1, whereby megalopae either settle in seagrass beds (primary nurseries), or when these are unavailable, in coarse woody debris adjoining salt marshes, in oyster reefs, or in other structured habitats. After settlement, megalopae and young juveniles in seagrass beds may exhibit density-dependent secondary dispersal to other seagrass beds or to alternative nursery habitats such as oyster reefs or the coarse woody debris in the subtidal zone of salt marshes. Once the young juveniles grow to ~20 mm CW, secondary dispersal occurs whereby these larger young juveniles emigrate from seagrass beds or alternative nursery habitats to the secondary nurseries (e.g., unstructured subtidal zone of salt-marsh fringed coves, oyster reefs and adjacent habitats) where survival and growth of these young juveniles is enhanced. In systems such as Delaware Bay or parts of the Gulf of Mexico, settlement occurs in alternative structured habitats such as salt marshes.

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. 19) 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 an early stage (1st-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 (>20 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. 19). 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 50 mm CW, as evidenced by the abundance of larger crabs feeding, molting, and mating in seagrass beds. Specifically, we posit that larger juveniles (>20 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. 2005b; 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 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.

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Chapter 14

Ecology of Juvenile and Adult Blue Crabs

ANSON H. HINES

INTRODUCTION

Life History

Newly settled blue crabs *Callinectes sapidus* generally grow through a series of early juvenile instars (developmental stages punctuated by ecdysis) within seagrass and other settlement habitats of lower estuaries (Orth and van Montfrans 1987; Williams et al. 1990; Olmi and Lipcius 1991; Perkins-Visser et al. 1996; Pile et al. 1996; Pardieck et al. 1999). They may also move upstream to settle in soft-bottom areas of some subestuaries, such as in lower Chesapeake Bay (Seitz et al. 2003a; Lipcius et al. 2005) and Mississippi Sound (Rakocinski et al. 2003) (see also Lipcius et al., Chapter 13). Upon attaining the 5th to 7th crab instar and ~20 mm carapace width (CW), juveniles typically disperse from their settlement site to exploit an array of habitats throughout the estuary (Pile et al. 1996; Moksnes et al. 1997; Pardieck et al. 1999; Etherington and Eggleston 2000, 2003). However, dispersal may occur as early as the 1st crab instar shortly after settlement in some estuaries, such as in North Carolina (Reyns and Eggleston 2004). Dispersed juveniles use a variety of micro-habitats where they forage on diverse food resources and grow for a typical period of 0.5 to 1.5 y (depending on temperature and food availability) until they reach sexual maturity in the 16th to 20th crab instar at ~110 to 180 mm CW (Van Engel 1958; Tagatz 1968a; Rugulo et al. 1998b). After mating, inseminated mature females cease molting and migrate back to the lower estuary, produce broods, and incubate eggs until larvae are released and transported out of the estuary onto the continental shelf (see Jivoff et al., Chapter 7; Epifanio, Chapter 12). By contrast, mature males may continue to molt and grow for 1 to 3 additional instars (typical large size is 180 to 200 mm, but occasionally some grow to >250 mm CW) (Van Engel 1958; see also Smith and Chang, Chapter 6). Unlike females, mature males tend to remain dispersed in the upper estuary without migrating directionally along the salinity gradient (Van Engel 1958; Hines et al. 1990, 1995).

Timing of life history events and life span appear to vary with latitude. In higher latitude estuaries with cold winter seasons, juvenile and adult stages may move into deeper water in channels to over-winter. This is a period of little activity, with movement, feeding, and molting proceeding slowly if at all, especially at temperatures below 9° or 10°C. Because of the shorter warm season, maturation typically occurs in the second season after settlement in Chesapeake and Delaware bays (e.g., see Ju et al. 2003 and Smith and Chang, Chapter 6). Most blue crabs are thought to die after a lifespan of about 3 y, although there is some debate as to whether death ensues from senescence or from high rate of fishing capture. In Chesapeake Bay, a small portion of the population lives to be 4 to 5 y old, with individuals rarely (<1%) living to 6 to 8 y (Sharov et al. 2003; see also Fogarty and Lipcius, Chapter 16). This pattern of timing and dispersal of life history stages along the estuarine salinity gradient is also evident in South Carolina (Archambault et al. 1990). However, in lower latitude estuaries of Florida and the Gulf Coast, blue crabs grow faster over a longer warm season to reach maturity within a year (Perry 1975; Tatum 1980). Although mature crabs in this region are presumed also to live to a typical age of 2 to 3 y and a maximum age of about 6 y (Perry et al. 1998; Steele and Bert 1998; Pellegrin et al. 2001), there are few data about lifespan along the Gulf Coast.

Ecological interactions of juvenile and adult blue crabs begin when juveniles disperse out of their settlement habitat and continue through the 1 to 3 y period of growth, maturation, and adulthood (e.g., Gillanders et al. 2003). This chapter addresses these ecological interactions during this complex period in the blue crab's life history. The interactions typically involve crabs that range in size from 20 to 200+ mm CW. This range includes crab instars 7 to 22 and ages of about 2 months to 3+ y post-settlement. Other chapters that link with this topic of juvenile and adult ecology include the biology of larvae (Epifanio, Chapter 12) and the ecology of early juvenile stages from settlement until dispersal from the settlement habitat (Lipcius et al., Chapter 13). Additional supplemental information can be found in the chapters on reproductive biology (Jivoff et al., Chapter 7), ecological aspects of disease and parasites (Shields and Overstreet, Chapter 8), and environmental physiology (Tankersley and Forward, Chapter 10). Aspects of population biology are important components of the ecology of blue crabs that I consider in this chapter; however, the topic of population dynamics, especially considered from the perspective of fishery models and stock management, is addressed in a separate chapter (Fogarty and Lipcius, Chapter 16). Overlap among these chapters is inevitable and valuable.

Previous Reviews and Historical Progression of Research

Previous reviews of the ecology of blue crabs in the context of their life history provide an historical perspective on the shifting emphasis of blue crab research. Early work focused on the life cycle and large-scale habitat use, primarily in Chesapeake Bay where the fishery was concentrated (Hay 1905; Churchill 1918, 1919; Cronin 1954; Cargo 1958; Van Engel 1958, 1987). A comprehensive review by Millikin and Williams (1984) not only summarized blue crab biology and ecology but also provided a key benchmark that integrated physiology and behavior into ecology by life stage in the context and terminology of modern demography, population dynamics, and standard crustacean physiological terms (e.g., molt stages, life stages) that were not idiosyncratic to fisher's colloquialisms (e.g., pink sign, sook, jimmy). Millikin and Williams (1984) also invoked modern statistical approaches to describe variability in population biology. Further, they considered geographical variation of blue crab biology, providing summaries of the fisheries and data on some aspects of biology for populations in estuaries along the East and Gulf coasts of North America.

As the blue crab fishery expanded geographically, fishery biologists developed reviews with a focus on state management of stocks along the East and Gulf coasts (e.g., Perry and Van Engel 1982; Guillory et al. 2001), including New York (Briggs 1998), New Jersey (Stehlik et al. 1998), Delaware (Kahn et al. 1998), Maryland and Virginia (Van Heukelem 1991; Miller and Houde 1998; Rugolo et al. 1998a, b), North Carolina (Henry and McKenna 1998; Eggleston et al. 2004), South Carolina (Archambault et al. 1990; Whitaker et al. 1998), Georgia (Evans 1998), Florida (Tagatz 1968a, b; Steele and Bert 1994, 1998), Alabama (Heath 1998), Mississippi (Perry 1975; Perry et al. 1998), Louisiana (Guillory and Perret 1998), Texas (Hammerschmidt et al. 1998), and the Gulf of Mexico (Perry et al. 1984; Steele and Perry 1990; McClintock et al. 1993; Guillory et al. 1998, 2001). Comparative analyses and proceedings flowed from meetings and colloquia that integrated scientists and managers across regions of the United States (e.g., Perry and Van Engel 1982), with proceedings of blue crab conferences appearing in the Bulletin of Marine Science in 1990, 1995, and 2003 (Smith et al. 1990; Olmi and Orth 1995; Eggleston 2003), and in the Journal of Experimental Marine Biology and Ecology in 2005 (Seitz 2005). Steele and Bert (1994) summarized information for latitudinal comparisons of reproductive and molting seasons, considering implications for population biology for the U.S. portion of the species' distribution. Interspecific comparisons also provided valuable insights into the ecology of *Callinectes sapidus* as the most widely distributed member of the genus, triggered especially by Williams' (1974; later updated in Williams 1984) systematic monograph of the genus that included summaries of the ecology of each species. Comparative studies of species of *Callinectes* in the Gulf Coast (Hsueh et al. 1992a, b, 1993) and Caribbean estuaries (Norse 1975, 1977, 1978a, b; Norse and Estevez 1977; Norse and Fox-Norse 1982; Haefner 1990a, b; Stoner and Buchanan 1990) extended the general ecology of *C. sapidus*. Comparative studies also recognized the valuable research contributions from Latin America (e.g., Paul 1981, 1982; DeVries et al. 1983; Ortiz and Gutiérrez 1992; Rosas et al. 1994; Oesterling and Petrocci 1995; Lazaro-Chavez et al. 1996; Oesterling 1998; Mantelatto and Fransozo 1999; Cházaro-Olvera and Peterson 2004). Limited reports also exist for *C. latimanus* in Africa (Kwei 1978). With the exception of a set of studies of *C. similis* (Hsueh et al. 1992a, b, 1993), reports for other species of *Callinectes* along North America remain unfortunately sparse and almost anecdotal (e.g., Daugherty 1952b; Tagatz 1967; Perschbacher and Schwartz 1979). Although the Chesapeake Bay population continues to receive the most intensive and comprehensive research on *C. sapidus*, blue crab research along the Gulf Coast is gaining in scope and breadth, and in this chapter I seek both to consider geographic variability as a key aspect of ecology and to encourage interspecific comparisons as a powerful tool to analyze blue crab ecology.

POPULATION BIOLOGY

Interaction of Population Dynamics and Community Ecology

Blue crab populations are characterized by three fundamental features that affect their dynamics and community interactions: (a) a distinctly bimodal population size structure resulting from seasonal reproduction and recruitment, which has marked effects on size-dependent interactions as predators and as prey that in turn affect habitat use and movement; (b) spatial variation in sex ratio that reflects differences between mature females and males in habitat use and movement; and (c) marked annual variation in abundance, which significantly affects density-dependent interactions, such as movement, habitat use, trophic interactions, competition, and sources of mortality. Careful description of these three variables — population structure, sex ratio, and abundance — is essential to understand the interaction between population biology and other aspects of the community ecology of blue crabs (e.g., see Wahle 2003 for comparison of blue crab dynamics with clawed and spiny lobsters). Hence, I summarize population structure (size and sex ratio) and spatial-temporal variation in abundance as basic descriptive elements of blue crab ecology that typically are prerequisites for mechanistic studies of complex community interactions, descriptions of which follow later in this chapter. The reader should refer to Fogarty and Lipcius (Chapter 16) for further detailed discussion of population dynamics.

Sampling Artifacts and Gear Efficiencies for Population Variables

The question, "How many blue crabs are there in a population or habitat?" is straightforward as a fundamental aspect of their ecology and fishery management. Similarly, size and sex composition of populations are basic elements that interact with both ecological processes and the fishery. However, quantifying and predicting variation in abundance and population structure of blue crabs are difficult, because numerous sampling artifacts confound accurate estimates of blue crab densities. The artifacts vary interactively among gear type, habitat, crab size, and activity levels (Barkley 1972; Allen et al. 1992).

A problem in the analysis of population size structure derives from sampling blue crabs with fishery gear, which is often designed to by-pass small juveniles, producing estimates of size-structure that are skewed to large, fishery-legal individuals (e.g., Caddy 1979). Thus, fishery gears selectively sample certain sizes and life stages of blue crabs that are targeted by commercial interests (e.g., Cargo 1954b; Van Engel 1962; Harris 1979; see also Kennedy et al., Chapter 15). Relative indicators of abundance have been derived from fishery catches, which may reflect fluctuations in fishery effort and size limits as much as variation in crab density (e.g., Rugulo et al. 1997, 1998a, b). Even when populations have been sampled consistently with fishery-independent surveys, artifacts in population structure and abundance also may be introduced by the sampling of habitats that do not include all sizes or ages of crabs.

At best, gears have different catch efficiencies in various habitats. Many sampling gears do not function well in structured habitat, where towed nets may become fouled or hung up. Traps deployed in structured habitat may have a different attraction to crabs than when deployed on bare sediment, where the trap itself provides more structure than the habitat. As noted, most sampling gears, including those employed in fishery-independent surveys, may fail to sample crabs of certain sizes (especially small juveniles), so they must be fitted with cod-end liners with mesh as fine as 6 to 7 mm to capture small crabs. Most gears selectively capture crabs that are active, so trawls pass over sedentary crabs buried in the sediments and baited traps do not attract crabs that are not feeding. This selectivity can result in estimates of higher abundance in warm summer months when crabs are active and feeding than during cold winter months when most are buried. To sample buried crabs as well as those on the surface, the gear requires features like tickler chains on trawls, or teeth projecting downward on leading edges of dredges (e.g., Chittenden and Van Engel 1972; Sulkin and Miller 1975), but effects of these modifications also vary with crab activity level.

Some studies have compared results among gears to determine which type of sampling will give the greatest relative index of crab abundance, or to consider trade-offs of sampling effort, mesh size, overall size of the mouth of the net, and the like (e.g., Sulkin and Miller 1975; Miller et al. 1980; Bishop et al. 1983; Rozas and Minello 1997). Compared to large mesh nets, small mesh nets create a large pressure wave in front of the gear when pulled through water or may clog with sediment, which may allow crabs to detect and escape the net. Large trawls may be better able than small ones to sample large crabs that evade capture by swimming out of the way. For seagrass beds with many small crabs, the gear that provides the best estimate of true densities has been suction dredges operated within enclosure rings or drop samplers (e.g., Orth and van Montfrans 1987; Ruiz et al. 1993; Pile et al. 1996; Rozas and Minello 1997; Rakocinski et al. 2003). However, although suction sampling works well for regions of higher crab densities where sampling area can be small, it typically does not work well for habitats (e.g., open sediment) that require large sampling areas because of low densities of crabs. Block nets provide good, unbiased samples of blue crab subpopulations in tidal marsh creeks (e.g., Hines et al. 1987; Hettler 1989; Rulifson 1991; Fitz and Wiegert 1992; Coen et al. 1999). The fishery-independent winter dredge survey in Chesapeake Bay, which provides the most comprehensive sample of the population, uses a Virginia crab dredge fitted with a fine mesh bag deployed at a time when crabs tend to be concentrated in deeper habitats lacking structure, and when crabs are not moving (Sharov et al. 2003).

Because most types of gear do not catch all of the crabs in the sampling area, providing instead a relative indicator of crab abundance, gear efficiencies have been estimated to allow catch data to be adjusted for absolute densities (e.g., Stokesbury et al. 1999). Gear efficiencies are estimated either by placing known densities of marked crabs into the sampling area, or by repeatedly sampling a set area until all crabs are removed, allowing back-calculation of the fraction of crabs caught in the initial sample. Orth and van Montfrans (1987) estimated 88% efficiency for 2 to 120 mm blue crabs sampled with a suction dredge within a drop ring enclosure deployed in seagrass habitat. By contrast, catch efficiency of trawls is generally much lower: 25 ± 5% for crabs >25 mm in soft bottom (Homer et al. 1980); 2 to 20% for crabs in unvegetated soft bottom (Orth and van Montfrans 1987); and only 0.4% for crabs <25 mm CW and 1.4% for crabs >25 mm CW in seagrass habitat (Orth and van Montfrans 1987). Seines with 7 mm mesh had catch efficiencies of about 50% for >25 mm CW, but only about 5% for crabs <25 mm in summer in shallow muddy bottoms of upper Chesapeake Bay (Davis and Hines, unpubl. data). Dredge sampling of blue crabs buried in sediments during winter samples have efficiencies of 22 to 47% (Endo 1992; Zhang et al. 1993; Zhang and Ault 1995; Vølstad et al. 2000).

Mark-recapture methods may be used to estimate true abundance of animals (Cormack 1968; Pollock et al. 1990). However, these methods require restrictive assumptions that rates of mortality, natality, immigration, and emigration are either nil or known (Pollock et al. 1990), which is usually not the case for blue crabs. Modified approaches of these methods are being tested for the Chesapeake Bay population (Hoenig et al. 2003).

Population Structure: Size and Sex

Blue crab populations in Chesapeake and Delaware bays typically exhibit a bimodal size-frequency distribution that derives from the seasonal pattern of summer to fall larval recruitment, retarded growth during cold winter months, and a 2-to-3 y life span at this northerly latitude of the species' distribution (Van Engel 1958; Hines et al. 1990). For example, seasonal cycles in the population structure of blue crabs in upper Chesapeake Bay (Fig. 1) show that crabs in the 0+ age-class enter the population in fall and disperse up the estuary from their settlement habitat as 20 mm juveniles, with possible further up-estuary dispersal in spring. The 0+ age-class grows to 80 to 90 mm during its first warm season of feeding in the subestuaries, and these juveniles become the 1+ age-class in their second summer, when they molt to maturity, with mature females ranging from 100 to 180 mm CW and mature males ranging from 110 to 200 mm CW. Males molt to maturity and may molt one to three times as adults, whereas females cease molting after attaining maturity. The winter dredge survey of crabs in Chesapeake Bay clearly shows the bimodal structure of the population, and allows for comparisons of age-class strength among years and estimates of annual survivorship (Sharov et al. 2003). This pattern of bimodal population structure and fall recruitment of the 0+ age-class is also evident in Charleston Harbor, South Carolina (Archambault et al. 1990). Although synchronous molting produces distinct modes for each instar in the population size structure of some crab species, such as the snow crab *Chionoecetes opilio* (Robichaud et al. 1989), this is not evident in blue crab populations.

At lower latitudes, a longer season of egg production, more continuous larval recruitment, and juvenile growth over a longer season results in less distinct age classes, making population size structure less bimodal (Steele and Bert 1994; Perry et al. 1995). However, bimodal population structure is still evident in Tampa Bay, Florida, where reproduction and molting tend to have seasonal peaks in both late spring and late summer (Steele and Bert 1994). Populations in Florida and the Gulf of Mexico are also subject to a cool winter period of low reproductive activity, but the extended recruitment season and variable growth rates appear to result in a size structure that is not distinctly bimodal (Perry et al. 1998).

Mean crab size of the 1+ age mode has declined significantly for males captured in pots in central Chesapeake Bay from 1968 to 1995 (Abbe and Stagg 1996; Abbe 2002) and for mature females in the spawning stock of the lower Bay (Lipcius and Stockhausen 2002). For males, the reduction in size appears to be attributable to fishery removals of large individuals (Abbe and Stagg 1996). For females, the cause arguably also may be related to short-term selection for physiological limits to growth (Lipcius and Stockhausen 2002; Sharov et al. 2003).

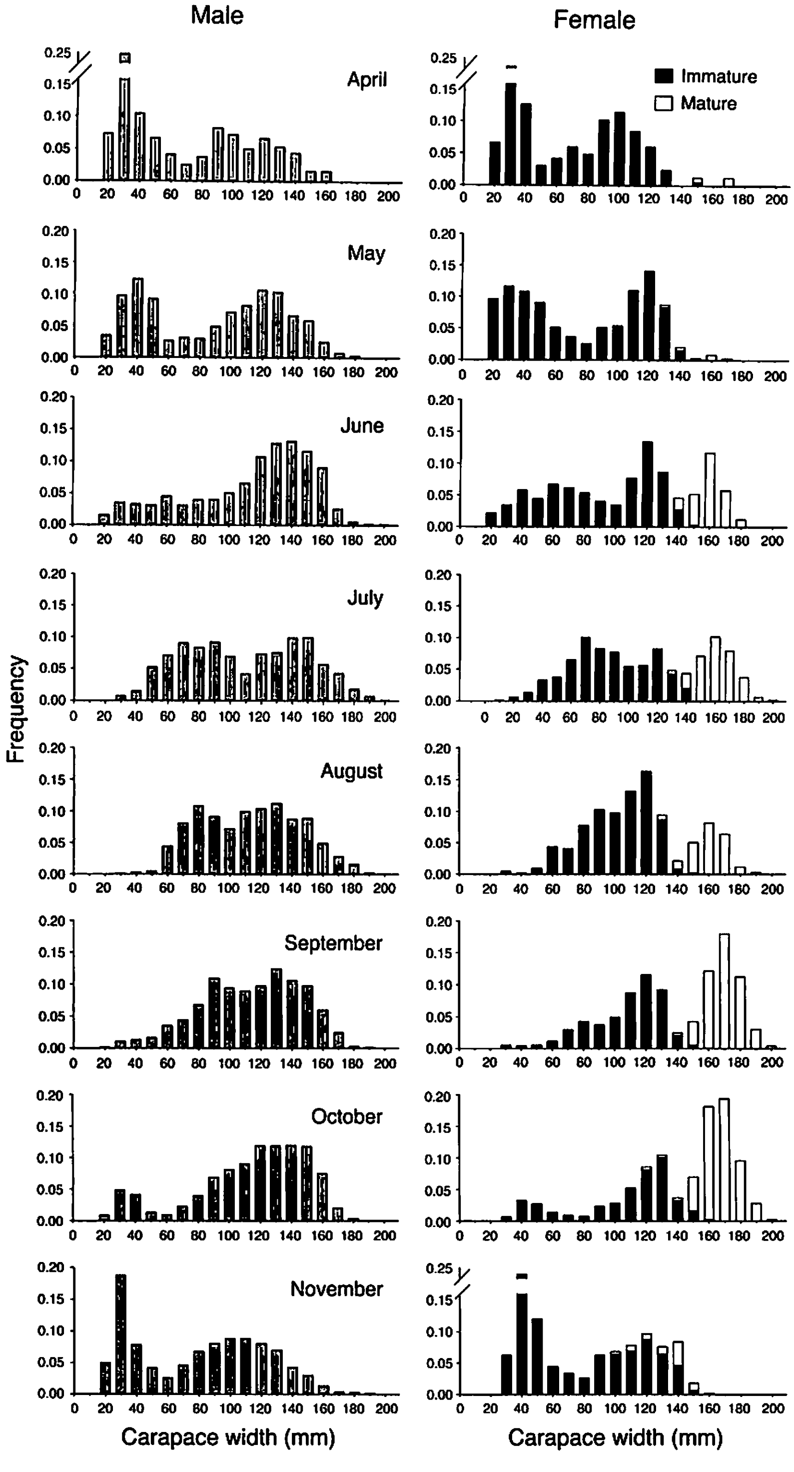

Figure 1. Seasonal variation in the size structure of the blue crab population in the Rhode River subestuary of Chesapeake Bay, Maryland. Long-term (25 y) average size-frequency distributions of crabs sampled in monthly otter trawls are shown for males (left) and females (right). The bimodal size structure reflects the two-year cycle of recruitment and growth to sexual maturity. Note recruitment of 0+ age cohort in the fall as 20-mm crabs disperse up the estuary into the juvenile nursery habitat, as well as growth of the 0+ and 1+ age cohorts as the season progresses. For females, solid columns indicate juveniles and open columns indicate sexually mature crabs. Note disappearance of mature females at the time of their fall departure and migration back down the estuary. See Hines et al. (1987, 1990).

The sex ratio is presumed to be balanced in most populations of blue crabs, especially at juvenile stages (e.g., Fitz and Wiegert 1992). However, quantitative assessment of sex ratio is difficult because males and females partition the available habitats along the estuarine salinity gradient (Hines et al. 1987). The habitats extend over large distances in many systems like Chesapeake Bay, which thus inhibits standardized sampling for all segments of the population. Moreover, the migratory behavior of females produces seasonal cycles in sex ratios at individual sites (Hines et al. 1987; Fitz and Wiegert 1992; Steele and Bert 1994). Apart from these difficulties, long-term fishery-independent sampling indicates that the composition of males in the population in central Chesapeake Bay declined significantly from 1968 to 1982, but leveled off from 1983 to 1995 (Abbe and Stagg 1996). System-wide sampling with a winter dredge survey indicates that the sex ratio was balanced and stable in Chesapeake Bay during the 1990s (Sharov et al. 2003).

Abundance

Seasonal and Annual Variation

Blue crab abundance in higher latitude estuaries, such as Chesapeake Bay, typically exhibits a strongly seasonal cycle (Miller et al. 1975; Hines et al. 1987, 1990; Orth and van Montfrans 1987; Pardieck et al. 1999), which reflects natural behavior and demography of the crabs. Trawling in shallow portions of the estuary (Fig. 2) shows fluctuating abundances of juvenile crabs that result from dispersal into the post-settlement nursery habitats up the Bay during fall and possibly spring (Hines et al. 1990). The seasonal cycle of catches also reflects declining abundances from the departure in fall of mature females that migrate down the estuary (Cargo 1958; Schaffner and Diaz 1988), as well as the movement of juveniles and mature males that shift into deeper waters over winter (Hines et al. 1987; Sharov et al. 2003; Aguilar et al. 2005). Since senescence of most crabs appears to result in death after about 2 to 3 y, the seasonal cycle of declining abundance may also reflect loss due to death of old crabs. However, there is little known about the seasonal timing of this source of mortality, except that cold temperatures interacting with low salinities during winters may take a significant toll, depending on crab age groups and distribution in the estuary (Sharov et al. 2003; Rome et al. 2005).

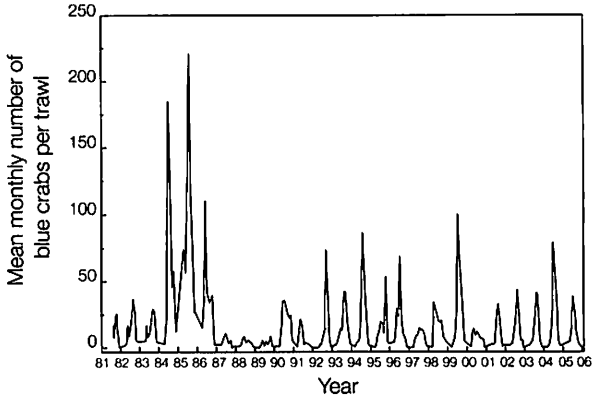

Figure 2. Long-term variation of mean monthly number of blue crabs caught in otter trawls in the mesohaline Rhode River subestuary of Chesapeake Bay, Maryland. Note seasonal fluctuation with peak abundances in summer, and large inter-annual variation. See Hines et al. (1987, 1990).

Fishery catches also track the seasonal cycle of blue crab activity and abundance, with peak catches of intermolt (hard) crabs in pots during summer and "hibernating" crabs caught with dredges in the lower Chesapeake Bay in winter (e.g., van Engel 1958; Rugulo et al. 1998; Sharov et al. 2003). Intense fishing pressure can also deplete the numbers of legal-size (mostly adult) blue crabs in large systems like Chesapeake Bay, both seasonally and annually (Lipcius and Stockhausen 2002; Sharov et al. 2003).

Seasonal peak abundance of blue crabs in Chesapeake Bay exhibits marked annual variation that may differ by an order of magnitude or more among years in fishery-independent trawl surveys (Hines et al. 1987, 1990; Lipcius and Van Engel 1990; Lipcius and Stockhausen 2002), fishery catches (Rugulo et al. 1998b), and in the fishery-independent winter dredge survey (Sharov et al. 2003). Annual variation in blue crab abundance is significantly correlated with salinity and temperature as environmental variables that are linked to broad climatic factors influencing estuarine ecosystems (Ulanowicz et al. 1982; Steele and Bert 1994). Variation in blue crab abundance among years mainly reflects large annual variations in larval recruitment (Orth and van Montfrans 1987; Goodrich et al. 1989; Olmi et al. 1990; van Montfrans et al. 1990, 1995; Lipcius and Stockhausen 2002), resulting in a significant recruit-stock relationship (Tang 1985; Lipcius and Van Engel 1990; Miller and Houde 1998) and in recruitment limitation at some low population levels (Lipcius and Stockhausen 2002). However, it is also recognized that factors affecting survivorship of juveniles after recruitment may decouple the recruit-adult relationship (Hines and Ruiz 1995; Pile et al. 1996; Rome et al. 2005). Long-term variation in blue crab fishery catches and scientific surveys indicate that abundance of the total adult population and mature females (spawning stock) declined drastically by 84% in Chesapeake Bay during the 1990s to early 2000s (Miller and Houde 1998; Lipcius and Stockhausen 2002). The extensive fishery-independent dredge survey throughout Chesapeake Bay conducted in winter also indicated significant declining crab abundance from 870 million to 240 million crabs during the 1990s (Sharov et al. 2003).

Variation among Estuaries

Blue crab abundance varies greatly among estuaries, which is often manifested by variation of fishery productivity. Historically, Chesapeake Bay has sustained North America's largest fishery catch of blue crabs, reflecting not only the large size of this estuary but also a highly productive combination of habitats (Van Engel 1958). The Chesapeake's extensive array of key nursery habitats, including seagrass beds, oyster reefs, and many large subestuarine tributaries with irregular shorelines of shallow water, provide refuge for juvenile blue crabs (Everett and Ruiz 1993; Ruiz et al. 1993; Hines and Ruiz 1995). Adjacent Delaware Bay is about one third the size of Chesapeake Bay but has produced disproportionately fewer blue crabs (~10-15% of Chesapeake Bay), perhaps because extensive seagrass beds are lacking in Delaware Bay (Kahn et al. 1998).

Blue crabs appear to depend more on extensive salt marsh habitats in estuaries along the southeast coast and much of the Gulf Coast than they do in Chesapeake Bay (Dudley and Judy 1973; Ryer et al. 1990; Thomas et al. 1990; Fitz and Wiegert 1991b, 1992; Zimmerman et al. 2000). However, abundances of newly settled juveniles (<10 mm CW) in Mississippi Sound were high (10-100 crabs m^{-2}) in both seagrass habitats and in bare sediments (Rakocinski et al. 2003), indicating that the role of these habitats may be similar to that in estuaries like Chesapeake Bay. Crab abundance in Chesapeake Bay has been greater than in other estuaries despite its somewhat limited extent of salt marshes; however within Chesapeake Bay, salt marshes that occur primarily along the central Eastern Shore have sustained the greatest production of crabs in this estuary. Further, even in tributaries of the western shore of the Chesapeake, habitats associated with up-river salt marsh appear to have the highest food resources and produce the fastest growth rates of juveniles, rivaling seagrass beds (Seitz et al. 2005).

Some of the variation in abundance among estuaries appears to result from differences in the dynamic balance of larval recruitment and rates of predation upon juveniles (Heck and Coen 1995). Gulf Coast estuaries experience levels of blue crab larval recruitment and abundance of early juveniles (<10 mm CW) that are one to two orders of magnitude greater than in East Coast estuaries, but predation by a large guild of predators also imposes a higher rate of juvenile mortality along the Gulf Coast (Heck and Coen 1995; Morgan et al. 1996; Heck et al. 2001; Heck and Spitzer 2001; Rakocinski et al. 2003).

Currently, published estimates of the total numbers of blue crabs in an estuary are available only for Chesapeake Bay. The number of mature female crabs comprising the spawning stock in 1200 km^{-2} of the lower Bay was estimated using trawling as varying from July to August peak levels of 9×10^6 crabs in 1986 and 1.5×10^6 crabs in 1987, declining in fall to 9×10^5 crabs in 1986 and 6×10^5 in 1987 (Jones et al. 1990; Prager 1996). Based on the Chesapeake's bay-wide fishery-independent winter dredge survey, Sharov et al. (2003) indicated that the total abundance of the Chesapeake population fluctuated between 240 million and 870 million crabs >15 mm CW from 1990 to 1999 (Fig. 3). During that decade, juveniles (0+ age class) fluctuated between ~100 million and 550 million crabs while adults (1+ age class) declined from ~350 million to 70 million crabs. Using a combination of 1990 to 1996 estimates from the winter dredge survey (Rothschild and Sharov 1997) and the Virginia summer trawl survey (e.g., Lipcius and Van Engel 1990), Seitz et al. (1998) estimated the number of mature female blue crabs to be ~33 to 182 million crabs. However, only ~3.7 million (2-11%) of these females appeared to reside within the spawning sanctuary of the lower mainstem of the Bay in summer, forming the core of the Chesapeake reproductive stock.

HABITAT USE

Habitat use after post-settlement dispersal varies by size, sex, and molt stage in blue crabs, such that densities of blue crabs vary greatly among habitats. Although the spatial interaction of life history stage and habitat use has been known for a long time, recent developments in quantitative population modeling have only just begun to incorporate these elements in an explicitly integrated way for large-scale systems (Miller 2003; Jensen and Miller 2005). Generally, crab densities are highest in association with structured habitats and lowest on non-structured soft-bottoms, but densities are also markedly affected by salinity, dissolved oxygen concentration, and other factors. Highest abundances have been recorded in seagrass habitats (up to 100 small crabs m^{-2}), especially in lower estuarine zones, where early post-settlement juvenile stages are often concentrated (Heck and Orth 1980a, b; Heck and Thoman 1984; Orth et al. 1984; Williams et al. 1990; Wilson et al. 1990; Etherington and Eggleston 2000; Rakocinski et al. 2003). Even where juvenile densities are low, the extent of non-seagrass habitats can provide accumulative importance to the population, especially at subsequent life stages (Hines and Ruiz 1995; Blackmon and Eggleston 2001; Rakocinski et al. 2003; Lipcius et al. 2005; Posey et al. 2005; Seitz et al. 2005). Non-seagrass, usually non-structured, habitats are crucial for intermolt adults (e.g., Wolcott and Hines 1989b; Hines et al. 1990). Thus, a wide range of estuarine habitats is required to complete the life cycle, typically involving sequential use of a series of habitats along the salinity gradient (e.g., Gillanders et al. 2003).

Structured Habitats and Juveniles

Juveniles >25 mm CW use an array of structural habitats that provide them with refuge from predation and cannibalism (see sections on these topics below) and with food resources (see section below). Throughout their geographic range, juveniles have used seagrass, including *Halodule wrightii* shoal grass, *Zostera marina* eel grass, *Thalassia testudinum* turtlegrass, and *Ruppia maritima* wigeon grass (Tagatz 1968a; Laughlin 1979; Heck and Orth 1980a, b; Penry 1982; Sheridan and Livingston 1983; Heck and Thoman 1984; Heck and Wilson 1987; Wilson et al. 1987; Thomas et al. 1990; Williams et al. 1990; Perkins-Visser et al. 1996; Pardieck et al. 1999; Hovel et al. 2002; Rakocinski et al. 2003; Hovel and Fonseca 2005). Densities of early juvenile crabs (<20 mm CW) range from 5 to 50 crabs m^{-2} in North Carolina sounds, with highest densities in seagrass habitats (Etherington and Eggleston 2000). Peak densities of 50 to 90 small juveniles m^{-2} occur in seagrass beds of Chesapeake Bay and the Gulf of Mexico (Miller et al. 1980; Sheridan and Livingston 1983; Orth and van Montfrans 1987; Thomas et al. 1990; Williams et al. 1990; Perkins-Visser et al. 1996; Pardieck et al. 1999; Rakocinski et al. 2003). Recovery and restoration of submerged vegetation habitat has often been considered vital to sustaining blue crab populations and fisheries (e.g., Anderson 1989). However, submerged vegetation in lower salinities of upper Chesapeake Bay was not important habitat for juvenile blue crabs (Heck and Thoman 1984), whereas juveniles were attracted to patches of seagrass as refuge habitat in a lower mesohaline estuary of upper Chesapeake Bay (Ruiz et al. 1993), so use of this habitat may depend on salinity.

Juveniles also obtain refuge in other vegetated habitats, especially drifting algae and salt marshes. Algal mats and drifting algae (Heck and Orth

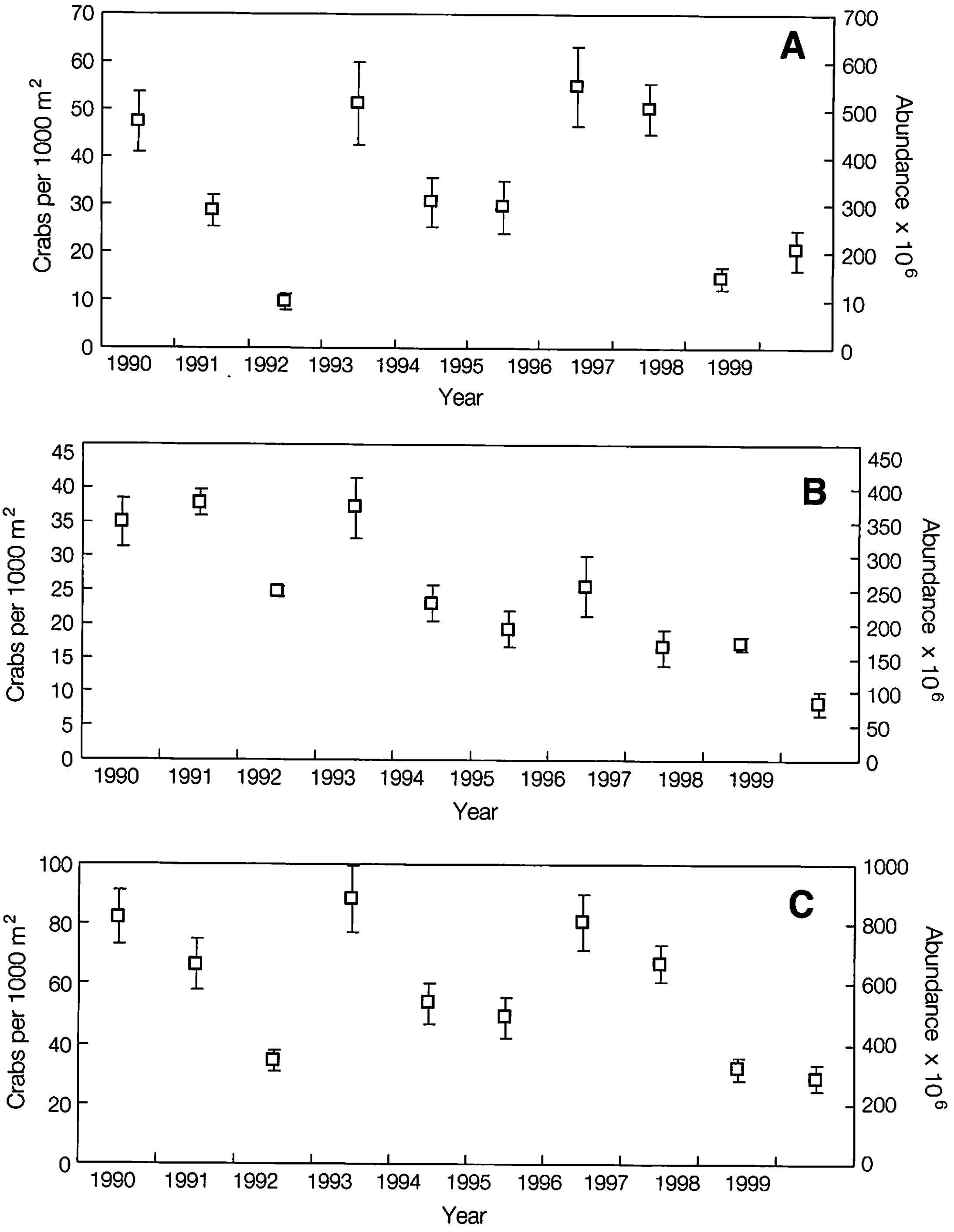

Figure 3. Annual variation in absolute density and population size of blue crabs in Chesapeake Bay, sampled with a fishery-independent winter dredge survey from 1990 to 1999. Data are adjusted for gear efficiency. (A) 0+ age class. (B) 1+ age class. (C) total population. Note large apparent annual variation in recruitment of juveniles (A) and long-term decline in adults (B). Error bars are 95% confidence intervals of the means; N = 1,500 dredge samples per year. From Sharov et al. (2003).

1980a), e.g., *Ulva lactea* sea lettuce (Wilson et al. 1990a, b; Sogard and Able 1991), may create important structured habitat for juveniles in some areas.

Juveniles use salt marshes and associated marsh creeks throughout much of their geographic range, including New Jersey (Tupper and Able 2000; Jivoff and Able 2003), Chesapeake Bay (Orth and van Montfrans 1987; Lipcius et al. 2005; Seitz et al. 2005), Georgia (Fitz and Wiegert 1991b), Louisiana (Peterson and Turner 1994), and Texas (Zimmerman and Minello 1984; Thomas et al. 1990; Minello and Webb 1997; Akin et al. 2003). Salt marshes in lower estuaries are generally thought to support variably high abundances of blue crabs (up to 13 crabs m^{-2}), particularly juveniles that move between marsh creeks and the marsh during the tidal cycle (Dudley and Judy 1973; Zimmerman and Menillo 1984; Hettler 1989; Ryer et al. 1990; Thomas et al. 1990; Fitz and Wiegert 1991b, 1992; Zimmerman et al. 2000). However, in sustained accurate sampling of a Georgia salt marsh, densities were relatively low: 1 to 10 small juveniles (<80 mm CW) ha^{-1}, and 10 to 50 crabs ha^{-1} of a size >80 mm CW (Fitz and Wiegert 1991b). Although juveniles moved well into the interior of marshes on high tides of some Louisiana systems (Peterson and Turner 1994), use of the marsh surface in many places appeared to be limited mainly to the edge habitat (Lin 1989; Fitz and Wiegert 1991b; Micheli 1997a), and juvenile abundance remained high in adjacent tidal creeks (Orth and van Montfrans 1987; Mense and Wenner 1989). In New Jersey, the species of emergent vegetation affected marsh use by blue crabs, with native species of *Spartina alterniflora* apparently being preferred by crabs over the invasive species *Phragmites australis* (Jivoff and Able 2003a). Densities of juvenile (5-10 mm CW) blue crabs in Hudson River estuary salt marshes dominated by this invasive reed averaged 0.06 to 0.39 crabs m^{-1} in summer (Hanson et al. 2002). Up-estuary habitats associated with, and adjacent to, salt marshes may be as important as seagrasses for blue crab nursery habitat, due to availability of food and lower predation levels (Seitz et al. 2003a; King et al. 2005; Lipcius et al. 2005; Seitz et al. 2005).

Blue crabs responded positively in growth, and in use of tidal creeks and other portions of restored salt marsh habitat in New Jersey (Jivoff and Able 2003b). Salt marsh restoration by increased tidal flushing also resulted in increased marsh use by blue crabs in Rhode Island (Raposa 2002). In Texas, however, densities of blue crabs were lower in created marshes than in natural *Spartina alterniflora* salt marshes, probably due to differences in elevation and tidal flooding duration of created marshes (Minello and Webb 1997).

In addition to submerged vegetation and salt marshes, juvenile blue crab densities are higher in two other structural habitats than in nearby bare sediments. Eastern oyster *Crassostrea virginica* reefs are used by juveniles over a wide range of salinities (Menzel and Hopkins 1956; Galtsoff 1964; Carriker 1967) and over much of their geographic range, including Florida (Marshall 1954), South Carolina (Lunz 1947; Coen et al. 1999; Lehnert and Allen 2002), North Carolina (Eggleston et al. 1998a, b; Posey et al. 1999a), and Chesapeake Bay (Van Engel 1958; Galtsoff 1964). However, some reports indicate relatively low abundances of blue crabs in oyster reef habitats (e.g., Coen et al. 1999; Lehnert and Allen 2002), so the role of this habitat for blue crabs is not well defined. Coarse woody debris, which is especially common in shallow waters of forested shorelines such as upper Chesapeake Bay, has provided still another structured habitat for juvenile blue crabs (Everett and Ruiz 1993).

Habitat value for blue crabs depends on complexity of structured patches (i.e., density of structural elements) (Bell and Westoby 1986). Blue crab response to habitat complexity varies with crab size and sex in habitat selection experiments (Williams et al. 1990; Schulman 1996). Juveniles 11 to 37 mm CW preferred high density of seagrass to low density. In the absence of potential large cannibalistic blue crabs, juvenile females selected low-density seagrass over high density while males selected high-density seagrass. In the presence of larger blue crabs, both female and male juveniles selected higher density seagrass. Larger (>45 mm CW) blue crabs selected low-density seagrass. However, effects of shoot density of seagrasses may vary seasonally as other factors, such as crab density and abundance of food resources within the seagrass habitat and the adjacent unvegetated sediment, come into play (Hovel and Lipcius 2002).

Availability of rocky substrates has been very limited in estuaries within the distribution of blue crabs along the East and Gulf Coasts until recent times when humans have added large quantities of rock to estuaries to reduce shoreline erosion and to create breakwaters and jetties. There is almost no information available on blue crab responses to rocky substrates, but juvenile blue crab densities increased in small experimental patches of rock rip-rap compared to bare sediment (Davis and Hines, unpubl. data).

Non-Structured, Soft-Bottom Habitats

Non-structured soft-bottom habitats are typically characterized by low crab abundances, with summer peak estimates (corrected for trawl catch efficiency) on muddy and sandy bottoms ranging from 0.08 to 0.63 crabs m^{-2} for juveniles >20 mm CW and adults in upper Chesapeake Bay (e.g., Hines et al. 1987, 1990), 0.02 to 0.36 crabs m^{-2} in lower Chesapeake Bay (e.g., Seitz et al. 2003a), and 0.1 to 1.7 juveniles m^{-2} on the Gulf Coast (e.g., Thomas et al. 1990; Rakocinski et al. 2003). In South Carolina, 15-mm juveniles were most abundant (0.32 crabs m^{-2}) in sandy-mud substrates of salt-marsh creeks, especially in oligohaline zones; these densities were more than twice those collected on shell hash or in marsh grasses (Mense and Wenner 1989). Densities of large juveniles range from 0.01 to 0.6 crabs m^{-2} and adults from about 0.008 to 0.038 crabs m^{-2} (after gear correction) sampled in sediments with dredges during winter throughout Chesapeake Bay (Sharov et al. 2003). Recent studies (Seitz et al. 2003a; King et al. 2005; Lipcius et al. 2005; Seitz et al. 2005) indicate that shallow muddy habitats adjacent to salt marshes in the low salinity reaches of subestuaries are of great value to juvenile blue crabs, probably because of their higher food resources (infaunal bivalves) and lower predator abundance.

Soft-bottom habitats >1 m deep are frequently used by large, adult crabs. In subestuaries, these habitats are the primary habitat for foraging males and females in the summer (Hines et al. 1987, 1990, 1995; Wolcott and Hines 1989a, 1990). Deeper (>10 m) soft-bottom habitats of the Chesapeake main stem are used extensively by females during fall migration (Aguilar et al. 2005) and by adult males and females for burial over-winter (Van Engel 1958; Schaffner and Diaz 1988; Sharov et al. 2003) and by mature females during the summer spawning season (Lipcius et al. 2003).

In upper Chesapeake Bay, Mississippi Sound, and many other estuaries, most structured habitats have been lost due to destructive over-fishing and disease effects on oyster reefs, major declines in seagrasses, and removal of woody debris as hazards to navigation (Orth and Moore 1984; Everett and Ruiz 1993; Rothschild et al. 1994; Moncreiff et al. 1998). In these systems, juveniles use non-structured shallow (<70 cm deep) water as refuge habitat (Ruiz et al. 1993; Dittel et al. 1995; Hines and Ruiz 1995). In a subestuary of upper Chesapeake Bay, juvenile densities peaked at <40 cm depth and diminished significantly with increasing depth, whereas densities of larger crabs increased at depths >70cm (Hines and Ruiz 1995).

Although densities in bare sediment are typically low (<1 crabs m^{-2}), these soft bottom habitats may support large portions of the blue crab population because of their great extent compared to high densities in limited structured habitats. In Mississippi Sound, for example, small juveniles (<10 mm CW) are abundant on bare sediments in correlation with, but at lower densities than, nearby seagrass habitats where post-larvae settled (Rakocinski et al. 2003). However, habitat use of non-structured habitat depends interactively on blue crab size and water depth (Ruiz et al. 1993) and on salinity zone (Posey et al. 2005).

Multiple Habitat Use

Most studies have focused on juvenile blue crab use of a single habitat at a time, or on comparison of a structured habitat with bare sediment. However, when multiple habitat use has been studied with balanced comparisons, juvenile blue crabs exploit all the available habitats in varying degrees.

Juvenile blue crabs in Texas exploit submerged vegetation, emergent salt marsh areas, and bare sediment in differing degrees for feeding and refuge from predation (Thomas 1989). On the Texas coast, juveniles <40 mm CW were found at highest density in seagrass, at intermediate density in salt marsh, and at lowest density in bare sediment; however, crabs were larger in salt marshes than in seagrass or non-vegetated habitat (Thomas et al. 1990; King and Sheridan 2006). Thus, in Gulf coast areas where seagrass habitat is infrequent, salt marsh provides important additional nursery habitat for juvenile blue crabs (Thomas et al. 1990), but *Vallisneria americana* beds may provide crucial habitat on low tides when marshes are exposed (Rozas and Minello 2006). In areas of Mississippi Sound, where seagrasses have undergone a severe decline, early juveniles can be abundant in soft sediments adjacent to seagrass patches, with abundance of small juveniles (<10 mm CW) in seagrass and bare sediment habitats exhibiting covariation (Rakocinski et al. 2003). Densities of post-settlement stages in structured habitat were considerably higher than in nearby sediment habitats, suggesting either "spill over" from settlement in seagrass patches or actual direct recruitment to bare sediments as a supplementary area. In South Carolina, juveniles used tidal creeks of salt marsh ecosystems, rather than going onto the marsh surface, probably avoiding exposure on low tides (Mense and Wenner 1989). Juvenile blue crabs in upper Chesapeake Bay used five habitat types (bare sediment, submerged vegetation, woody debris, oyster shell, and rocky rip-rap) deployed simultaneously as experimental patches, with variable but significantly higher densities in structured habitat (Davis and Hines, unpubl. data). In New Jersey, juveniles used seven types of habitats including seagrass, algal habitat, and bare sediment as well as adjoining salt marsh at densities that varied temporally, but attained similar peak densities among all of the habitats (Wilson et al. 1990b; Meise and Stehlik 2003). However, another study showed greatest juvenile blue crab abundance in macroalgal *Ulva lactuca* areas compared to seagrass *Zostera marina* and saltmarsh *Spartina* spp. creeks (Sogard and Able 1991).

Shifting Habitat Use by Life History Stage

Newly recruited juveniles (<5th instar) are found at highest densities in seagrass beds and only at very low densities in unvegetated habitats (Orth and van Montfrans 1987; Williams et al. 1990; Pile et al. 1996; Pardieck et al. 1999; Heck et al. 2001). A reduction in the density of later stage crabs (11-25 mm CW) in seagrass beds and increasing abundance in marsh creeks indicate that juvenile blue crabs undergo a shift in habitat use (Orth and van Montfrans 1987; see also Pardieck et al. 1999; Rakocinski et al. 2003). The shift appears to be triggered by attainment of a size refuge from predation, because tethering of 1st through 9th instar juveniles showed that predation rates diminished significantly between 5th (7-9 mm) and 9th (14-16 mm) instars (Pile et al. 1996). Similarly, although small (<10mm CW) juveniles exhibited strong affinity for shoal grass habitat compared to bare sediment, larger juveniles did not exhibit strongly preferential association with seagrass along the Gulf Coast (Williams et al. 1990). However, other Gulf Coast estuaries showed variable, often high, abundances among seagrasses and bare sediment areas (Sheridan and Livingston 1983; Rakocinski et al. 2003).

During summer, habitat use by blue crabs varies with size, sex, and molt stage as they feed, grow, molt to maturity, and mate, as illustrated within the Rhode River, a subestuary of Chesapeake Bay (Hines et al. 1987, 1995). There, large, intermolt, 1+ age class crabs (>100 mm CW) primarily use nonstructured soft bottom habitat in deeper (1-4 m) water of estuarine channels and basins when foraging on infaunal prey, whereas 0+ age class juveniles (30-70 mm CW) primarily use shallow (>70 cm) water along the shoreline, where they escape predation or cannibalism by large crabs (Hines et al. 1987, 1990, 1995; Ruiz et al. 1993; Hines and Ruiz 1995). Juveniles (30-70 mm CW) seek woody debris primarily along the shoreline as refuge for molting (Hines et al. in prep.). As prepubertal males approach their molt to maturity, they move up into tidal creeks, where >90% of the crabs are male and in active molt stages (Hines et al. 1987). These males select the shallow tidal marsh edge along the creek as the microhabitat for molting (Wolcott and Hines 1990). After molting to maturity, males move back out into the subestuarine basin to forage and mate.

In contrast, prepubertal females molt to maturity within the estuarine basin and especially at the mouth of the subestuary, where they couple with intermolt mature males. This mate guarding affords females protection from predation or cannibalism and allows males to block competitive insemination of their mates by other males (Jivoff 1997a, b; Jivoff and Hines 1998a, b; Carver 1999; Carver et al. 2005). Mated females remain to forage in deeper waters near the subestuary through the summer until the fall migration (Turner et al. 2003; Aguilar et al. 2005). During migration to the spawning area in the lower estuary, females tend to use habitat along the deep channel of the mainstem of Chesapeake Bay (Aguilar et al. 2005). Thus, the deeper waters of the mainstem of the estuary form a migration corridor for females (Lipcius et al. 2001).

In lower Chesapeake Bay, over-wintering blue crabs are mostly mature females that are least abundant in shoal and spit habitats, at intermediate abundance in deep channels, and most abundant in basin habitats of the mainstem, especially at depths >9 m in sediments composed of 40 to 60% sand (Schaffner and Diaz 1988). This survey indicated that over-wintering females occur primarily in areas of the lower mainstem estuary characterized by moderate energy regimes and fine but sandy sediments. In contrast, wintering juveniles and males bury into sediments of deeper channels and the mainstem of the middle and upper estuary (Sharov et al. 2003). During the summer spawning season in Chesapeake Bay, mature females exhibit peak abundance in the mainstem at depths of 6 to 14 m, with nearly half of all adult females in the lower Bay found deeper than 10 m (Lipcius et al. 2003).

Salinity Zone

Blue crab abundance varies along the salinity gradient, with highest densities occurring in the settlement habitats of the polyhaline zone (Orth and van Montfrans 1987; Fitz and Wiegert 1991b; Moksnes et al., 1997; Zimmerman et al. 2000; King et al. 2005). After they disperse from their settlement habitat, the abundance of juveniles and males tends to be more evenly distributed across a broad range of salinities from polyhaline to mesohaline waters. In river-dominated estuaries of the southeastern United States (North Carolina to Georgia) where structured habitats for refuge are often largely absent, abundances of small juveniles (13-24 mm CW) were negatively correlated with salinity (Posey et al. 2005). Juveniles encountered lower predator abundance and lower mortality rates (tested by tethering), implying that low salinity areas may be important nursery habitat for food and reduced predation. By contrast, abundances of larger juveniles (>24 mm CW) were uncorrelated with salinity or juveniles were more common at higher salinity sites (Posey et al. 2005). Juvenile blue crabs in Chesapeake Bay can be abundant up-estuary in lower salinity zones where they feed on dense infaunal invertebrates associated with detrital production of adjacent salt marshes (Seitz 1996; Seitz et al. 2003a; King et al. 2005; Lipcius et al. 2005; Seitz et al. 2005). Juvenile blue crabs may be abundant in oligohaline salinities and tidal freshwater marshes, where they appear to obtain osmotic advantage for larger molt increments (Haefner and Shuster 1964; Ettinger and Blye 1981; deFur et al. 1988) as well as refuge from predators (Rozas and Odum 1987). Activities vary with salinity, and movement of mouth parts, antennules, and the abdomen increases at lower salinity (McGaw et al. 1999), which are associated with blue crab behavior and use of various habitats along the estuarine gradient. In higher latitude estuaries like Delaware and Chesapeake bays, mature females become concentrated over the winter in deep waters of the polyhaline zone, where they migrate before brood production the following spring or summer (Schaffner and Diaz 1988; Lipcius et al. 2001, 2003; Sharov et al. 2003; Aguilar et al. 2005). At lower latitudes, mature and ovigerous females also aggregate in high salinity zones, because they incubate and hatch eggs near the mouths of estuaries (Tagatz 1968a; Tankersley et al. 1998).

In the Caribbean basin, species of *Callinectes* partition the habitat by salinity along the estuarine gradient (Norse 1978a, b). *Callinectes maracaiboensis, C. bocourti,* and *C. sapidus* are most tolerant of low salinities and extend into oligohaline salinities (0-10[1]), with all three of these species also extending into mesohaline and polyhaline salinities. The mesohaline zone includes (in order of euryhalinity) *C. exasperatus, C. danae,* and *C. marginatus*, and these three species extend into polyhaline and near-marine waters. Again in order of tolerance to low salinities, *C. exasperatus, C. marginatus*, and *C. ornatus* occur in near marine and marine salinities (>30). *Callinectes similis* also occurs in polyhaline and near-marine salinities. Along estuaries of the Pacific Coast of Central America and Columbia, *C. toxotes* dominates in low salinities whereas *C. arcuatus* is dominant in the mesohaline to polyhaline zones.

Hypoxic Habitats

Blue crab densities are zero in anoxic waters of eutrophic estuaries, such as areas deeper than 10 m in major tributaries and the central channel of Chesapeake Bay (Pihl et al. 1991) and in the Neuse River in North Carolina (Eby and Crowder 2002), as well as delta areas of the Mississippi plume (Rabalais et al. 2001). Crab densities are diminished in hypoxic areas because crabs may move into very shallow waters during hypoxic events, such as nocturnal hypoxia in summer or during plankton blooms (e.g., Loesch 1960; Pihl et al. 1991). Juveniles of both *C. sapidus* and *C. similis* readily detect and avoid hypoxic waters (Das and Stickle 1994). Similarly, adults avoid hypoxic habitats <4 mg dissolved O_2 L^{-1} (Bell et al. 2003a). As hypoxic waters have extended inshore from deeper waters, suitable blue crab habitat has been "compressed" into shallower areas, as seen in the Neuse River estuary and Pamlico Sound (Selberg et al. 2001; Eby and Crowder 2002) and modeled for the Patuxent River tributary of Chesapeake Bay (Mistiaen et al. 2003).

Spatial and Temporal Variation in Habitat Use

In estuaries like Chesapeake Bay, significant seasonal and long-term variation in area and composition of structured habitats has occurred, including long-term declines in submerged aquatic vegetation (Orth and Moore 1984), oyster reefs (Mann et al. 1991; Rothschild et al. 1994), and coarse woody debris (Everett and Ruiz 1993). The evidence for the crucial nursery function of these habitats indicates that their loss imposes significant negative effects on survival and growth for blue crab populations. However, the combined effects of multiple habitat loss and fragmentation creating a mosaic of refuges are complex, because juvenile blue crabs, their prey, and their predators may respond differentially and with fluctuating densities to such habitat changes (Irlandi 1997; Eggleston et al. 1998a, b; Micheli and Peterson 1999; Hovel and Lipcius 2001; Hovel et al. 2002; Hovel 2003; Hovel and Fonseca 2005). The interaction of transport processes, movement, and habitat value at multiple scales indicates that landscape-level factors should be considered in analyses of habitat use (e.g., Stockhausen and Lipcius 2003; Hovel 2003).

Habitat value for blue crabs also depends interactively on patch size and complexity (i.e., density of structural elements within the patch) (Heck and Orth 1980a; Irlandi 1997; Hovel et al. 2002; Hovel and Fonseca 2005). Seagrass patches as small as 0.25 m^2 support higher densities, higher growth, and higher survival of juvenile blue crabs than do bare sediments adjacent to seagrass patches (Perkins-Visser et al. 1996; Eggleston et al. 1998a, b; Hovel and Lipcius 2001). Smaller patches also afford greater access to bivalve prey, such as the hard clam, *Mercenaria mercenaria* (Irlandi 1997). Survival rates of tethered juvenile crabs vary interactively with patch size and landscape configuration, such that survival is higher in small (1-3 m^2) than in large (>100 m^2) patches, and is higher in patchy than in continuous seagrass beds (Hovel and Fonseca 2005). Effects of patch size of seagrass habitat vary temporally with seasonal changes in predator or cannibal use of patches (Hovel and Lipcius 2001; Hovel et al. 2002).

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[1] Salinity is presented as a pure ratio with no dimensions or units, according to the Practical Salinity Scale (UNESCO 1985).

These studies indicate that patchy seagrass landscapes are valuable refuge habitat for juveniles, and that effects on survival can only be understood when larger scales of habitat structure are considered.

Habitat fragmentation may favor ecological interactions at the edges of structural habitats because smaller patches have greater ratios of edge to interior. Higher ratios may increase probability of key attributes of patch use, such as habitat encounter by recruiting crabs, supply of food items that are moving past, and predators moving around the patch edges (Eggleston et al. 1998a, b; Blackmon and Eggleston 2001). Greater relative habitat edge may allow large mobile predators (such as large blue crabs) to gain access to smaller prey (such as small blue crabs) that receive refuge from interiors of larger patches (e.g., Eggleston et al. 1998a, b, 1999; Davis and Hines, unpubl. data). The complex dynamics of benefits and disadvantages of edges and interior zones of patchy habitats like seagrass may result in marked short-term (seasonal) changes in abundances of blue crabs and their prey (Bologna and Heck 2002).

Habitat configuration and connectivity also interact to affect habitat use and value for blue crabs. Vegetated habitats (both seagrass and salt marsh patches) act as corridors for blue crabs to gain access to oyster reefs for food, with both seagrass and fringes of emergent marsh plants providing refuge from predation upon the crabs by mobile predators such as birds (Micheli and Peterson 1999). Features that increase juvenile use of Gulf Coast salt marshes are reticulated marsh geomorphology, low tidal amplitude, and long periods of tidal inundation (Thomas et al. 1990). In subestuaries of Chesapeake Bay, blue crab abundance is related to the interaction of salinity zone, presence of adjacent salt marsh habitat, and watershed land use (King et al. 2005). Juveniles are most abundant in higher salinities and in areas adjacent to salt marshes of subestuaries with watersheds that are predominantly forested or in agriculture, whereas suburban and urbanized watersheds have lower juvenile densities. Thus, sites with connection to marsh habitats providing detritus sources for blue crab food, especially deposit feeding bivalves like the Baltic macoma *Macoma balthica*, favor blue crab abundance, whereas human development of watersheds appears to reduce blue crab abundance, albeit through indirect ways (Seitz et al. 2003a; King et al. 2005).

At higher latitudes, blue crabs undergo marked seasonal shifts in habitat use with the onset of cold winter temperatures and cessation of feeding, movement, and molting. Juvenile crabs in New Jersey appear to shift their habitat over winter from unvegetated habitat to eelgrass roots and debris in marsh creeks (Wilson et al. 1990b). In Delaware Bay and Chesapeake Bay, crabs move into deeper water in fall (late September, October, and November), with inseminated females migrating from shallow nursery habitats to higher salinity zones in the lower bay. Migrating females move down deeper (13-25 m) water along the Bay's main channel and not along the shallow shoulders of the mainstem (Turner et al. 2003; Aguilar et al. 2005.). Over-wintering blue crabs in lower Chesapeake Bay (90-98% female) were most abundant in water deeper than 9 m where sediments are composed of 40 to 80% fine silty sand (Schaffner and Diaz 1988). Winter dredge surveys throughout Chesapeake Bay confirm the concentration of mature females in the lower bay, with large males in deeper water of lower salinities and small juveniles in depths of 2 to 13 m (Sharov et al. 2003).

Much less is known about temporal variation in habitat use of blue crabs in estuaries at lower latitudes, probably because seasonal temperature changes are much less pronounced in these systems. Even so, these systems are subject to seasonal changes, and general patterns of habitat use along estuarine salinity gradients appear to be similar among estuaries along the East Coast of North America and also in Gulf Coast systems (e.g., Van Engel 1958; Darnell 1959; Tagatz 1968a; Archambault et al. 1990; Steele and Bert 1994; Guillory and Perret 1998; Kahn et al. 1998). However, many of the assessments for lower latitude estuaries tend to cite literature from the mid-Atlantic region, and in the absence of comparably detailed studies for a particular region, such inferences may not be valid. For example, mature females along the Gulf Coast of Florida often exhibit seasonal shifts in habitat as they migrate northwest alongshore for long distances in a pattern that appears distinctly different from East Coast estuaries (see Adult Movement section below). In addition, predation rates upon post-settlement juveniles are much higher in estuaries of the central Gulf of Mexico than in mid-Atlantic estuaries, which severely regulate blue crab abundance and distribution among habitats (Heck and Cohen 1995).

MOVEMENT

Approaches and Methods for Movement Studies

Blue crab movement varies with life stage and molt stage, and depends on habitat and geographic region, as well as on tidal and seasonal cycles (Gillanders et al. 2003). Movement patterns may be deduced indirectly from spatially disjunct distributions of life stages, as when settling larvae occur mainly in the lower estuary but larger juveniles are distributed throughout the estuary. Movement is also inferred by temporal variation in the distribution of a life stage, as when immature females molt to maturity and mate in upper estuarine zones but ovigerous females later occur primarily near the mouth of estuaries (e.g.,Van Engel 1958).

Movement between points (without knowing the route traveled) can be estimated directly by mark-recapture studies involving large numbers (thousands) of crabs marked with inexpensive external or internal tags (e.g., Cronin 1954; Judy and Dudley 1970; van Montfrans et al. 1986; Fitz and Wiegert 1991a; Steele 1991; Davis et al. 2004b; Aguilar et al. 2005) (Fig. 4). External tags are readily visible to fishers and typically cause little harm to crabs, but they are lost during molting. As a result, external tags usually have been applied to large mature crabs that do not molt (females) or only molt infrequently (males). Internal tags that are retained during molting also have been used, but these may require expensive equipment to insert the tags (e.g., micro-wire tags; van Montfrans et al. 1986; Fitz and Wiegert 1991a; Davis et al. 2004b) or to detect them (e.g., "pit tags"; Wolcott and Hines 1996). Internal tags are often not seen by fishers, and also may cause significant mortality (e.g., dart tags; Fannaly 1978; Souza et al. 1980) or may induce limb autotomy (e.g., elastomer injection; Davis et al. 2004b). However, some forms of internal tags (especially micowire or coded wire tags and elastomer injection) work well for juveniles as small as 10 mm CW (van Montfrans et al. 1986; Fitz and Wiegert 1991a; Davis et al. 2004b).

External ultrasonic telemetry tags, which are expensive and usually are applied to small numbers of crabs >60 mm CW, allow acquisition of detailed data on the path of movement and other selected aspects of behavior and physiological functions (Nye 1989; Wolcott and Hines 1989a, b, 1990, 1996; Hines et al. 1995; Clark et al. 1999a, b, 2000; Terwin 1999; Bell et al. 2003a, b) (Fig. 5). Ultrasonic tags may also be used to transmit data on environmental variables (temperature, conductivity, depth, light) that crabs encounter, and they have been developed to signal physiological variables (muscle action potentials, posture, suture breaks of the exoskeleton) that are integral components of crab behaviors (locomotion, feeding, fighting, mating, molting) in relation to location and time (Wolcott 1995; Wolcott and Hines 1996) (Fig. 6). Electronic tags that record data about environmental variables to micro-chips that can be down-loaded to a computer when the tag is recaptured have been applied recently to blue crabs to deduce movement and behavior (Wolcott et al. 2004).

Post-Settlement Dispersal of Juveniles

Dispersal of juveniles after settlement increases the array and extent of nursery habitats. Our knowledge of the characteristics of secondary, post-settlement dispersal varies among estuarine systems, with some important contrasts among Mobile Bay, Pamlico Sound, and Chesapeake Bay, for example. In Mobile Bay, Mississippi, post-settlement dispersal is largely limited by intense predation on juveniles (J1 to J5), to the extent that few dispersing juveniles are collected (Heck et al. 2001). However, densities

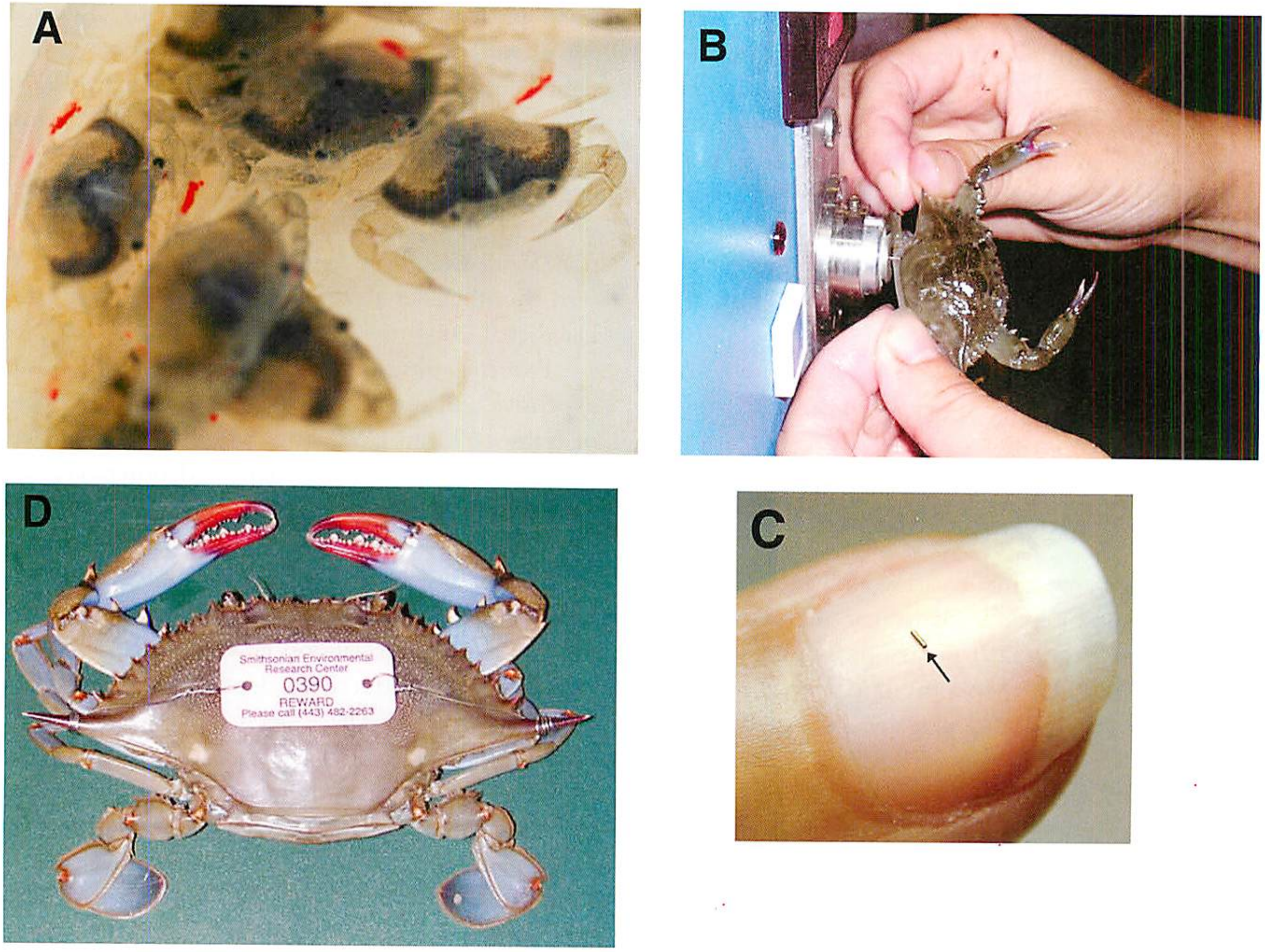


Figure 4. Tagging methods for blue crabs. (A) Juveniles with red elastomer injected into swim paddle legs. (B) Micro-wire injection of crabs by a specialized machine that inserts a tiny segment of magnetized wire into the muscle at the base of a swimming leg; the tag persists through the molt cycle. (C) Close up of micro-wire (arrow) that can be detected by magnetic sensor. (D) Highly visible plastic tag attached to dorsal carapace of a mature female, which will not molt. Photos by Alicia Young-Williams, SERC.

of larger juveniles (J5 to J9) in various nursery habitats (seagrasses, marshes, and adjacent bare sediment) in various Gulf Coast estuaries occur at levels similar to similar habitats in East Coast estuaries (Heck and Coen 1995; Heck et al. 1995; Morgan et al. 1996; Heck et al. 2001; Rakocinski et al. 2003).

In North Carolina sounds, field collections of dispersing juveniles provide contradictory results. Some studies indicate dispersal occurs at the earliest instars (J1, and well before J5) (Etherington and Eggleston 2000, 2003; Blackmon and Eggleston 2001; Etherington et al. 2003; Reyns and Eggleston 2004), whereas other studies indicate that dispersal occurs at later stages (J4-5) (Forward et al. 2004). Juvenile crabs emigrate rapidly after settlement in a density-dependent process that redistributes them from high-density settlement sites to areas with low larval supply. Dispersal from seagrass settlement habitats occurs pelagically by a circadian rhythm of swimming on nighttime flood tides (Forward et al. 2003, 2004). Although secondary dispersal is a consistent process across a broad range

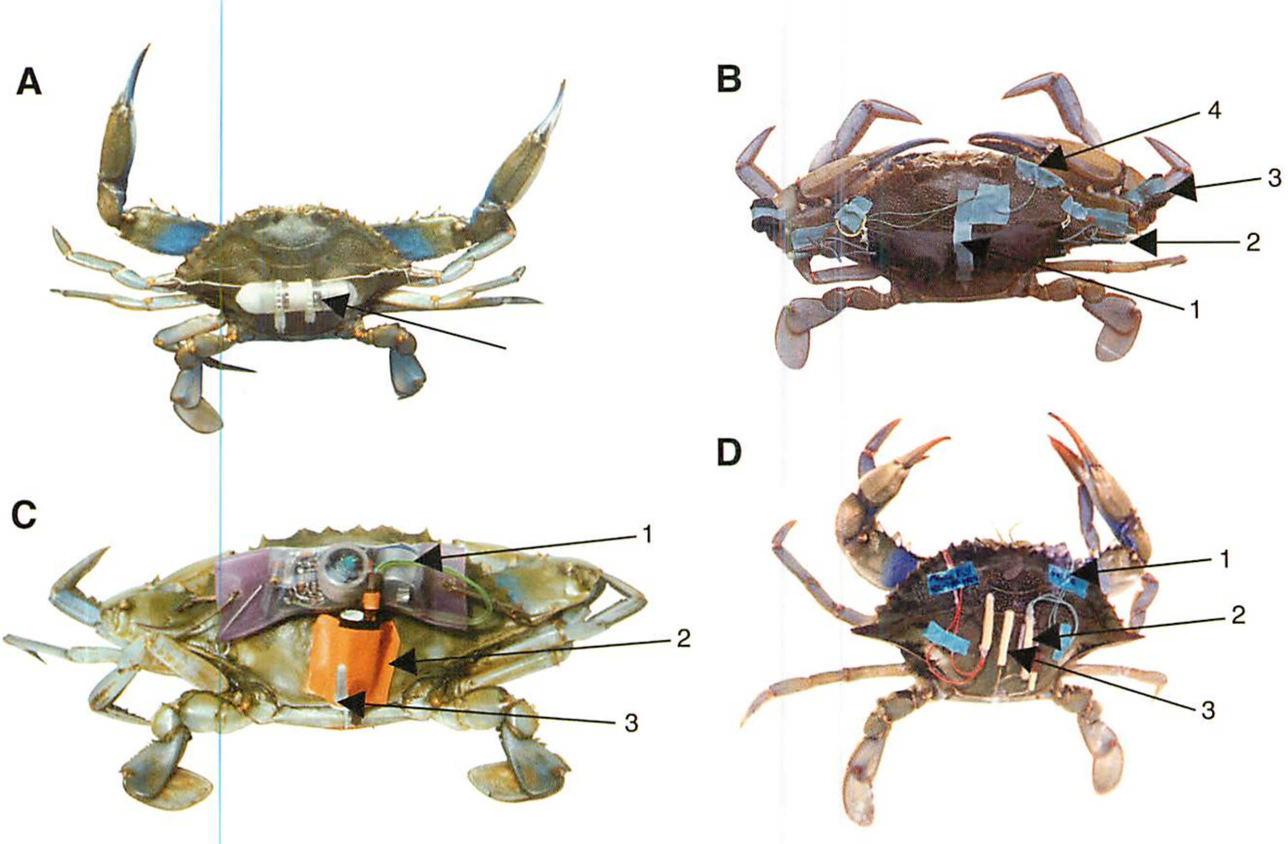
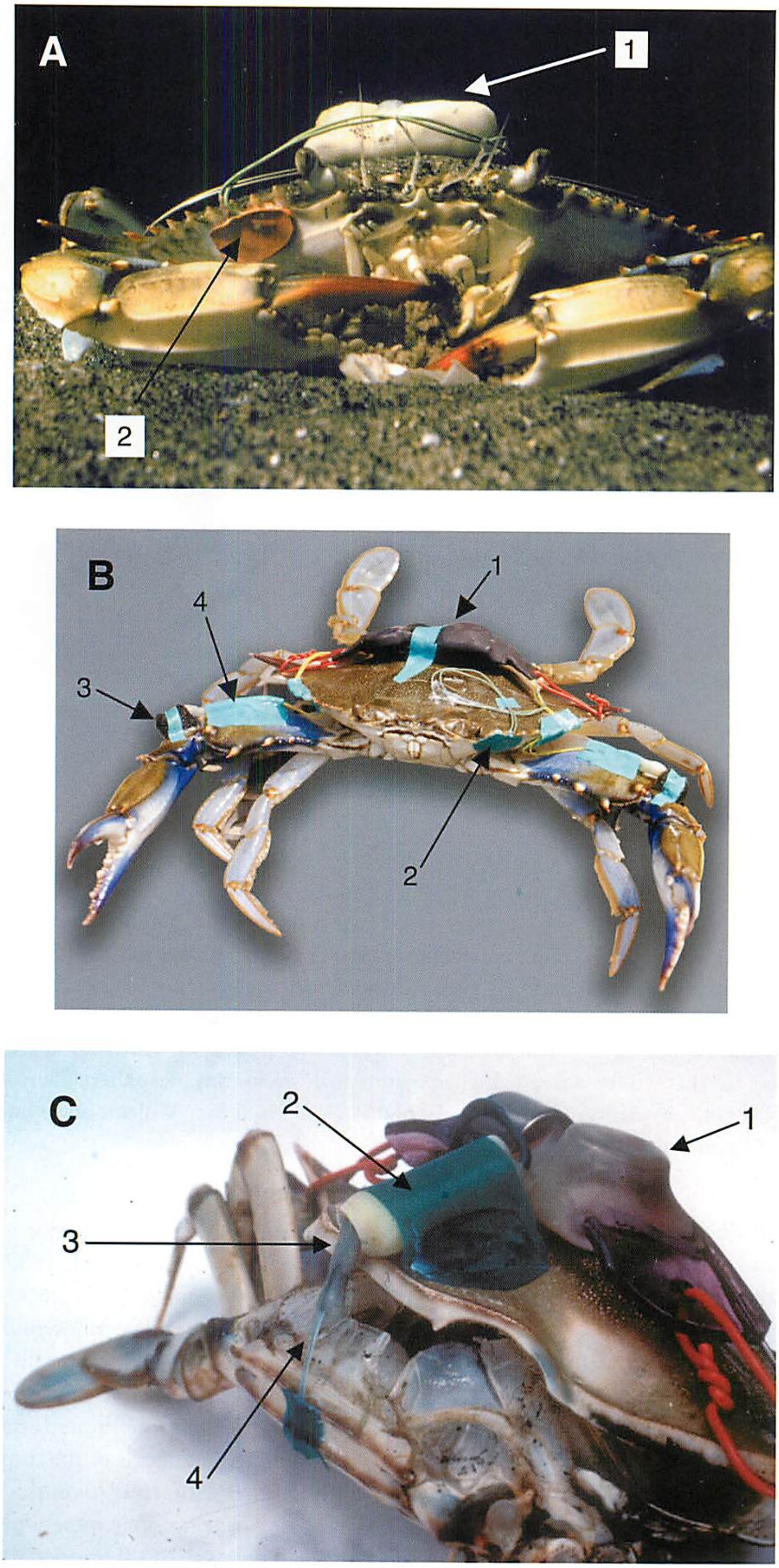


Figure 5. Dorsal views of blue crabs equipped with ultrasonic biotelemetry tags that signal location and selected behaviors and physiological functions. (A) Commercial transmitter (arrow) for location. (B) Customized transmitter for location, feeding, and fighting. 1 = transmitter; 2 = reed switch on merus of right chela; 3 = magnet on carpus of right chela; 4 = electrode wires for detecting contraction of the right mandibular muscle. (C) Customized transmitter for location and molting; 1 = transmitter; 2 = reed switch and adjacent tube for magnet; 3 = magnet in post-molt position on spring connection to ventral carapace. (D) Customized transmitter for location and sensing of pre-copulatory mate guarding during mating. 1 = wires running to transmitter located on ventral carapace; 2 = reed switches; 3 = magnet on spring bar that will be depressed when mature male grasps this pre-pubertal female. Tags designed by Thomas G. Wolcott. Photos by Anson H. Hines and Thomas G. Wolcott. See Wolcott and Hines (1989a, b, 1990); Clark et al. (1999b); Carver (2001).

of wind conditions (Etherington and Eggleston 2003), hurricanes and storm events may modify the dispersal, moving a range of life stages at wider spatial scales throughout the sounds, but effects depend on seasonal timing, amount of rainwater runoff causing flushing, salinity declines, and low dissolved oxygen (Etherington and Eggleston 2000, 2003; Eby and Crowder 2002; Mallin et al. 2002; Posey et al. 2005).

In Chesapeake Bay, dispersal of juveniles from the settlement habitat appears to reflect ontogenic change in activity and behavior at about the 5th to 7th crab instar (Hines et al. 1987; Pile et al. 1996; Etherington and Eggleston 2000, 2003; Diaz et al. 2001). It is clear that, following some lag interval after settlement, juveniles typically disperse. This dispersal may occur over several months in lower latitudes and during more limited seasons at higher latitudes, but timing details of the dispersal are not clear. In northern estuaries, juveniles do not undergo migratory dispersal in winter when water temperatures fall below 10°C (Hines et al. 1987). In Chesa-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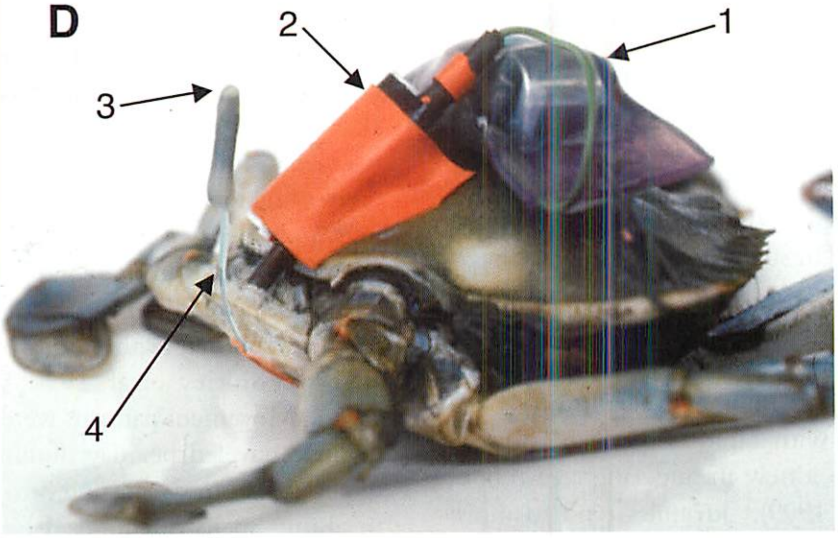

Figure 6 (Opposite page and above). Side views of biotelemetry tags that signal location and selected behaviors and physiological functions of blue crabs. (A) Feeding tag, which signals location and contraction of the mandibular muscle. 1 = transmitter; 2 = waterproof patch covering insertion of electrode through the anterior-lateral carapace into the right mandibular muscle and the haemocoel, to detect the myopotential of muscle contraction. (B) Feeding and threat display tag, which signals location, contraction of the mandibular muscle, and meral spread of the chelae. 1 = transmitter; 2 = waterproof patch covering the insertion of electrodes through the carapace into the left mandibular muscle; 3 = magnet on carpus of right chela; 4 = reed switch on merus of right chela. Threat displays are signaled when the magnets are positioned close to the reed switches. (C) and (D) Molting tags. 1 = transmitter; 2 = reed switch and parallel insertion tube for magnet; 3 = magnet; 4 = spring-like attachment of magnet to ventral carapace. As the crab swells during ecdysis (C) and backs out of the old carapace, the magnet is pulled from the tube and springs into post-molt position (D) away from the reed switch, changing the telemetry signal. Photos by Thomas G. Wolcott and Anson H. Hines. See Wolcott and Hines (1989a, b, 1990); Clark et al. (1999b).

peake Bay, juveniles disperse from lower Bay settlement habitats to arrive in upper Bay subestuaries during fall and late in the following spring (Hines et al. 1987, 1990). Although the behavioral and physical mechanisms have not been studied explicitly for the post-settlement dispersal, juvenile movement up the estuary may involve selective tidal-stream transport, as exhibited by megalops and small juveniles entering lower estuaries (Lipcius et al. 1990; Little and Epifanio 1991; DeVries et al. 1994; Tankersley and Forward 1994; Forward et al. 2003a, b; see also Tankersley and Forward, Chapter 10) or by ovigerous females moving out of estuaries to hatch their eggs (Tankersley et al. 1998). Alternatively, juveniles may ride the salinity wedge up-estuary like mud crab larvae (Cronin 1982), some fish species (McCleave and Whipplehouser 1987), invertebrate larvae (de Wolf 1974), and some phytoplankton species (Tyler and Seliger 1978); or, small crabs may simply swim up-estuary under their own navigational mechanism and power. Post-settlement dispersal also may be driven by storms in North Carolina sounds (Etherington and Eggleston 2000). Although the seasonal timing of juvenile dispersal appears to be consistent among years, the abundance of juveniles dispersing up the estuary varies greatly among years, with fluctuations in numbers of recruits settling into the estuary (Hines et al. 1987, 1990; Lipcius and Van Engel 1990; Pile et al. 1996; Rakocinski et al. 2003).

Juvenile Movement among Habitats within Subestuaries

Once dispersed, juveniles >20 cm CW tend to remain within subestuaries. Juvenile movement reflects their shifting habitat use within subestuaries and may involve active locomotion over distances from 10 m to a few km (Hines et al. 1995, unpubl. data; Terwin 1999). In subestuaries of upper Chesapeake Bay, telemetry studies showed that juveniles (60-80 mm CW) move along shorelines within subestuaries, with a typical pattern of periods of meandering slowly (2 m h^{-1}) in shallow (<1 m) water interspersed with rapid (>50 m h^{-1}) directional movement to a new meandering area (Hines et al. 1995; Terwin 1999). Juveniles tend to move rather directly and rapidly across channels, and not to meander in deeper water where they are most vulnerable to cannibalism by large crabs; however, small juveniles do not seem to move in a net direction along the axis of the subestuary as do larger pre-pubertal and adult crabs (Hines and Ruiz 1995; Hines et al. 1995; Terwin 1999; Hines and Wolcott, unpubl. data). Tagged juveniles released experimentally into small (1-10 ha) coves of Chesapeake Bay remained within the release sites and did not move away until molting to maturity (Davis et al. 2005b).

Juveniles often exhibit short-term movement into salt marsh habitats, depending on tidal fluctuations. Tagging studies in Georgia showed that juveniles move with the tide into salt creeks and onto salt marsh surfaces, but they do not move far (<100 m) into the interior of the marsh habitat (Fitz and Wiegert 1991b, 1992). In Texas and North Carolina, juveniles also move onto salt marshes with tidal flooding (Zimmerman and Minello 1984; Hettler 1989). In lower Chesapeake Bay, daily exchange of tagged juveniles was minimal (5-8% d^{-1}) among adjacent types of habitats, including small (<100 m) tidal marsh creeks, seagrass beds, and unvegetated habitats (van Montfrans et al. 1991). Crabs buried on low tides to remain in a creek for 8 to 12 d, resulting in a population turnover time (exchange with new juveniles from surrounding areas) of >65 d (van Montfrans et al. 1991).

Premolt juveniles typically move in advance of ecdysis to refuge habitats for molting. Juvenile are thought to move cyclically into and out of seagrass beds in many areas as the primary site for molting (Van Engel 1958). In subestuaries of Chesapeake Bay that have lost submerged aquatic vegetation, telemetry showed that juveniles moved up to hundreds of meters in shallow water along shore to molt in woody debris (Hines et al., in prep.). In other telemetry studies in the same subestuary, pre-pubertal males moved 1 to 3 km into salt creeks during the few days before the molt to maturity (Hines et al. 1987; Shirley et al. 1990; Wolcott and Hines 1990). Movement patterns were highly variable, but distance traveled per day diminished from averages of about 200 m d^{-1} during 3 to 6 d before molting to about 50 m during 1 d before ecdysis, when movement ceased (Wolcott and Hines 1990). In subestuaries of North Carolina Sounds, pre-pubertal males and females similarly moved an average total distance of about 2 km (net distance about 1 km) over 7 d (Shirley and Wolcott 1991). Distance traveled per day similarly diminished markedly at 3 d before ecdysis, but movement did not differ significantly by sex and males did not appear to orient to salt creek habitats as in upper Chesapeake Bay (Shirley and Wolcott 1991).

Laboratory experiments demonstrate that juveniles of both *C. sapidus* and *C. similis* readily detect hypoxic water and move to avoid low oxygen levels (Das and Stickle 1994). However, responses to hypoxia may depend on severity and timing of low oxygen events, as it does for adults (Bell et al. 2003a, b).

Juvenile movement among estuaries and even among adjacent subestuaries appears to be minimal (e.g., van Montfrans et al. 1991; Hines et al. 1995; Terwin 1999). However, with declining water temperatures in fall in higher latitude systems like Chesapeake Bay, juveniles move from shallow (<1 m) water to deeper (>2 m deep) channels where they spend the winter months (pers. obs.).

Movement of Adults

Adult blue crab movement can be considered in two categories. The first is small-scale short-term movement that occurs within estuaries over distances typically <10 km over days to weeks for both males and females. The second is large-scale, seasonal migratory movement, which may involve distances of 10 to 800 km, especially for females moving from mating areas to areas of brood incubation and egg hatching.

Adult Short-term, Small-scale Movement

Short-term, tidal movement and orientation have been studied along beaches of the Gulf Coast by observation and tracking experiments (Nishimoto and Herrnkind 1978, 1982). Using blindfolded crabs and experimental beaches of different orientation, these studies indicated that blue crabs orient well to surge direction and that they use a sun-compass for orientation with tidal fluctuations and irregular shorelines.

Short-term and daily movement within estuaries has been estimated with tagging-recapture studies. In North Carolina, Judy and Dudley (1970) estimated that short-term (42 d) movement averaged about 6 km (range 3.5-11.6 km) d^{-1}, but this included a large proportion of migrating females, and the report does not provide the ability to separate the data for males and non-migrating females. Tagging studies in Florida showed that mature males rarely moved more than 10 km from the tagging site (Oesterling and Adams 1982). In a study near a power plant in Chesapeake Bay, Souza et al. (1980) estimated that blue crabs moved 400 to 900 m per day, although the study crabs endured a high level of mortality (19-39%) from handling and dart tags. However, these mark-recapture studies only indicate the net distance traveled and provide little information about the path taken by the crab, which is key to understanding small-scale, non-migratory movement.

Using ultrasonic telemetry, the path and detailed characteristics of non-migratory movement of adult and juvenile (>60 mm) blue crabs have been studied in the Rhode River, a subestuary of upper Chesapeake Bay (Wolcott and Hines 1989a, 1990; Hines et al. 1995; Terwin 1999; Turner et al. 2003) (Fig. 7). Intermolt crabs moved at an average speed of about 10 m h^{-1} during the warm season, but speed varied by month from a high average speed of about 15 m h^{-1} in July to about 5 m h^{-1} in May or late September, and no movement of males by late November to March. Speed also varied by size and life stage, with large males (>140 mm CW) moving faster (15 m h^{-1}) than similar sized females (8 m h^{-1}) or large juveniles (100-120 mm CW) (5 m h^{-1}). As indicated above for molting juveniles, movement of mature males decreased markedly at premolt stage D_2-D_3 about 3 d before ecdysis (Wolcott and Hines 1990). Although movement was highly variable among intermolt individuals, male and female crabs exhibited a characteristic pattern of slow meandering (0-10 m h^{-1}) within a radius of 50 to 200 m over a period of 1 to 5 d interspersed by sudden rapid (50 to 700 m h^{-1}) movement for a distance of 0.5 to 4 km that was directionally oriented along the axis of the subestuary. Unlike juveniles, this intermittent rapid, directional movement by adults resulted in their moving from the subestuary into the Chesapeake mainstem in about 2 to 3 weeks. As discussed under the section on Foraging below, slow meandering is associated with foraging in patches of higher density prey, whereas fast directional movement is apparently triggered by agonism among crabs competing for food.

Short-term mass shoreward migrations of blue crabs, described as "jubilees," occur in small-scale areas within subestuaries in response to hypoxic or anoxic conditions during early morning hours of summer plankton blooms, or possibly in response to seiches of deeper anoxic water (Loesch 1960). Ultrasonic telemetry showed that movement which is less extreme than jubilee events may also result in less visible shifts in depth distribution toward shore (Bell et al. 2003a, b). This movement appears to be an avoidance response that puts crabs into more oxygenated shallow water. However, blue crabs exposed to hypoxia during sudden upwelling events were not successful at moving to normoxic water, sometimes resulting in their remaining in severely hypoxic waters (<2 mg L^{-1}) for several hours (Bell et al. 2003a).

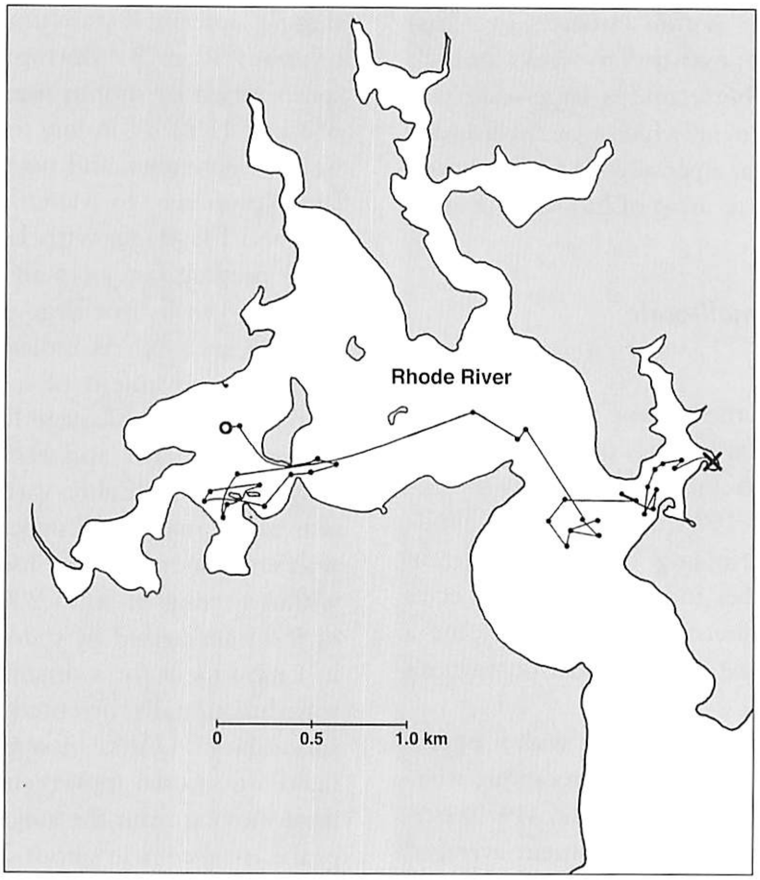

Figure 7. Example of a track of a large male blue crab fitted with an ultrasonic biotelemetry tag (as shown in Fig. 5A) in the Rhode River subestuary of Chesapeake Bay. The crab was released at the open circle (left end of track line); dots are locations about 12-h intervals over several days. Crab was recaptured at "X" (right end of track). Note meandering locations alternating with directional movement along channel of the subestuary.

Adult Large-scale and Seasonal Migratory Movement

Tagging studies of large, mostly mature crabs have been conducted over the past 80 y in many estuaries along the East and Gulf coasts of North America, both to understand seasonal patterns of movement that explain cyclical and spatial variation in catch of males and females within estuaries and to determine whether blue crab movement between estuaries is a key factor in defining stocks for fishery management. Such tagging studies typically achieve only low recapture rates. Initial studies in Chesapeake Bay included Fiedler's (1930) tagging of nearly 1,800 crabs with a recapture of 10.8%, Truitt's (1939) tagging of 4,600 crabs, and Cronin's (1949) test of various tags to obtain up to 22.6% return. These early researchers determined the basic annual cyclical pattern that mature female crabs move directionally to the mouth of the Bay after mating to overwinter near the spawning area. By contrast, males showed a non-directional, random movement within the estuary. Initial tagging studies for Delaware Bay (Cronin 1954; Porter 1956) indicated more variable movement by mature females, without clear directional migration seaward, though much of the movement occurred near the already wide mouth of the bay.

Most tagging studies have found a general pattern of retention of males and females within a home estuary, with females typically moving directionally down estuary over greater distances (depending on where they were released), males showing little net directional movement, with only a small fraction of individuals of either sex moving into neighboring estuaries, and no large-scale migration along the coast. For example, Judy and Dudley (1970) estimated movements of tagged blue crabs in North Carolina sounds, with a 30% return of all released crabs comprised of 17,237 females and 5,691 males. For males, 88 to 100% of returns occurred within 24 km of their release site, whereas females had 64 to 90% recovery in the area of release. Few recaptured crabs (2.2% of males and 6.2% of females) moved >24 km from release sites, with no males moving substantial distances alongshore and about 1% of females moving 65 to 258 km along inland waters from Oregon Inlet to Chesapeake Bay and about 1% moving alongshore 25 to 210 km from southern North Carolina estuaries to South Carolina. Similarly, in Chincoteague Bay, Virginia, Cargo (1958) tagged nearly 400 crabs in late summer and showed that mature females move southward within the bay to more saline waters over the subsequent months. In coastal South Carolina, Fischler and Walburg (1962) tagged 4,353 crabs >125 mm CW and showed no migration between estuaries. Tagatz (1968a) tagged >11,500 blue crabs in the St. John's River estuary, Florida. Most of his 35% recaptures, especially mature females, showed downstream movement, with only about 5% of the recaptures occurring outside the home estuary – mostly as movement within 50 km along the intra-coastal waterway, with two individuals being recaptured about 500 km away after a year. Along the west coast of Florida, Oesterling (1976) tagged 6,287 crabs and found that 95% of recaptured males were caught within 18 km of their release site. In Lake Borgne, Louisiana, and Mississippi Sound, Perry (1975) tagged and released 1,023 adults (155 males, 868 females) with a 30% return that showed crabs traveled 3 to 60 km over 4 to 261 d (mean = 40 d) at large, and that females moved from low salinities in Louisiana to over-winter in high salinities of Mississippi Sound. Within the Sound, movements appeared random, with little movement between adjacent estuaries. In bay and lagoonal systems of Texas, adult male crabs with tags moved <8 km and females moved <20 km (More 1969; Benefield and Linton 1990).

For estuaries along the Atlantic East Coast as well as the central and western regions of the Gulf Coast, tagging studies indicate that, sometime after mating, females typically migrate along the axis of the estuary to spawn near the mouth or just outside the starting estuary, but migratory movement among estuarine systems is minimal (see tagging studies for Delaware Bay [Cronin 1954; Porter 1956], Chincoteague Bay [Cargo 1958], Chesapeake Bay [Churchill 1919; Fielder 1930; Truitt 1939; Van Engel 1958; McConnagha 1993], North Carolina sounds and estuaries [Fischler 1965; Judy and Dudley 1970; Schwartz 1997], South Carolina [Fischler and Walburg 1962], St. John's River estuary of northeast Florida [Tagatz 1968a], Mississippi Sound [Perry 1975), Louisiana [Darnell 1959], and Texas [Daugherty 1952a; More 1969]). In studies that tagged large numbers of crabs, a small percentage were occasionally recaptured long distances from the release estuary. For example, Schwartz (1997) tagged 22,781 crabs in the Cape Fear River estuary, North Carolina, over 2 y. Of the 13.4% crabs (1,338 males, 1,723 females) that he recaptured, 2,985 were caught locally, and only 10 (0.3%) moved north to other estuarine systems while 66 crabs (2%) moved south. One female moved as far south as Key West, Florida (1,256 km), and one male was recaptured as far north as Hoopersville, Chesapeake Bay, Maryland (617 km). One crab was caught in an adjacent North Carolina sound as late as 6.5 y later.

In contrast to the pattern of females remaining in association with their mating estuaries in most regions, tagging studies along the west coast of Florida showed that a significant proportion of mature females move long distances from their mating estuary, although many reproduce near their home estuary as well (Oesterling 1976; Oesterling and Adams 1982; Steele 1991). Oesterling (1976) tagged and released 6,287 crabs during warm months along the west coast of Florida with a 10.7% return rate. Many females were recaptured substantial distances from release sites, often well away from their home estuary: 43% were recovered >16 km away, 25% were caught >48 km away, and 4% traveled >322 km away. Mature females that left their home estuary moved in a northerly direction along the peninsular coast and westerly along the panhandle; however, there appeared to be a westward barrier to further migration in the vicinity of Apalachicola Bay, which was deduced to be a primary spawning ground for the region. Similarly, Steele (1991) tagged more than 13,000 blue crabs during 2 y in Tampa Bay, with a recapture rate of nearly 25%. Mature females tended to move out of estuaries alongshore in a northerly direction, with 29% of recoveries occurring >765 km up the coast, and with several individuals traveling >800 km in approximately 100 d. In further tagging studies, Steele (1991) showed that females released along the southwest coast from Key Largo to Sarasota Bay contributed to the northwestward migration and moved as far as Apalachee Bay. In contrast, of 2,767 tagged crabs released in Apalachee Bay, 38% were retained in the Bay and only 5% were recaptured west of the release Bay, suggesting that the low salinity flow from the Apalachicola River impedes further westward migration of mature females (Steele 1991). Crabs tagged near Key Largo that moved in the other direction along the east coast of the peninsula moved as far as Biscayne Bay (Steele 1991).

With seasonal declines in water temperature at higher latitude (e.g., Chesapeake Bay, Delaware Bay), mature males, like juveniles, move into deeper channels of subestuaries and main estuarine basins, where they cease moving for the winter months. Males do not appear to move long distances during this seasonal shift (Hines and Wolcott, unpubl. data), but movement into deeper water in winter reduces exposure to lethal combinations of severely cold, low salinity surface waters (Rome et al. 2005).

Mature female blue crabs typically exhibit two phases of migratory movement after mating (Tankersley et al. 1998). The first phase (phase I) involves movement from mating locations to the lower estuary before brood production. The second phase (phase II) occurs during brood incubation just before egg hatching and involves movement to the mouth of, or off-shore from, the estuary. In large estuaries like Chesapeake and Delaware bays, phase I migration may occur over distances of 200 km or more, whereas in smaller estuaries and for females mating in the lower portions of large systems, crabs may only migrate fewer than tens of km during phase I migration. In Chesapeake Bay, this initial phase of migration occurs during late September through November and not earlier in the season (Turner et al. 2003; Aguilar et al. 2005). Both over-the-back tags and ultrasonic telemetry show that after mating during July through September, mature females forage and move about in subestuaries in the typical small-scale pattern of alternating meander and short directional movement (Turner et al. 2003; Aguilar et al. 2005). Although this period of foraging before migration allows a female to recover from her molt to maturity, the migration appears to occur in seasonal synchrony rather than being triggered by completing a non-synchronized period of physiological preparation after molting (Aguilar et al. 2005). In Chesapeake Bay, migration is manifested by relatively fast seaward movement that involves walking on the bottom, or swimming in the water column, or both (Wolcott et al. 2004), typically along the deeper channel of the Bay's mainstem (Aguilar et al. 2005) (Fig. 8). In Chesapeake Bay, females cease migrating for the winter and settle into bottom sediments of the mainstem as water temperatures drop below about 9° to 10°C, with some females remaining in the mesohaline zone and others arriving in the polyhaline zone for winter. As water temperature rises in spring and females become active, those that over-wintered in the mesohaline zone complete phase I seaward migration. Although fishers in Chesapeake Bay report a "wave" of mature females moving up the estuary in spring, this movement reflects increases in female activity and feeding as temperatures increase northward, thus increasing their vulnerability to fishing rather than reflecting actual movement of females up-estuary.

In phase II of migration, ovigerous females exhibit selective tidal-stream transport (see Tankersley and Forward, Chapter 10) by a tidal rhythm of swimming at the surface on nocturnal ebbing tides, thus moving near to, or out of, the mouth of estuaries, where they hatch their eggs (Tankersley et al. 1998, in review; Forward et al. 2003a, b; Carr et al.

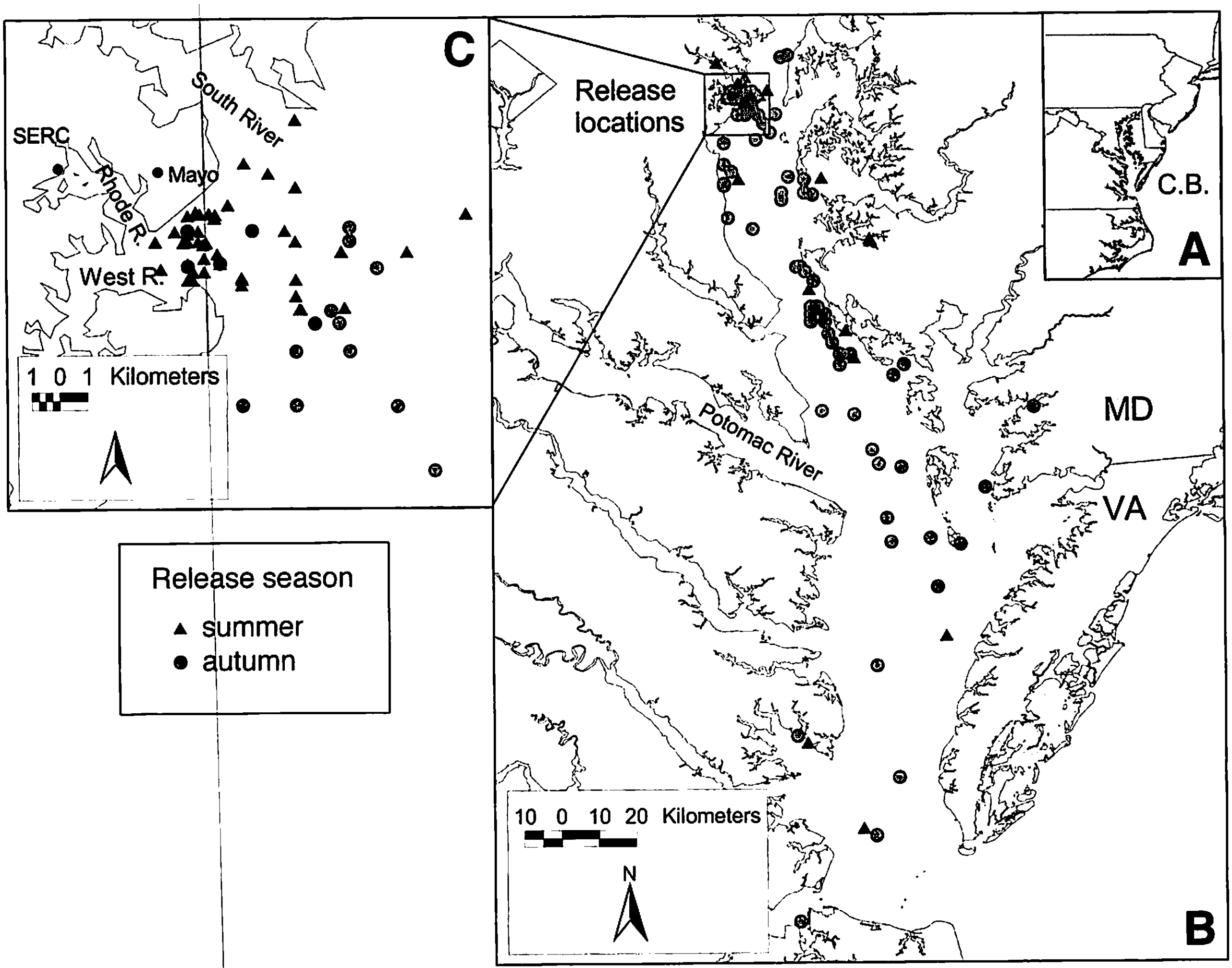

Figure 8. Locations of tagged female crabs recaptured by fishers. Crabs were tagged and released in summer and fall off the mouth of the Rhode River subestuary. Recapture sites indicate that migration occurs during fall and that the migration route follows the eastern side of the deep channel of the mainstem of the estuary. From Aguilar et al. (2005). CB = Chesapeake Bay; MD = Maryland; SERC = Smithsonian Environmental Research Center; VA = Virginia.

2004; Forward and Cohen 2004; Ziegler et al. in review). After their eggs hatch, some females reverse their tidal-stream transport on flooding tides to move back into the lower estuary, where they may produce subsequent broods (R.A. Tankersley, Biology, Florida Institute of Technology, pers. comm.; Tankersley et al., in review). Other females may remain outside the estuary (D. Ritschoff, Duke University Marine Laboratory, pers. comm.), which may account for some of them moving to neighboring estuaries. However, mature females do not move back to lower salinity zones of estuaries (Fischler 1965; Hines et al. 1987, 1990). For very large estuaries like Chesapeake Bay and Delaware Bay, female spawning migration out of the mouth of the bays is not well documented or understood. For example, Prager (1996) assumed that females had a mean residence time of 4 to 21 d in the spawning area of Chesapeake Bay, but there are no empirical measures of this, and other studies indicate that mature females remain in the lower Bay spawning sanctuary throughout the summer (Hoenig et al. 2003; Lipcius et al. 2003). For Chesapeake Bay during the summer, peak abundances of egg-bearing females move progresssively from northern to southern portions of the lower bay spawning area, but there is little evidence of females migrating out of the mouth of the bay proper (Lipcius et al. 2003). In Delaware Bay, which has a large, progressively widening mouth, spawning females occurring over a broad area of the mouth may move out onto the shelf as well (C. Epifanio, University of Delaware College of Marine Studies, Lewes, pers. comm.).

DIET AND FORAGING

Diet

General

Blue crabs are epibenthic generalist predators that forage on a diversity of sessile infaunal and epibenthic invertebrates and on motile fish and crustaceans, as well as feeding omnivorously on plant material, detritus and scavenged carrion (Darnell 1958;Tagatz 1968a; Odum and Heald 1972; Laughlin 1982; Alexander 1986; Ryer 1987; Hines et al. 1990; Hsueh et al. 1992a; Mansour 1992; Meise and Stehlik 2003; Stehlik et al. 2004) (Fig. 9). The diet of blue crabs can be assessed by observations of feeding and behavior (e.g., Hughes and Seed 1981; Moody 1994), but the murky water of estuarine habitats often makes this impossible. Although food items are typically disassembled by the chelae, maxillipeds, and mandibles during feeding, identification of recently consumed stomach contents is readily possible if foreguts are preserved in the field before the gastric mill pulverizes identifiable chunks of food (e.g., Laughlin 1982; Hines et al. 1990; Mansour 1992). However, variation among food items in digestibility, gut clearance time, and regurgitation (e.g., of shell fragments) may affect this approach (e.g., see Custer 1985; Haefner 1990b). Tests of foregut clearance rates for three types of prey (mussel, fish, shrimp) indicate that contents should be sampled within 2 h of feeding (Custer 1985). Some researchers advocate adjusting diet composition to give more weight to crabs with fuller stomachs than nearly empty stomachs, and some studies quantify diet by presence-absence of items to quantify the frequency of individuals in a sample that includes food items (e.g., Hines et al. 1990; Stoner and Buchanan 1990; Mansour 1992). Others studies do not make such adjustments, or they use weights of stomach contents to assess dietary importance (e.g., Laughlin 1982). In any case, analysis of stomach contents allows reasonably accurate quantification of diet for crabs from a full array of habitats, with or without direct observation of feeding.

As reflected by stomach contents and other feeding observations (Table 1), blue crab diet includes at least 99 species from several phyla, especially molluscs (typically 20-40% of stomach content weight or volume), arthropods (10-26%), chordates (fishes; 5-12%) and annelids (polychaetes; 1-7%). Stomach contents also often include detritus and unidentified, partially digested matter, as well as sediment that may be ingested incidentally. Juvenile blue crabs have the digestive enzymes to utilize plant detritus, but the importance of such low quality food is not evident for blue crabs except, perhaps, when restricted to certain refuge habitats (McClintock et al. 1991). Xanthid crabs, blue crabs themselves, and fish are important secondary components of the diet. In a trophic web analysis of Chesapeake Bay (Baird and Ulanowicz 1989), the diet of blue crabs was described as consisting of about 60% bivalve molluscs, with the remainder comprising polychaetes, amphipods, dead fish, and juvenile blue crabs (Darnell 1958; Tagatz 1968a; Virnstein 1977; Nelson 1981; Paul 1981). Although blue crabs certainly exhibit a broad diet, quantitative studies show that bivalve molluscs are dominant prey that consistently comprise the largest volume or weight of juvenile and adult diet in many habitats (Laughlin 1982; Hines et al. 1990; Eggleston et al. 1992; Mansour 1992; Meise and Stehlik 2003). Importantly, however, the diet of blue crabs exhibits significant ontogenetic, temporal, and spatial variation.

Because they are readily attracted by baits that release oily chemical plumes (e.g., Atlantic menhaden *Brevoortia tyrannus* and other alosid fish, American eel *Anguilla rostrata*, and various shellfish), blue crabs are often considered to be primarily scavengers and predators on the species used by fisheries in traps or trotlines. However, stomach contents of crabs sampled by methods independent of baits (e.g.,

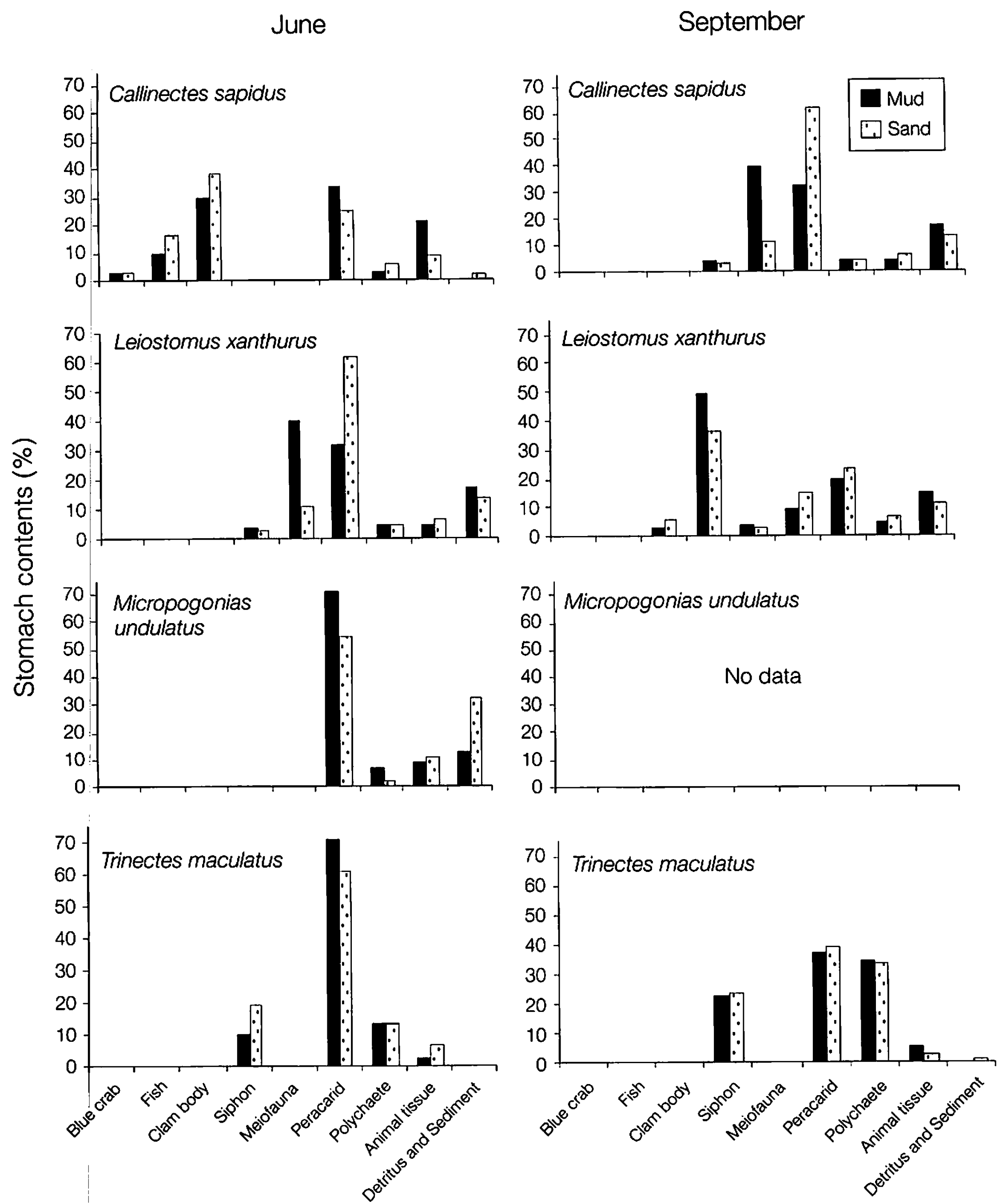

Figure 9. Diet of blue crabs and three species of common demersal fish (*Leistomus xanthurus*, *Micropogonias undulatus*, *Trinectes maculatus*) that comprise the guild of epibenthic predators in upper Chesapeake Bay. Composition of stomachs weighted by stomach fullness for nine food categories are shown for crabs and fish collected with otter trawls on muddy and sandy sediments in early (June) and late (September) season. Note that blue crab diet is more diverse in June than September, with an increasing specialization from June to September on clams, which comprise 60% of their diet. From Hines et al. (1990).

Table 1. Prey items fed on by, or found in stomachs of, juvenile and adult blue crabs.

Prey Species	References
Foraminifera	Fitz & Wiegert (1991b), Laughlin (1982), Ropes (1989)
Porifera	Mansour (1992)
Cnidarians	
hydroids	Mansour (1992)
Actinaria	Mansour (1992)
Polychaeta	Fitz & Wiegert (1991b), Laughlin (1982), Ropes (1989)
Glycera sp.	Mansour (1992)
Laeonereis culveri	Hines et al. (1990), Laughlin (1982)
Nereis spp.	Hines et al. (1990), Mansour (1992), Ropes (1989)
Nereis succinea	Hines et al. (1990), Laughlin (1982)
Pectinaria sp.	Mansour (1992)
Mollusca	Darnell (1958, 1961), Eggleston (1990a,b,c), Menzel & Hopkins (1956), Tagatz (1968a)
Bivalvia	Laughlin (1982), Ropes (1989)
Anadara sp.	Mansour (1992), Orth et al. (1984)
Argopecten irradians	Irlandi et al. (1995)
Brachidontes exustus	Custer (1985)
Brachidontes sp.	Laughlin (1982)
Crassostrea virginica	Abbe & Breitburg (1992), Carriker (1951), Eggleston (1990a,b,c), Krantz & Chamberlin (1978), Laughlin (1982), Lunz (1947), Mansour (1992), Marshall (1954), Menzel & Nichy (1958), Micheli & Peterson (1999)
Dreissena polymorpha	Boles & Lipcius (1997)
Gemma gemma	Ropes (1989)
Geukensia demissa	Hughes & Seed (1981), Irlandi et al. (1995), Laughlin (1982), Lin (1989, 1991), Seed (1982)
Ischadium recurvum	Ebersole & Kennedy (1995)
Macoma balthica	Hines et al. (1990), Mansour (1992), Mansour & Lipcius (1991, 1993)
Macoma mitchelli	Hines et al. (1990), Mansour (1992), Mansour & Lipcius (1991, 1993)
Macoma spp.	Laughlin (1982), Mansour (1992), Mansour & Lipcius (1991, 1993)
Mactra sp.	Laughlin (1982)
Mercenaria mercenaria	Arnold (1984), Carriker (1951), Irlandi (1994), Micheli (1997a,b), Micheli & Peterson (1999), Ropes (1989), van Engel (1958)
Mulinia lateralis	Mansour (1992), Orth et al. (1984)
mussels	Lin (1991), Mansour (1992)
Mya arenaria	Ebersole & Kennedy (1995), Hines et al. (1990), Mansour (1992), Mansour & Lipcius (1991, 1993), Ropes (1989)
Mytilus edulis	Ropes (1989)
Ostrea sp.	Lunz (1947)
Rangia cuneata	Ebersole & Kennedy (1995), Laughlin (1982)
Tellina sp.	Laughlin (1982)
Gastropoda	Eggleston (1990a,b), Laughlin (1982)
Astyris lunata	Cote et al. (2001)
Bittium sp.	Laughlin (1982)
Bittium varium; Billiolum varium	Cote et al. (2001), Mansour (1992), Wright et al. (1996)

Table 1, continued.

Prey Species	References
Gastropoda, continued	
Cephalaspidea	Mansour (1992)
Hydrobia sp.	Ropes (1989)
Ilyanassa (Nassarius) obsoleta	Tagatz (1968a)
Littoraria irrorata	Hamilton (1976), Heard (1982), Seed (1982)
Littoraria littorea	Heard (1982), Laughlin (1982)
Melampus coffeus	Darnell (1958, 1961)
Mitrella lunata	Mansour (1992), Martin et al. (1989)
Neritina virginea	Darnell (1958, 1961)
Neritina reclivata	Laughlin (1982)
Odostomia sp.	Krantz & Chamberlin (1978)
Pyramidellidae	Mansour (1992)
Crustacea	
Ampelisca sp.	Martin et al. (1989)
Amphipoda	Hines et al. (1990), Laughlin (1982), Mansour (1992), Ropes (1989)
brachyuran larvae	Fitz & Wiegert (1991b)
Callinectes sapidus	Heck & Spitzer (2001), Hines & Ruiz (1995), Laughlin (1982), Moksnes et al. (1997), Orth et al. (1984), Peery (1989), Ryer et al. (1997)
Cirripedia	Laughlin (1982), Mansour (1992), Ropes (1989)
Clibinarius sp.	Laughlin (1982)
Copepoda	Fitz & Wiegert (1991b)
Corophium sp.	Laughlin (1982)
crabs	Ropes(1989)
Gammarus sp.	Laughlin (1982)
hermit crabs	Laughlin (1982)
Isopoda	Hines et al. (1990), Laughlin (1982), Mansour (1992)
majid crabs	Mansour (1992)
Mysidacea	Laughlin (1982)
Mysidopsis sp.	Laughlin (1982)
Neopanope sp.	Laughlin (1982), Mansour & Lipcius (1993)
Ostracoda	Fitz & Wiegert (1991b), Laughlin (1982)
Palaemonetes sp.	Laughlin (1982)
Palaemonidae	Fitz & Wiegert (1991b)
Penaeidae	Fitz & Wiegert (1991b)
Penaeus duorarum	Custer (1985)
Penaeus sp.	Laughlin (1982)
Peracaridea	Fitz & Wiegert (1991b)
Rhithropanopeus harrisii	Hines et al. (1990)
shrimp	Laughlin (1982), Mansour & Lipcius (1993)
Uca spp.	Fitz & Wiegert (1991b), Heard (1982), Hughes & Seed (1995)
Xanthidae	Fitz & Wiegert (1991b), Heard (1982), Hines et al. (1990), Hughes & Seed (1995), Laughlin (1982), Mansour (1992)
Insecta	
Chironomidae (larvae)	Hines et al. (1990), Laughlin (1982), Mansour (1992)
Coleoptera	Tagatz (1968a)
Dicrontendipes	Tagatz (1968a)
Diptera	Tagatz (1968a)
Hemiptera	Tagatz (1968a)

Table 1, continued.

Prey Species	References
Insecta, continued	
Hymenoptera	Tagatz (1968a)
Odonata	Tagatz (1968a)
Bryozoa	Mansour (1992)
Echinodermata	
Ophiuroidea	Mansour (1992)
Ascidiacea	Mansour (1992)
Molgula manhattensis	Beaven (1956)
Pisces	Fitz & Wiegert (1991b), Hines et al. (1990), Laughlin (1982), Mansour (1992), Ropes (1989)
Anchoa mitchelli	Laughlin (1982), Mansour (1992)
Bairdiella chrysoura	Custer (1985)
Etropus sp.	Laughlin (1982)
Fundulus heteroclitus	Kneib (1982), Martin et al. (1989)
Leiostomus xanthurus	Mansour (1992)
Microgobius sp.	Laughlin (1982)
Micropogonias undulatus	Laughlin (1982)
Trinectes maculatus	Laughlin (1982), Mansour (1992)
Aves	
duck	Milne (1965)
Plant material	Hines et al. (1990), Laughlin (1982), Ropes (1989)
algae	Ropes (1989)
Spartina sp.	Fitz & Wiegert (1991b), Ropes (1989)
submerged aquatic vegetation	Laughlin (1982)
Detritus	Hines et al. (1990), Laughlin (1982)

by trawling) reflect their natural diet (e.g., Laughlin 1982; Hines et al. 1990; Mansour 1992), which does not frequently include these bait items. Blue crabs scavenge many species in the by-catch of near-shore fisheries, including many species of fish and decapod crustaceans, but these food resources are clearly enhanced by human activities.

Ontogenetic Variation in Diet

Blue crab diet changes during ontogeny, with juveniles feeding on smaller, more diverse epibiota and infauna of shallow sediments, and large adults feeding on larger, less diverse, epifauna and often on more deeply buried infauna (Laughlin 1982; Stoner and Buchanan 1990; Mansour 1992). Although Tagatz (1968a) reported that all sizes of crabs ate the same food types, the preponderance of evidence indicates that as crabs grow larger than about 70 mm CW, their diet becomes more focused on bivalve molluscs, particularly infaunal clams. For example, Laughlin (1982) found that bivalves increased in stomach contents from about 24% in small juveniles

(<31 mm) to 39% in large crabs (>60 mm) in Apalachicola Bay, Florida. In upper Chesapeake Bay, small infaunal Baltic macoma comprised more than 60% of the diet of large crabs (Hines et al. 1990). Where or when bivalve prey are not common, fish, shrimp, gastropods, and crabs become important for larger blue crabs. Plant material is common in the stomach contents (10-12%) of small (<60 mm) blue crabs in seagrass habitat, but much less so for large (>60 mm) crabs. The diet of small blue crabs rarely includes other blue crabs, whereas they are a significant dietary component (10-15%) of larger blue crabs (Laughlin 1982; Hines et al. 1990). Diets of all sizes of juvenile to adult blue crabs commonly include xanthid crabs (Laughlin 1982; Mansour 1992). Large blue crabs evidently are also capable of capturing several species of estuarine fishes (5-15% of stomach contents), although small juveniles typically do not (Laughlin 1982; Hines et al 1990; Mansour 1992). In Puerto Rico at a site where bivalves were uncommon, variation in the diet of *C. sapidus* clustered into four crab size classes (10-20 mm, 21-30 mm, 31-80 mm, 81-150 mm CW) (Stoner and Buchanan 1990). Stomachs of small crabs included mainly amphipods, foraminiferans, polychaetes, and detritus, whereas larger crabs ate more fish, crabs, and bivalves (Stoner and Buchanan 1990). Thus, the diet diversity of blue crabs tends to decrease during ontogeny, with stomach contents of small blue crabs including more species of smaller prey and larger crab stomachs including fewer species but with increasing composition of bivalves, juvenile blue crabs, and fish.

Temporal Variation in Diet

Blue crab diet shows temporal variation on several time scales. Although blue crabs feed throughout the diel cycle (see Foraging Behavior and Activity below), diet composition generally does not exhibit significant diurnal-nocturnal variation (Laughlin 1982; Ryer 1987; Hines, unpubl. data) Diet may vary temporally with tidal fluctuations that provide blue crabs with access to prey species of intertidal habitats like salt marshes, mangroves, ribbed mussel *Geukensia demissa* beds, and sand flats (Ryer 1987; Lin 1989; Fitz and Wiegert 1991b; pers. obs.). Blue crabs readily move into intertidal habitats to forage on ribbed mussels, and their foraging success may be limited by duration of high tide and distance needed to travel to reach prey from the subtidal zone (Lin 1989). Conversely, motile species that also forage or seek refuge in the intertidal habitats may become more important in the diet of blue crabs on low tide as both prey and blue crabs become concentrated in shallow subtidal habitat. In areas like upper Chesapeake Bay where tidal amplitudes are small and intertidal habitats are not used by blue crabs, tidal variation in diet may be concomitantly small (pers. obs.).

Over longer time periods, blue crab diet shows significant seasonal variation, probably reflecting changing prey availability through seasonal recruitment and depletion (Laughlin 1982; Hines et al. 1990; Meise and Stehlik 2003). In Apalachicola Bay, Florida, molluscs comprised a greater portion of blue crab diet in winter-spring than in summer-fall, especially in small crabs that fed on small, shallowly buried bivalves (Laughlin 1982). In upper Chesapeake Bay, infaunal bivalves and juvenile blue crabs formed a greater portion of the diet of large blue crabs in late summer to early fall, as the abundance of surface-dwelling infauna declined markedly with increasing predator activity in the early season (Hines et al. 1990). Mansour (1992) found significant annual variation in blue crab diet in Chesapeake Bay (two-fold difference among years in some prey items such as cannibalized crabs), reflecting variation in prey availability because ontogenetic shifts in diet were similar among years. Similar large annual variation in diet was found in New Jersey salt marsh systems (Meise and Stehlik 2003).

Spatial Variation in Diet

Because blue crabs forage opportunistically over large spatial extent, diet may vary along with prey species available in diverse habitats. Diet varied significantly among sites within Apalachicola Bay (Laughlin 1982) and Chesapeake Bay (Mansour 1992), and among estuarine systems (e.g., Tagatz 1968a; Heard 1982; Laughlin 1982; Hines et al.

1990; Stoner and Buchanan 1990; Mansour 1992; Meise and Stehlik 2003; Stehlik et al. 2004). For example, whereas molluscs form the main part of the diet in most estuaries, xanthid crabs formed a large part of the diet in the Hudson-Ruritan estuary (Stehlik et al. 2004) and in some locations and times in Chesapeake Bay (Mansour 1992). On the other hand, broad categories of the diet of blue crabs remain similar across the full latitudinal range of the species (e.g., Tagatz 1968a; Laughlin 1982; Hines et al. 1990; Stoner and Buchanan 1990; Mansour; 1992; Cesar et al. 2003; Meise and Stehlik 2003; Stehlik et al. 2004). Although bivalves appear to be important in the diet in most areas (Menzel and Hopkins 1956; Darnell 1958; Tagatz 1968a; Alexander 1986; Hines et al. 1990; Mansour 1992; Meise and Stehlik 2003; Stehlik et al. 2004), the species of bivalves shift among habitats to include eastern oysters in oyster reefs (Eggleston 1990a, b, c), ribbed mussels in salt marshes (Lin 1989), and infaunal Baltic macoma and soft clam *Mya arenaria* in subtidal soft-bottom habitats (Hines et al. 1990; Mansour 1992). Many food items are taken opportunistically as they are encountered by crabs moving among habitats. For example, in salt marshes fiddler crabs (*Uca* spp.) and periwinkles *(Littoraria* spp.*)* are important components of the diet (Heard 1982). Plant material is common in stomach contents of blue crabs associated with seagrass beds *(Halodule wrightii, Ruppia maritima*) (Darnell 1958; Tagatz 1968a; Laughlin 1982; Alexander 1986) and salt marshes *(Spartina* spp.*)* (Alexander 1986), whereas plant material in stomachs is almost absent in estuarine habitats lacking plants (Hines et al. 1990). Juvenile blue crabs may use structured habitats like seagrasses because those habitats provide diverse and abundant food resources, as well as refuge from predation (Laughlin 1982; Thomas et al. 1990; Perkins-Visser et al. 1996). Seagrass habitats provide abundant infaunal and epifaunal prey in the root-rhizome and canopy regions, as well as detritus (Heck and Orth 1980a; Orth et al. 1984; Mansour 1992).

Interspecific Variation in Diet

The diets of other species of *Callinectes* appear to be similar to *C. sapidus* and to show similar ontogenetic and spatial variation (Paul 1981; Haefner 1990a; Stoner and Buchanan 1990; Hsueh et al. 1992a). In diets of *C. arcuatus* and *C. toxotes* on the Pacific coast of Central America, plant material and detritus decreased with increasing crab size whereas shrimp, fish, and bivalves increased (Paul 1981). The diet of *C. toxotes* appears to be more carnivorous and less varied than that of *C. arcuatus* (Paul 1981). In Mobile Bay, Alabama, fish, bivalves, brachyuran crabs, and gastropods comprised 85% of the diet of *C. similis* and 91% of the diet of *C. sapidus* (Hsueh et al. 1992a). In a comparative study of diet ontogeny in four species of *Callinectes* in Puerto Rico (Stoner and Buchanan 1990), *C. danae* showed the least varied diet, which was relatively low in detritus and higher in mostly large motile prey. For *C. danae*, crabs (mostly hermit crabs) were most important in the diet of small individuals up to 125 mm CW and less important for larger individuals. Fish increased with significant seasonal variation in the stomachs of smaller to larger sizes of *C. danae*, and shrimp importance increased with crab size up to 125 mm but was unimportant in large crabs. In *C. bocourti*, crab remains and detritus decreased as crab size increased, polychaetes were common in smaller crabs, and bivalves were variable but present in all sizes of crabs (Stoner and Buchanan 1990). In *C. ornatus*, detritus and shrimp decreased with crab size, bivalves and gastropods increased with crab size, amphipods were proportionately high in small crabs, and fish and crabs were common in mid-sized crabs (Stoner and Buchanan 1990). By comparison, in *C. ornatus* in Bermuda, stomach contents were dominated (~40%) by cerithiacean gastropod mollusc species (including *Modulus modulus* and two others), with carbonate substrate, plant material, crustaceans, nereid polychaetes, fish, and bivalve molluscs comprising other important components (Haefner 1990b).

Of the *Callinectes* species studied, the diets of *C. bocourti* (Stoner and Buchanan 1990) and *C. similis* (Hsueh et al. 1992a) appear to be most similar to that of *C. sapidus*. This diet similarity may reflect morphological and behavioral similarities, as these species are thought to be most closely related to each other (Norse and Fox-Norse 1982; Williams 1984).

Blue crab diet is similar to that of portunid crabs other than *Callinectes* spp., many of which are predators of soft-bottom habitats and often take molluscs and decapod crustaceans. This similarity is evident in European green crabs *Carcinus maenas* (Ropes 1968, 1989), *Ovalipes* spp. (Caine 1974; Haddon et al. 1987; Sponaugle and Lawton 1990), *Portunus pelagicus* (Williams 1981; deLestang et al. 2000), and *Scylla serrata* (Hill 1976).

Foraging Behavior and Activity

Blue crabs are capable of using visual cues to track and catch prey, particularly faster-moving prey like fishes, fiddler crabs, and other blue crabs. On occasion they have been observed climbing out of water for prey (Abbott 1967), or reaching out of water to capture *Littoraria* spp. snails on emergent salt marsh vegetation (Hamilton 1976). There are several records of crabs cruising along the water's edge of salt mashes with their eyestalks extended out of water like periscopes to track fiddler crabs (*Uca* spp.), and then making quick dashes out of the water to grab their quarry and return to the water to eat (Hughes and Seed 1995; W. Herrnkind, Florida State University, pers. comm.; T. Wolcott, North Carolina State Universtiy, pers. comm.). Prey movement seems to be of paramount importance in attracting the initial attention of the predator (Hughes and Seed 1995; Mascaro et al. 2003), and crabs appear strongly attracted to even slowly moving prey such as snails (Hughes 1989), sometimes resulting in distraction of the crab from items already being handled (Hughes and Seed 1995). The reverse case where visual behavior is modified by chemical cues also may occur (Diaz et al. 1999, 2001). Although the ability to distinguish colors has been attributed to blue crabs, in part based on mating and threat displays, the physiological (optic pigment) basis for this is not established (Bursey 1984), and there is no record of blue crabs using prey color in foraging behavior.

Foraging in blue crabs is typically mediated by chemotactile cues, as their chemo-sensory abilities are very sensitive to trace dilutions of chemicals (Pearson and Olla 1977). Chemical cues modulate feeding behavior in already active crabs rather than initiating foraging from a quiescent state (Zimmer-Faust et al. 1996). Small juveniles (4th-5th instar) exhibit a hierarchy of responses to flow, odors, and visual cues during orientation (Díaz et al. 2003). Larger blue crabs orient well in slow currents and move in a zig-zag pattern back and forth across odor plumes to locate food (Weissburg and Zimmer-Faust 1993, 1994; Zimmer-Faust et al. 1995; 1996; Powers and Kittinger 2002). This orientation to odor plumes is very sensitive to turbulence and current speed (Weissburg and Zimmer-Faust 1993, 1994; Zimmer-Faust et al. 1995; Finelli et al. 1999; Powers and Kittinger 2002; Weissburg et al. 2003). Flow properties and turbulence affect the ability of crabs to orient to odor plumes emanating from actively pumping bivalves (hard clams, bay scallop *Argopecten irradians*), and high flow speed or large sediment particle size increase boundary layer turbulence, thereby decreasing crab success at chemo-orientation. In addition to these boundary layer effects, high flow speed also lessens the probability that crabs contact odor plumes, so that crabs orient best in very slow (<3 cm s^{-1}), smoothly flowing currents and perform poorly in fast currents or no flow.

When they are orienting in odor plumes from distant food, blue crabs use both cephalic and thoracic appendages for olfactory-mediated foraging, and the combination of these may provide elements of redundancy that are valuable when chemical signals are weak or intermittent and also may provide a more three-dimensional perception of the chemical plumes (Keller et al. 2003). For orienting to prey at a distance and in currents, crabs typically use chemo-sensory structures on their antennules, involving antennule flicking and increased pumping of the scaphognathite (Hazlett 1971; Pearson and Olla 1977; Eggleston 1990a; Keller et al. 2003). As they reach the location of prey they use chemotactile receptors on the dactyls of their walking legs (Lipcius and Hines 1986; Eggleston 1990a; Keller et al. 2003). They may probe the sediment with their chelae pointed down and then proceed to excavate prey to sediment depths of 10 to 15 cm (Blundon and Kennedy 1982a, b; Alexander 1986; Lipcius and

Hines 1986). Prey are manipulated with their claws and maxillipeds to allow the mandibles to take bites for ingestion. Once prey are obtained, blue crab claws are capable of exerting large forces to crack and open shells of most bivalves (Blundon and Kennedy 1982a). Although some bivalves (e.g., large Atlantic rangia clams *Rangia cuneata* and hard clams) are armored heavily enough to prevent cracking (Blundon and Kennedy 1982a; Seitz et al. 2001a), some crabs develop handling techniques to chip the edges of shells (a "can-opener" technique) and gain entry to soft tissues of prey (Blundon and Kennedy 1982a; Eggleston 1990a, b; Hughes and Seed 1995). Repeated application of relatively moderate force to an area of molluscan shell creates micro-fractures that eventually cause fatigue failure (Elner 1978; Boulding and LaBarbera 1986).

Wolcott and Hines (1989a) used ultrasonic biotelemetry equipped with electrodes inserted into the origin of blue crab mandibular muscles to transmit muscle action potential during contraction; this allowed the recording of the number of bites used to consume prey items (Fig. 10). The number of bites was positively correlated with prey size, with ~200 bites typically required to consume the small clam *Macoma balthica*. In general, feeding bouts for a variety of prey involved ten to several hundred bites (Nye 1989; Wolcott and Hines 1989a). When consuming prey with a hard exterior (e.g., bivalves), crabs typically had pauses in mandibular bites at the start of a feeding bout as prey were manipulated by the chelae, for example, to open shells; for prey with a hard interior structures (e.g., fish), pauses in biting occurred at the end of the feeding bout when food was most manipulated to tear apart the skull and vertebral column (Nye 1989).

Foraging is markedly affected by the molt cycle. Feeding ceases during late post-molt stages (D_2-D_4), ecdysis (E), and soft post-molt stages (A, early B), but crabs are voracious feeders from late post-molt through early pre-molt stages (late B, C, D_0, D_1). Cessation of feeding around the time of molting allows the soft-crab fishery to hold high densities of premolt crabs without fear of cannibalism while waiting for the crabs to molt to the commercial soft crab stage.

Feeding activity exhibits significant variation on diel, tidal, and seasonal cycles. Although nocturnal feeding activity is often attributed to blue crabs (Warner 1976), sampling crabs on a 24-h cycle for analysis of stomach contents showed only a weak trend for increased feeding at dusk in lower Chesapeake seagrass beds (Ryer 1987). Feeding was related to the tidal cycle in adjacent salt marsh creeks, with crab guts being fullest on high tides. Ultrasonic biotelemetry transmitters equipped with electrodes to record mandibular muscle contractions of free-ranging crabs in upper Chesapeake Bay showed that blue crabs feed in distinct feeding bouts 4 to 7 times throughout the diel cycle, but with significant peaks of feeding during crepuscular times of morning and evening (Nye 1989; Wolcott and Hines 1989a). Similarly, a congener, *C. arcuatus*, fed most actively at night in the laboratory, with a prominent peak at dusk and a lesser peak at dawn (Paul 1981). Insofar as foraging success of blue crabs is related to their use of currents to orient to odor plumes of prey (Weissburg and Zimmer-Faust 1993, 1994; Zimmer-Faust et al. 1995; 1996; Weissburg et al. 2003), tidal currents may produce cycles of foraging. Seasonal cycles of feeding activity are clearly related to temperature because feeding rates decline with low temperatures and appear to cease below 7° to 8°C (pers. obs.).

Predator-Prey Population Interactions, Community Effects, and Food Web Dynamics

Direct Effects of Blue Crab Predation

Covariation of Predator-prey Populations. Foraging of blue crabs has major effects on prey populations and benthic community structure. Negative correlations of predator and prey abundances often reflect these effects. Densities of infaunal prey increase seasonally during winter-spring recruitment and decline markedly as blue crabs and other epibenthic predators become active during warm summer-fall months, especially in high latitude estuaries like Chesapeake Bay (Virnstein 1977, 1979; Holland et al. 1980; Hines et al. 1990). In estuaries at lower latitudes, seasonal effects are less marked but still evident (Livingston 1976; Laughlin 1982). The abundance and habitat use of prey such as eastern oysters may be limited by blue crab predation that can lead to local extinction of oyster spat in Louisiana (Menzel and Hopkins 1956), South Carolina (Lunz 1947), Florida (Marshall 1954), and Chesapeake Bay (Eggleston 1990a, b, c) over a wide range of salinities (Menzel and Hopkins 1956; Carriker 1967). Similarly, blue crab foraging exerts great negative influence on abundance of clams such as wild hard clams (Van Engel 1958; Sponaugle and Lawton 1990), cultured hard clams (Gibbons and Castagna 1985; Kraeuter and Castagna 1985a, b), Atlantic rangia (Darnell 1958), soft clams (Blundon and Kennedy 1982a, b; Eggleston et al. 1992), ribbed mussels (Seed 1980), Baltic macoma (Eggleston et al. 1992; Hines et al. 1990), and bay scallops (Bologna and Heck 1999; Bishop et al. 2005). Blue crab and bivalve prey densities (e.g., Baltic macoma) also may exhibit inverse covariation over longer intervals of several years (Hines et al. 1990).

Blue crabs appear to limit abundances of certain invasive species. Experiments indicate that predation by large blue crabs may limit abundances of young rapa whelks *Rapana venosa*, a species which has been recently introduced in lower Chesapeake Bay (Harding 2003), although the rapa whelk appears to

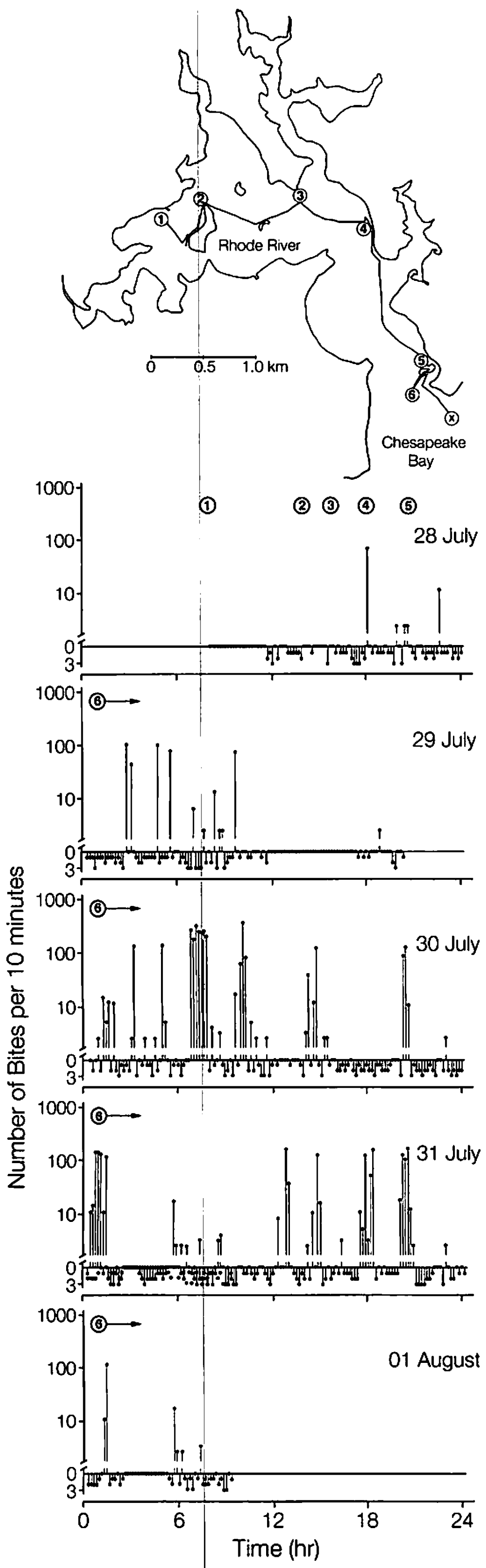

Figure 10. Biotelemetry record of movement and feeding of a large male blue crab in the Rhode River subestuary of Chesapeake Bay in 1986. The crab was equipped with a telemetry tag like that shown in Fig. 6A that transmits mandibular muscle contraction and location. Map at top shows the track of the crab, which was released at position 1 and moved along the numbered sequences over 96 h, spending most of the time feeding at position "6" before being recaptured in a pot at "X." The 4-d feeding record is shown below the map, with circled numbers corresponding to the numbered positions along the track. Lines extending upward from the axis show feeding during feeding bouts at 10-min intervals, with the number of bites presented on a log scale. Lines below the axis represent single, non-feeding bites in each 10-min interval.

be well-established as an invasive species within areas of abundant crabs (Mann and Harding 2000). Blue crabs also appear to limit the geographic distribution of the long-established invasive European green crab along the East Coast of North America (deRivera et al. 2005). Although green crabs extend to lower, warmer latitudes within their native range in the eastern Atlantic, the southern limit of the invasive green crab population along the northwestern Atlantic occurs between Delaware and Chesapeake Bays, where blue crab abundance increases markedly. Moreover, the abundance of green crabs is inversely related to blue crab abundance within bays in the region of overlap of the two species between Cape Cod and Chesapeake Bay. Mortality of green crabs tethered at sites spanning the geographic overlap increased in correlation with abundance of blue crabs, and carapace remains of tethered crabs were indicative of blue crab predation. Tidal amplitude drops dramatically in the vicinity of Chesapeake Bay, which greatly diminishes the intertidal zone that appears to afford green crabs refuge from subtidal blue crab predation. Blue crab predation is predicted to limit the down-stream spread of invasive zebra mussels *Dreissena polymorpha* in the Hudson River estuary (Boles and Lipcius 1997).

Community Structure: Predator Exclusion Studies. Direct effects of predation by blue crabs are readily evident from predator exclusion experiments in soft-bottom habitats, such that infaunal species diversity and density increase markedly within cages placed over patches of the bottom to exclude the suite of blue crabs and other large epibenthic predators (Virnstein 1977, 1979; Holland et al. 1980; Woodin 1981; Hines et al. 1990; Silliman and Bertness 2002). Although unarmored prey species dwelling on or near the surface of sediments are fed on by blue crabs, other decapods, and fishes, blue crabs have a major effect on deeper burying or armored prey (especially bivalves) (Virnstein 1979; Hines et al. 1990; Eggelston et al. 1992; Micheli 1997a, b; Seitz et al. 2001). Note that the horseshoe crab *Limulus polyphemus* and the cow-nose ray *Rhinoptera bonasus* may also feed on the same deeply buried prey in some habitats (Orth 1975; Woodin 1981). Survivorship of infaunal bivalves in habitats dominated by blue crabs increased markedly when these prey were placed in sediment patches protected by cages (Hines et al. 1990; Eggleston et al. 1992; Seitz et al. 2001a; Kuhlmann and Hines 2005). Similarly, experiments excluding wading birds and blue crabs on North Carolina salt marshes showed that predation by blue crabs, not birds, caused major mortality of mummichog *Fundulus heteroclitus*, especially for the largest (>70 mm) fish, which suffered 90% mortality in 24 d (Kneib 1982). These experimental studies show clearly that when crabs and other motile epibenthic predators are excluded in Chesapeake Bay and other locations, the diversity and densities of infaunal species remain high; conversely, predation by blue crabs and other epibenthic predators drastically reduces infaunal prey abundance and diversity. Blue crab predation on infauna thus exerts "top-down" control of benthic communities, although food availability as patches of infaunal prey support higher densities of blue crabs than areas with low food resources (e.g., Seitz and Lipcius 2001). The balance of relative effects of bottom-up control of community structure by nutrients and food resources versus top-down control by blue crab predation may vary in space and time (Posey et al. 1999b; Seitz and Lipcius 2001).

Indirect Effects of Blue Crab Predation

In some soft-bottom communities, responses to experimental manipulation of blue crabs and other large epibenthic predators are more complex, reflecting indirect effects of predation. For example, in Georgia salt marshes experimental manipulation of the dominant grazer the marsh periwinkle *Littoraria irrorata* and its consumers (blue crabs and terrapins *Malaclemys terrapin*) demonstrated that plant biomass and production were largely controlled by the trophic cascade of grazers and their predators, rather than by nutrient supply (Silliman and Bertness 2002). In the absence of the crab and terrapin predators, the periwinkles were able to convert one of the most productive marshes in the world into a barren mudflat within 8 months.

In some ecosystems, however, trophic interactions are more complex and top-down effects of blue crabs and other large predators may be modulated by other species. Predator exclusion experiments in the Indian River Lagoon, Florida, showed that infaunal prey abundance and diversity did not increase in the absence of large blue crabs and fishes (Virnstein 1978). Instead, exclusion of the large predators removed predation on smaller decapods and fishes that function as an intermediate guild of predators on infauna. The small, intermediate predators increased markedly within the cages and continued to maintain the abundance and diversity of infaunal prey at low levels. The relative importance of predation by large blue crabs and fishes compared to that by smaller, intermediate epibenthic and infaunal predators has been sometimes debated with no clear conclusion (e.g., see Virnstein 1978; Ambrose 1984, 1986; Commito and Ambrose 1985a, b; Wilson 1986). However, the regions where the smaller predators appear to have greatest effects compared to blue crab effects appear to be at higher salinities or lower latitude where these smaller predators have high species diversity compared to their diversity in lower salinities and northern estuaries.

Oyster toadfish *Opsanus tau* may limit mud crab and blue crab predation on juvenile hard clams (Flagg and Malouf 1983; Gibbons and Castagna 1985; Bisker and Castagna 1989; Bisker et al. 1989). For example, hard clams in experimental trays with oyster toadfish had nearly 70% survival and the trays contained significantly fewer blue crabs, whereas clams in trays without toadfish had only 2% survival and more blue crabs were present (Bisker and Castagna 1989). However, other experimental tests in cages indicated that oyster toadfish caused only slightly lower blue crab predation upon oysters set on cultch and had no effect on blue crab predation on cultchless oyster spat (Abbe and Breitburg 1992).

Blue crabs may facilitate predation by other species in the community. Using enclosures in a North Carolina Sound, Martin et al. (1989) showed that blue crabs enhanced survival of spot *Leiostomus xanthurus* by removing the algae *Enteromorpha intestinalis*, providing access for the fish to feed upon the invertebrates in bottom sediment. In Mississippi waters, blue crabs have been reported to carry many (1-17) oyster drills *Thais haemastoma* on their backs during their movement within subestuaries and their longer-distance migration along estuaries (Cake 1983). Thus, the crabs transport these important predators of bivalves, snails, and barnacles to various salinity zones and among prey patches.

Blue crabs also cause extensive indirect effects on soft-bottom communities through bioturbation (sedimentary disturbance by animals) by their burrowing activities (Woodin 1981; Hines et al. 1990). Experiments using exclusion cages placed in upper Chesapeake Bay in summer showed that blue crab digging activity thoroughly re-worked patches of dyed surface sediments down to depths of 10 cm (Hines et al. 1990) (Fig. 11). Such bioturbation has major effects on sediment stability and biogeochemistry, which in turn regulates many aspects of infaunal community structure, such as composition of deposit- versus suspension-feeders (e.g., Rhoads and Young 1970; Rhoads 1974).

Blue crab foraging is affected markedly by indirect effects of other predator species in soft-bottom communities. Browsing by epibenthic fishes (especially flatfish and sciaenid species) and shrimp can cause intense siphon nipping of infaunal bivalves (deVlas 1985; Zwarts 1986; Zwarts and Wanink 1989; Kamermans and Huitema 1994; Whitlatch et al. 1997), including infaunal bivalves within the estuarine communities of blue crabs (Hines et al. 1990; Irlandi and Mehlich 1996). Deposit-feeding bivalves with cropped siphons (particularly Baltic macoma) reside nearer to the sediment surface (Hodgson 1982; deVlas 1985; Zwarts 1986; de Goeij et al. 2001) and change their feeding activity (Lin and Hines 1994; Peterson and Skilleter 1994; Skilleter and Peterson 1994). *Macoma balthica*, which comprises much of the diet of blue crabs in many parts of Chesapeake Bay (Hines et al. 1990; Mansour 1992), undergoes a seasonal cycle of burial depth as intense cropping by epibenthic fishes (spot, Atlantic croaker *Micropogonias undulatus*, hogchoker *Trinectes maculatus*) reduces siphon size faster than siphons can regenerate during summer (Hines and Lipcius, in prep.). Clams with partially nipped siphons (<40% intact weight) still tend to reside at refuge burial

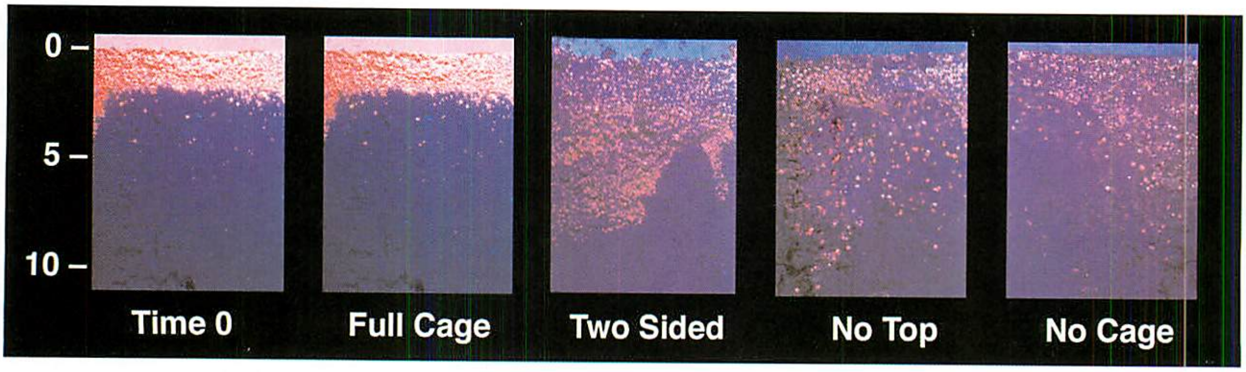

Figure 11. Bioturbation of sediments in the Rhode River subestuary of Chesapeake Bay, Maryland. Vertical profiles traced from representative photographs show sections through patches of dyed sand place on sediment surface in late August (Time 0) and subjected to 4 cage treatments for 2 weeks. Crabs and fish were excluded (full cage) or allowed access to patches in partial cages (2-sided, no top) and uncaged areas. Note extensive bioturbation that extends to a sediment depth of 10 cm, which is the approximate limit of blue crab digging and is much deeper than disturbance by sciaenids and flatfishes. From Hines et al. (1990).

depths >12 cm. However, as cropping increases (>40% removal), the clams move up to sediment depths <12 cm where they become accessible to excavation and predation by blue crabs. Thus, the accumulating non-lethal siphon nipping by epibenthic fishes causes a threshold response in the lethal predation by blue crabs feeding on the clams (Hines and Lipcius, in prep.).

Spatial Variation

Predator exclusion experiments show that effects of predation by blue crabs and epibenthic fishes on prey populations and infaunal community structure are qualitatively similar across several spatial scales, but with significant quantitative variation within subestuaries (Hines et al. 1990), among salinity zones of Chesapeake Bay (Virnstein 1977, 1979; Holland et al. 1980; Hines et al. 1990), and among estuarine systems along the east coast of North America (Virnstein 1978, 1979; Holland et al. 1980; Woodin 1981; Hines et al. 1990). In some habitats, blue crabs are the numerically dominant predators regulating benthic community structure (e.g., upper Chesapeake Bay), whereas in other locations they may be one member of a diverse guild of abundant predators (e.g., Indian River Lagoon, Florida) (Virnstein 1978; Hines et al. 1990).

Blue Crab Responses to Prey Resources

Selection of Individual Prey

Although blue crabs feed upon a wide range of prey, they select prey with certain preferred characteristics that vary by species, size, morphological armor, and passive and active modes of escape. Attributes of the habitat also affect predation success and individual prey selection by blue crabs. Blue crabs and other crab species have been used as good experimental models to test theoretical hypotheses about mechanisms of prey selection by predators. Experimental studies also show that blue crab foraging behavior and selection of individual prey can be conditioned by environmental variables and the crabs' experience (e.g., Seed and Hughes 1997; Terwin 1999).

Prey Species. Blue crab foraging rates in comparative laboratory experiments vary significantly among prey species that differ substantially in their vulnerability to blue crabs, such as large eastern oysters and small hard clams (Bisker and Castagna 1987; Eggleston 1990b); heavy-shelled Atlantic rangia clams and similar-sized thin-shelled soft clams (Ebersole and Kennedy 1995); mobile fiddler crabs

(*Uca* spp.) and sedentary ribbed mussels (Hughes and Seed 1981; Micheli 1997; Seed and Hughes 1997); and deeply buried bivalves (soft clam) and a surface-dwelling species (hooked mussel *Ischadium recurvum*) (Ebersole and Kennedy 1995). In Alabama salt marshes, blue crabs preyed most frequently on epifaunal periwinkles *Littoraria irrorata* and, to a lesser extent, killifish *Fundulus similis*; they rarely selected semi-buried ribbed mussels (West and Williams 1986). However, foraging rates of blue crabs are similar among species that do not differ much in vulnerability, such as small bivalves when they are at or near the sediment surface (Atlantic rangia, hard clams, soft clams, Baltic macoma, ribbed mussels, hooked mussels) (Bisker and Castagna 1987; Sponaugle and Lawton 1990; Eggleston et al. 1992; Ebersole and Kennedy 1995; Seitz et al. 2001a). These differences and similarities suggest that blue crabs respond to various traits that contribute to differences in profitability among prey species, such as costs of capture success and handling time, as well as energetic gains (Seed and Hughes 1997).

Prey Size. Although crabs consume a wide size range of prey, laboratory experiments show that blue crabs exhibit size selection of prey when feeding on various molluscs, including periwinkles (Schindler et al. 1994), hard clams (Arnold 1984; Peterson 1990; Micheli 1995), ribbed mussels (Seed 1980, 1982; Hughes and Seed 1981; Bertness and Grosholz 1985; Lin 1991), Atlantic rangia clams (Ebersole and Kennedy 1994), and eastern oysters (Bisker and Castagna 1987; Eggleston 1990b, c). When offered hard-shelled prey (molluscs), blue crabs and other decapods often select smaller sizes than the predicted optimum (see optimal foraging section below) (Juanes 1992). For example, blue crabs prefer smaller than larger individuals of the ribbed mussel (Hughes and Seed 1981) and the hard clam (Micheli 1995). Blue crabs in the laboratory readily crush very small mussels, and feed on slightly larger mussels by crushing them more slowly across the umbonal region, whereas they open larger mussels gradually by chipping the posterior edges of the shell, severing the adductor muscle, and tearing the valves apart (Hughes and Seed 1981). For each prey species, blue crab foraging is also dependent on relative predator:prey size (Schindler et al. 1994). For some prey such as penaeid shrimp, large crabs are more successful at capturing larger prey; however, prey activity also affects prey capture rates (Mascaro et al. 2003).

Prey Armor. Successful attack on molluscan and other prey species by crabs often depends on the prey's armor (evolution of thick shell with ridges or spines) (Vermeij 1987). Many infaunal prey lack effective armor and are readily attacked by blue crabs (e.g., thin-shelled bivalves such as soft clams, *Macoma* spp.) (Blundon and Kennedy 1982a, b) and must rely on other methods of avoiding or reducing crab predation (see prey escape section below) (Seitz et al. 2001a). Even for species that have evolved armor against predators, shell thickness and armor strength are closely correlated with size, so that juvenile prey become less vulnerable to blue crabs as they grow and attain armor strength that is effective against even large blue crabs (e.g., hard clams, Atlantic rangia clams) (Blundon and Kennedy 1982a, b; Arnold 1984). Other prey increase the crab's handling time through other aspects of morphological barriers to crab manipulation, such as attachment in groups by shell cementation (oysters) (Eggleston 1990b) or by byssal threads (mussels) (Bertness and Grosholz 1985; Lin 1991).

Prey Escape. Mobile prey (fish, other decapod crustaceans) typically escape crab predation by fleeing. Although unsuccessful attacks by blue crabs are not usually documented, autotomy (limb loss) of juveniles often leaves a record of unsuccessful cannibalistic attacks (Smith and Hines 1991a; Dittel et al. 1995; Hines and Ruiz 1995).

Some prey escape blue crabs by moving into refuge habitats either where they are less accessible to blue crabs or where blue crabs are less effective at foraging. Avoiding vulnerability during tidal inundation, some prey (e.g., *Littoraria* spp.) climb emergent vegetation, although blue crabs will reach out of the water to take prey off *Spartina alterniflora* plants (Hamilton 1976; Stanhope et al. 1982; Warren 1985). Similarly, sea scallops *Placopecten magellanicus* attach to seagrasses at levels off the bottom (e.g., Barbeau et al. 1994) where blue crabs may encounter them less frequently than if they remained on the bottom. Other prey position themselves on marsh surfaces where they are less vulnerable to predation by blue crabs. For example, fiddler crabs (*Uca* spp.) hide in burrows on high tide and forage on marsh surfaces on low tides; however, blue crabs sometimes will emerge briefly from marsh creeks on low tide to catch fiddler crabs and take them back into the creek to feed on them (Hughes and Seed 1981; W. Herrnkind, pers. comm.; T. Wolcott, pers. com.). Ribbed mussels in the interior of salt marshes suffer less mortality from blue crab predation than those on the edge of tidal creeks, and those mussels within the interior of mussel clumps are less vulnerable to blue crabs (less accessible to manipulation by crabs) than those on the outside of clumps (Lin 1989, 1991). Escape of juvenile blue crabs from cannibalistic large crabs appears to be more effective in shallow water than in deep water (Hines and Ruiz 1995).

Thin-shelled molluscs and other unarmored infauna escape predation by burying to sediment depths below detection or digging capabilities of blue crabs (Blundon and Kennedy 1982b; Lipcius and Hines 1986; Hines et al. 1990; Seitz et al. 2001; Hines and Lipcius, in prep.). Vulnerability of infaunal bivalves (soft clams, Baltic macoma) to blue crab predation increases markedly at sediment depths shallower than 10 to 12 cm (Blundon and Kennedy 1982b; Hines and Lipcius, in prep.).

Effects of Habitat Characteristics. Vulnerability of infaunal prey to predation by blue crabs is greatly reduced by structure, such as rhizomes of submerged aquatic vegetation (Heck and Thoman 1981; Blundon and Kennedy 1982b), polychaete tubes (Woodin 1981), and by shell rubble within or overlying the sediment (Virnstein 1979; Arnold 1984; Gibbons and Castagna 1985; Kraeuter and Castagna 1985a, b; Sponaugle and Lawton 1990). Rate of blue crab foraging upon infaunal bivalves also differs by sediment type (sand, mud) depending on the prey species (soft clams, Baltic macoma) (Lipcius and Hines 1986; Eggleston et al. 1992; Seitz et al. 2001a). Added structure in the sediment appears to interfere with the crabs' ability to detect the prey with the chemotactile senses of their dactyls, or the crabs' ability to excavate the prey items, or both (Lipcius and Hines 1986; Eggleston et al. 1992). Similarly, blue crab foraging rates are reduced by fronds of submerged aquatic vegetation (Heck and Thoman 1981; Wilson et al. 1990a; Heck and Crowder 1991) and probably by drifting algae (Wilson et al. 1990b).

Hypoxia causes reductions in foraging activity in blue crabs and other predators, which generally move to avoid hypoxic water (Pihl et al. 1991; Bell et al. 2003a) and reduce feeding rates (Das and Stickle 1993; Seitz et al. 2003a). However, foraging in response to hypoxia may depend on complex predator-prey interactions modified by hypoxia. For example, hypoxia may cause infaunal soft clams to decrease their burial depth and extend their siphons, making them more vulnerable to crabs (Taylor and Eggleston 2000). However, agonistic interactions between crabs reduced foraging on these clams (Taylor and Eggleston 2000). Further, blue crab foraging also depends on hydrodynamics and duration of episodic events. Foraging activity of telemetered blue crabs in the field declined slightly when they were exposed to mildly hypoxic water (dissolved oxygen concentrations 2-4 mg L^{-1}) and severe hypoxia (<2 mg L^{-1}), but they continued to feed with dissolved oxygen concentrations as low as 1 mg L^{-1} (Bell et al. 2003b). These crabs reduced their proportion of time spent feeding during hypoxic upwelling conditions, but feeding ceased during the most severe upwelling of very hypoxic water.

Optimal Foraging on Individual Prey: Time Minimizer or Energy Maximizer? Optimal foraging theory hypothesizes that predators select prey with characteristics that maximize their net rate of energy (or biomass) intake, optimizing a balance in energy gained in successful consumption against energy costs of searching for and handling prey (Hughes 1980). The relative importance of some prey characteristics and profitability for blue crab foraging can be tested experimentally by providing crabs with choices in the laboratory and by use of "sham prey" such as dead bivalve shells of various sizes filled with artificial tissues of differing food quality (e.g., Micheli 1995). Certain crab species appear to conform to predictions of their ability to evaluate prey and to choose a diet according to encounter rates with prey of differing values, e.g., *Carcinus maenas* feeding on blue mussels *Mytilus edulis* (Elner and Hughes 1978). Blue crabs also select bivalve prey species with preferences that optimize prey profitability with respect to handling time, prey location, and prey refuge use (Ebersole and Kennedy 1995; Seed and Hughes 1997). Even for very small species of snail *Bittiolum varium* and *Astyris lunata*, blue crabs selected prey that were most profitable (Cote et al. 2001). Blue crabs, however, appear to select individual prey with behavior that simultaneously minimizes time spent handling prey and maximizes net rate of energy intake; smaller mussels that are easily crushed are preferred over larger ones that require significantly more handling time and technique for the crabs to open (Hughes and Seed 1981; Seed and Hughes 1997). Minimizing foraging time has adaptive advantages for blue crabs by reducing risk of exposure to predators and increasing time for other activities (e.g., hiding, searching for mates). The relative importance of time minimization versus energy maximization is not resolved for blue crabs.

At least five models attempt to explain prey size-selection behavior of crabs feeding on hard-shelled molluscs (Hughes and Seed 1995). (1) The chelar-wear model predicts that crabs prefer smaller prey sizes because larger sizes present a risk of chelar damage or wear that would select against future foraging capability (Juanes 1992). This model does not provide a comprehensive explanation of size-selection because intermediate prey sizes are sometimes selected and because sometimes smallest prey are also most profitable. (2) The prey-evaluation model predicts that preferred prey are most profitable, such that crabs appear to evaluate prey for a period of manipulation with chelae or mouth parts before accepting or rejecting an item (Elner and Hughes 1978; Jubb et al. 1983). This model does not provide a mechanistic definition of "evaluation," in that whereas most large prey are actively rejected, small prey may appear to be accidentally dropped and lost, leaving mid-sized prey selected by default. (3) The relative-stimulus model predicts that retention or rejection of prey depends on the strengths of tactile or olfactory stimuli from prey held in the chelae relative to stimuli simultaneously contacted by the pereopods (Jubb et al. 1983). It assumes that simultaneous contacts accumulate, so that several small prey present stronger stimuli than a single large item. Although explaining why theoretically optimally-sized prey are rejected, this model only applies when crabs are in contact with numerous prey at once, such as a clump of mussels or an oyster reef. (4) The mechanical-selection model assumes that crabs have difficulty manipulating small prey and breaking or opening large ones, such that lack of dexterity may cause accidental loss of small items, whereas the long time needed to break large prey may exceed the crab's motivation to persist (Hughes and Seed 1981; Lawton and Hughes 1985; ap Rheinallt 1986). According to this model the crab would select for intermediate prey sizes. (5) The key stimulus model combines features of the mechanical selection and relative-stimulus models to propose that crabs adopt an opportunistic strategy of responding to the strongest stimuli from tactile or visual cues (Hughes and Seed 1995). When using tactile stimuli to forage, crabs attack each sequential item irrespective of size, whereas prey encountered simultaneously may lead to size selection based on competing stimuli. In each case, the attack persists until the crab loses motivation, though damage to the prey acts as a reinforcing stimulus to persist longer (Hogan and Roper 1978; Abby-Kalio 1989; Seed and Hughes 1997). Many aspects of the five models are not mutually exclusive.

Prey Sequestration and "Kleptoparasitism"

In laboratory settings, blue crabs sometimes hold prey for variable periods without eating it promptly (pers. obs.). Also in laboratory conditions, blue crabs sometimes steal food (kleptoparasitism) (Brockman and Barnard 1979) from other crabs, especially when crab densities are high (pers. obs.). However, it is not clear whether prey sequestration and kleptoparasitism occur in field conditions.

Conditioning Modifies Prey Selection. Components of blue crab foraging can be conditioned adaptively with respect to the crabs' experience and traits of both the environment and prey (Seed and Hughes 1997). Blue crabs may adjust their foraging behavior through learned improvement of handling efficiency (e.g., Cunningham 1983). This occurs, not necessarily by modifying technique, but by developing more directed sequences of standard components of attack behavior (Abby-Kalio 1989), which shortens handling time and increases the probability of success within a given persistence time (the time needed to successfully overcome and handle a prey item by repeated attack, e.g., to open a bivalve) (Hughes and Seed 1995). Persistence time is adjusted through experience to local prey quality and availability for both sedentary prey (ribbed mussels) and mobile prey (fiddler crabs) (Hughes and Seed 1995; Seed and Hughes 1997). When offered a choice between two prey species (juvenile hard clams and juvenile eastern oysters) in the laboratory, blue crabs modified their foraging based on previous experience (Micheli 1997a). The crabs consumed more clams than oysters when conditioned on a diet of clams or a mixed diet of clams and oysters than when conditioned on oysters alone; conversely crabs conditioned on oysters ate fewer oysters or clams when tested with single prey diets. Conditioning also significantly affects size selectivity of blue crabs, such that crabs ate larger clams when conditioned with greater proportions of larger clams before feeding trials, whereas they ate smaller clams when conditioned with smaller proportions of small clams (Micheli 1995).

Physiological status of blue crabs, as well as environmental conditions and experience, can modify prey selection by blue crabs. Hunger can broaden their diet (Micheli 1995). Conditioning responses should be considered in experiments with blue crabs. Feeding test crabs with one type of prey, or with prey supplied in a density or other particular circumstance, before starting a trial may affect the outcome of the experiment (Terwin 1999).

Selection of Prey Patches

Although blue crabs and other predators clearly feed on individual prey, their foraging behavior typically responds to prey resources with patchy distributions (Clark et al. 2000). As with most predators, interactions of blue crabs with their patchily distributed prey depend on densities of prey and predators, affecting prey persistence and blue crab distribution in the environment. Other characteristics of prey patch scale (e.g., patch size, distance apart) also affect predator-prey dynamics.

Prey Density: Functional Response and Aggregative Response. Density of prey in a patch affects predator-prey dynamics through the predator's functional response, which describes the predator's per capita feeding rate as a function of prey density (Holling 1959; Hassell 1978). Blue crabs feeding on bivalves in the laboratory exhibit variable functional responses that differ by prey species and habitat type (e.g., sediment, dissolved oxygen conditions), with responses distinguished most readily by considering prey mortality as a proportional rate (percentage) (Lipcius and Hines 1986; Eggleston 1990a, c; Sponaugle and Lawton 1990; Eggleston et al. 1992; Dittel et al. 1995; Taylor and Eggleston 2000; Seitz et al. 2001a). Blue crabs foraging on soft clams (Fig. 12) exhibited an inversely density-dependent (Type II) functional response in mud, in that the percentage of prey consumed by blue crabs increased as prey density declined. When feeding on soft clams in sandy sediments, however, the crabs exhibited a sigmoidal density-dependent (Type III) functional response, such that proportional mortality of prey declined markedly at low densities (Lipcius and Hines 1986). By contrast, blue crabs feeding on Baltic macoma in the laboratory exhibited a sigmoidal density-dependent functional response in both sand and mud (Eggleston et al. 1992). This variation in functional responses implies that blue crabs are capable of driving localized patches of soft clams to extinction in mud, whereas the declining predation at low prey densities should help soft clams to persist in sand, and Baltic macoma to persist in both sand and mud.

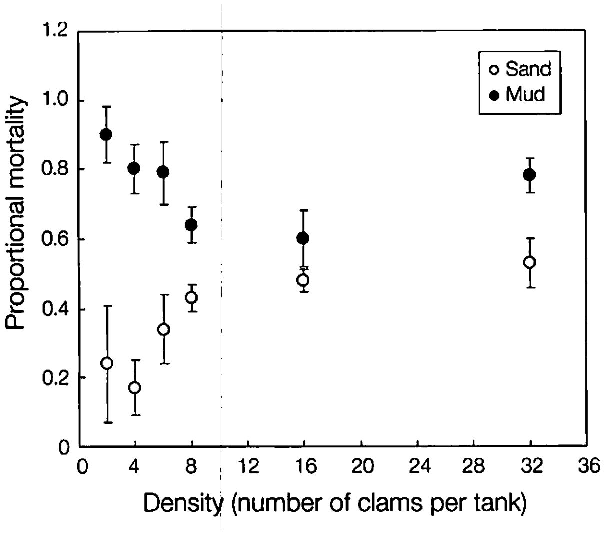

Figure 12. Functional responses of blue crabs foraging on varying densities of soft clams *Mya arenaria*. Foraging rate of crabs depends on prey density and sediment type, as indicated by proportional mortality rates of clams at six densities exposed to crab predation in two sediments in the laboratory. Blue crabs caused increasing proportional mortality of clams in mud and decreasing proportional mortality in sand. Means ± one standard error are indicated. From Lipcius and Hines (1986).

Experimental field tests of varying clam densities in small patches in muddy and in sandy areas confirmed the extinction of soft clams in mud and persistence at low densities of soft clams in sand, and persistence of Baltic macoma in both mud and sand (Seitz et al. 2001a). Moreover, long-term population dynamics of these two prey species in Chesapeake Bay reflect these predicted patterns of localized persistence and extinction (Eggleston et al. 1992; Seitz et al. 2001a). The background densities of prey also regulate the foraging response of blue crabs, as density-dependent mortality of Baltic macoma varied when deployed in small experimental patches placed into areas of differing natural clam densities where crab predation dominated (Kuhlmann and Hines 2005). Density dependence of blue crabs foraging on Baltic macoma was weaker in laboratory treatments with two crabs than with a single crab, and foraging time at low prey densities increased when two crabs were present (Kuhlmann and Hines 2005). Exposure of soft calms to moderately low oxygen levels also caused shifts in blue crab functional response as the bivalves moved up in the sediment and became more vulnerable to crabs (Taylor and Eggleston 2000).

The blue crab functional response while feeding on juvenile eastern oysters varied by sex, with females exhibiting a positively density-dependent (Type III) response and males having an inversely density-dependent (Type II) response (Eggleston 1990a, c). The differences in functional response were due to features of both predator (males have proportionately larger chela height than females) and prey (numbers of oyster spat on the accessible edges of cultch decline at lower density). These behavioral studies indicated that juvenile oysters gradually attain a partial prey refuge at low densities and large shell size before attaining an absolute prey refuge from all blue crabs at ~50 mm shell size.

Cannibalistic large crabs foraging on juvenile crabs exhibited an inversely density-dependent functional response, with juveniles suffering increasing proportional mortality at low densities in the laboratory and in shallow near-shore waters (Dittel et al. 1995). This study used the density-dependent foraging pattern of the crab's functional response to test for the effectiveness of shallow water as a refuge, showing the value of even a partial refuge in reducing intense cannibalism.

Blue crabs adjust their foraging rate in response to previous experience and conditioning by prey densities (Terwin 1999). When provided with Baltic macoma at low prey density in laboratory experiments, blue crabs conditioned at low clam densities foraged more effectively than those conditioned at high clam densities. The functional response of blue crabs (or other such predators) in the context of this shift in foraging efficiency depends on the rate of crabs' learning or conditioning relative to their rate of movement over patches of differing prey density (Terwin 1999).

Predator aggregation as a function of density of prey patches is termed the aggregative response (Holling 1959; Hassell and May 1974; Hassell 1978). Blue crabs clearly aggregate on prey patches (Moody 1994; Clark et al. 1999a, b, 2000; Terwin 1999; Hines and Wolcott, unpubl. data), although the quantitative function of the aggregative response to prey density is not well measured. Biotelemetry of location, feeding, and agonistic displays of blue crabs in Chesapeake Bay shows that blue crabs aggregate on patches of Baltic macoma prey, causing agonistic interactions among crabs to increase markedly at feeding times (Nye 1989; Wolcott and Hines 1989a; Clark et al. 1999a, b, 2000). If agonistic interactions increase sufficiently, blue crabs distribute themselves among prey patches, thus reducing agonistic interactions and increasing foraging efficiency (Clark et al. 2000), perhaps similar to an "ideal free distribution" in which predators are distributed among patches in proportion to prey resources (Kennedy and Gray 1993). The "numerical response," or the population reproductive response to system-wide fluctuations in prey resources (Holling 1959), is not known to hold for blue crabs, due to the complexities of many interacting and confounding factors at such a large scale.

Optimal Foraging on Prey Patches. In addition to tests of feeding on individual prey, blue crab foraging on prey patches has also been studied with innovative tests of optimal foraging theory. When foraging on patchy prey, predators are predicted to optimize their energy intake by selecting the most rewarding patches in which to concentrate their foraging efforts (Hassell and May 1974; Stephens and Krebs 1986). As prey are depleted within a patch, predators foraging optimally must depart to seek a new, more profitable prey patch, based on the predator's knowledge or experience about the environment, "rules of thumb" developed from their past experience, or both combined (Hassell and May 1974; Stephens and Krebs 1986). Predators using knowledge of their surrounding are predicted to abandon a prey patch when prey density falls below the overall mean density (the "marginal value") of the environment (Charnov 1976). Predators that do not have complete knowledge about prey resources are predicted to depart patches according to optimality rules based on the predator's experience of the quality, variability, and distribution of prey patches (Alonso et al. 1995).

Blue crabs equipped with biotelemetry tags provided detailed information about foraging responses to infaunal prey patches (Nye 1989; Wolcott and Hines 1989a, 1996; Bell et al. 2003b). Adult crabs spent more time meandering slowly on patches of higher densities of prey, particularly infaunal Baltic macoma, where they exhibited significantly more feeding activity than where they moved rapidly between prey patches. The crabs typically departed from a prey patch after foraging for hours to a few days, well before the patch exhibited prey depletion. The crabs above may have left an undepleted prey patch as a result of agonistic interactions interfering with feeding (Clark et al. 1999a). In an experimental test of optimal foraging behavior on patchy prey resources, Clark et al. (1999a, 2000) conducted field experiments using blue crabs foraging on small patches of Baltic macoma within large (400 m^2) enclosures in upper Chesapeake Bay. The field enclosures allowed experimental manipulation of the number of blue crabs and the number of clam patches, while telemetry recorded crab location, feeding, and threat displays. The density of blue crabs and the distribution of their prey interacted to affect the foraging behavior and success of the crabs. When only a single clam patch was available, blue crabs at high density interfered with each other's foraging success, such that clam consumption decreased as agonistic encounters increased. However, when clams were provided in two patches, blue crabs at high density dispersed between patches, thus reducing agonistic interactions and increasing foraging rate. The crabs reduced agonistic interactions disproportionately more than the 50% attributable to halving their densities on the patches, and quickly moved off a clam patch when another crab approached. Residence time of crabs on a prey patch was shorter when there were two patches than when there was a single patch, and the crabs divided their foraging time between patches and consuming prey from each patch at a similar rate. As a result, the crabs provided with two prey patches more than doubled their consumption of clams, which is consistent with optimizing behavior rather than more simple opportunistic response to increased prey availability.

Response to Prey Patch Characteristics Other Than Density. Spatial pattern of predators foraging on prey patches is determined by three components of ecological scale: "Grain" (patch size), "Lag" (distance between patches), and "Extent" (distance the predator-prey interaction is manifested). Hines et al. (2003) evaluated these components for blue crabs foraging on Baltic macoma in Chesapeake Bay by using a large grid of benthic cores for estimating spatial variation in clam density, biotelemetry of crab movement and foraging activity, and field experiments testing spatial effects of crab predation effects on clams. Geostatistics of the benthic prey grid showed that the Grain of dense clam patches averaged 200 m diameter, which was similar to what was revealed by biotelemetry data that showed crabs aggregated to feed on 140-m diameter clam patches (Nye 1989; Clark et al. 1999a; Hines and Wolcott, unpubl. data). As fighting among crabs increased with aggregation, the crabs dispersed to new clam patches at a Lag of 0.5 to 5 km. Clam out-planting experiments showed that Lag affected crab foraging efficiency (Terwin 1999; Hines et al., unpubl. data). A Lag distance of 7 m resulted in highest foraging success, apparently as odor plumes from clams dismantled by crab feeding facilitated aggregation of crabs to prey patches. Prey mortality decreased both at shorter Lags as crab agonism increased and at longer Lags as detection of prey odor plumes diminished (Clark et al. 1999b; Hines et al., unpubl. data). The Extent of the blue crab-clam interaction was 50 to 200 km, as deduced from crab stomach contents and similar results of predator exclusion experiments within Chesapeake Bay (Virnstein 1977; Holland et al. 1980; Hines et al. 1990). The Extent of the interaction is modified by addition of competing predator species at high salinity and in more tropical zones (Virnstein 1977, 1978). Predicting blue crab-prey dynamics requires consideration of interactive effects of all three components of scale (Hines et al. 2003).

Habitat location of prey patches affects foraging rates of blue crabs (Leber 1985; Sponaugle and Lawton 1990; Eggleston et al. 1992; Micheli 1996; Seitz et al. 2001). Effects of habitat may vary with season, as shown with field experiments contrasting foraging on experimental hard clams in adjoining intertidal salt marshes and sand flats in North Carolina (Micheli 1996, 1997a). In winter, crabs spent more time in salt marshes than sand flats, and predation rates were highest on clam patches within the edge of salt marshes, where the emergent vegetation provided the crabs some protection from gull predators. In summer when avian predators were rare and abundance of other competing blue crabs increased, crab predation intensity was similar between the two habitats.

Blue crabs selected clam patches depending on conditioning for habitat location of prey (Michelli 1997b). When tested with clams in equal experimental patches in differing habitats, crabs conditioned to feed on clams in salt marsh habitat ate more clams in salt marsh habitat than in sand flat habitat, whereas crabs conditioned to feed in sand flats ate approximately equal numbers of clams in both habitats. Patch preference persisted for more than 24 h between conditioning and testing.

Food Webs for Blue Crabs

Analysis of food web structure using stable isotopes of carbon and nitrogen has provided insight into trophic levels and sources of the food as it passes through the feeding paths for juvenile blue crabs in Delaware Bay ecosystems (Fantle et al. 1999; Dittel et al. 2000). Early juveniles living in the bay habitat fed primarily on zooplankton, whereas marsh-dwelling crabs, which were enriched in ^{13}C relative to bay juveniles, used carbon derived from marsh plants *(Spartina alterniflora).* Nitrogen isotope data suggested that juvenile blue crabs in marsh habitat also fed on primary consumers, such as fiddler crabs (*Uca* spp.) or marsh periwinkles (*Littoraria* spp.)

Two major food web models place blue crabs at a central position of Chesapeake Bay trophic dynamics. In the first, Baird and Ulanowicz (1989) considered blue crabs as the foremost benthic scavenger or predator in Chesapeake Bay and developed a three-season analysis of carbon biomass and flows for a food web model (Fig. 13 depicts the annual carbon standing crop). In their model, average blue crab biomass carbon varied from 500 mg C m^{-2} in

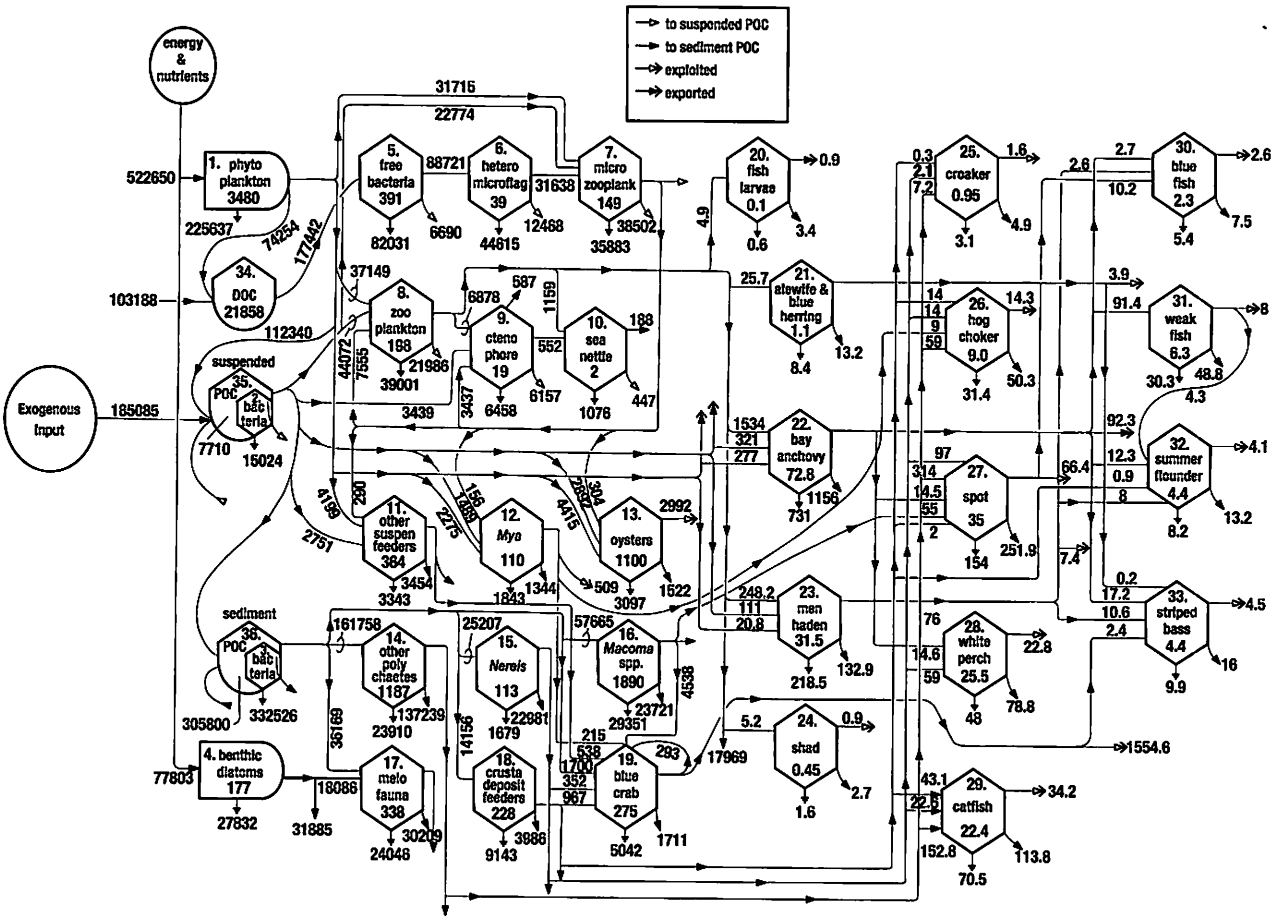

Figure 13. Complex schematic food web of annual carbon standing crops and flows for 36 principal components of the Chesapeake Bay's mesohaline zone. Carbon standing crops are indicated within the compartments in mg m^{-2} and the indicated carbon flows are in mg m^{-2} y^{-1}. Note that blue crabs (bottom center compartment) are major benthic consumers with a standing stock much larger than that of any of the fish species. From Baird and Ulanowicz (1989).

summer to 300 mg C m^{-2} in fall and 100 mg C m^{-2} in winter. They calculated indirect as well as direct trophic dependencies for each of the 36 "model compartments" of the food web, including blue crabs. Blue crabs were ranked at 27 out of a possible 36 in trophic hierarchy, and had an average annual effective trophic level of 3.51 (only behind the trophic levels of top predatory fishes, the highest of which was bluefish *Pomatomus saltatrix* at 4.59), with 71% of their trophic interactions occurring at Level IV, due to essentially no feeding in winter. At this high level, blue crabs contributed carbon only in small quantities to few trophic groups; however, carbon in blue crabs was derived (directly and indirectly) from a varied "extended diet" composed of lower trophic levels, including phytoplankton, sediment bacteria, polychaetes, *Macoma* spp., and particulate organic carbon (Table 2). The indirect carbon flows indicated that the blue crab is at the hub of carbon recycling and transfers for the benthic subsystem of the food web, and accordingly blue crabs were grouped into a "Benthic Deposit Feeder" category that is dominant in a simplified food web for the Chesapeake mesohaline ecosystem. Although rates of carbon flow in the food web model varied greatly on a seasonal basis, the overall structure of the food web did not change much seasonally.

A second model of the Chesapeake food web that emphasizes fishery species also places blue crabs in a central position (NOAA Chesapeake Bay Program, H. Townsend, pers. comm. 2004) (Fig. 14). This food web is constructed using "EcoPath with EcoSim" modeling software. The portion of the food web model that includes the species and trophic groups with direct interactions with adult and young-of-the-year blue crabs (Fig. 14) shows hard clams, soft clams, and eastern oysters as prey species with commercial importance. It lumps all other prey species as "other infauna and epifauna" and "other suspension feeders," and includes "benthic algae" as a food source. This food web illustrates predation by adult blue crabs on juveniles (young-of-the-year), as well as by Atlantic croaker, migratory and resident striped bass *Morone saxatilis*, sandbar shark *Carcharhinus plumbeus*, American eel, "littoral forage fish," and "piscivorous birds."

COMPETITION

Competitive interactions can be difficult to prove because they require demonstration that resources (e.g., food, refuge habitat) both are used simultaneously and are limiting to at least one of the users (i.e., result in displacement or reduced growth, reproduction, or survivorship). Definitive experimental analysis of interspecific competition for blue crabs is limited and some experiments only provide indirect indications of competition. For example, Bisker et al. (1989) reported that oyster toadfish reduced blue crab and xanthid crab predation on juvenile hard clams in field cultures, suggesting that blue crabs and xanthids competed for bivalve prey.

Nevertheless, interspecific competition in blue crabs may be inferred from niche overlap and resource partitioning among other species, especially

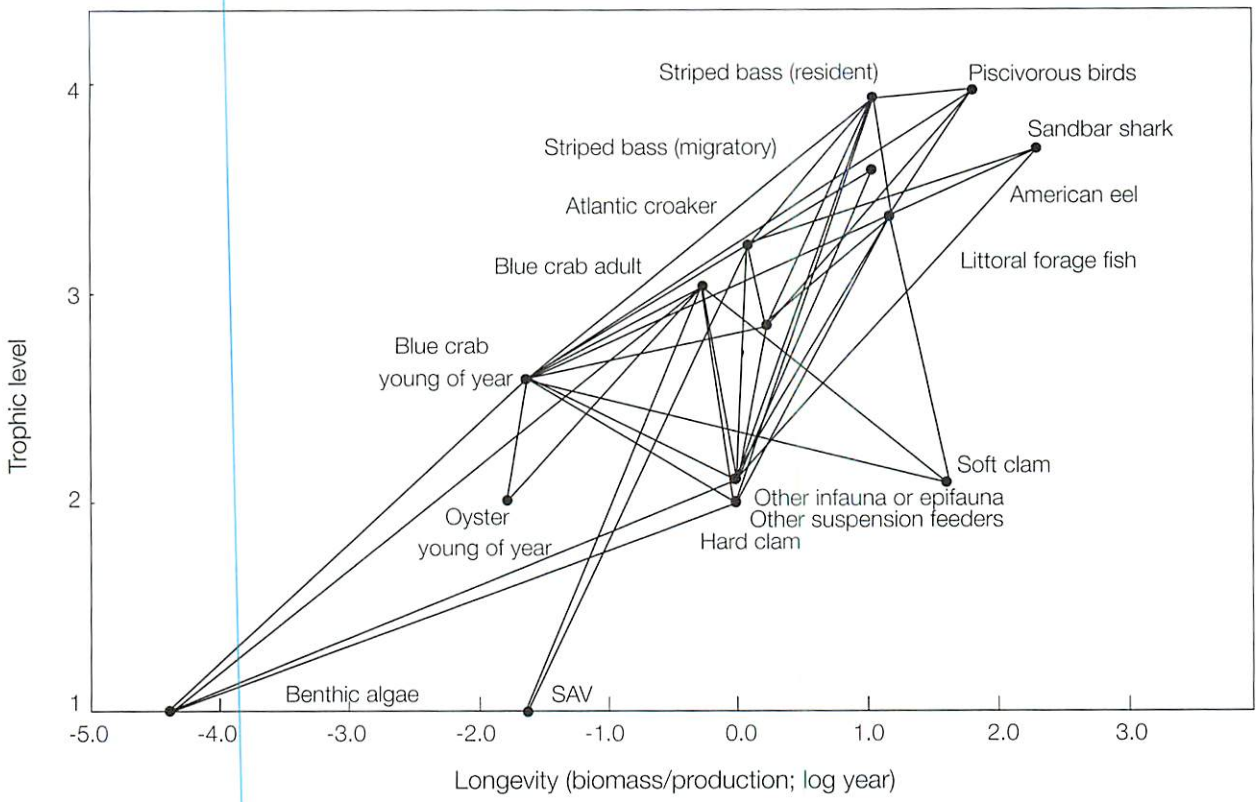

Figure 14. Food web of Chesapeake Bay developed using "EcoPath with EcoSim" modeling software, showing the model segment that focuses on trophic interactions associated with blue crabs. SAV = submerged aquatic vegetation. From NOAA Chesapeake Bay Program.

Table 2. Extended diet of blue crabs in Chesapeake Bay (Baird and Ulanowicz 1989). Because the carbon flow of the diet item passes through several compartments of the food web (see Fig. 13) before it is consumed by blue crabs (or other consumers), the sum of the diet derivation exceeds 100%.

Trophic Category	Diet Derivation (Direct and Indirect) Percent
Phytoplankton	35.2
Bacteria attached to suspended particles	3.2
Sediment bacteria	79.5
Benthic algae	9.1
Free bacteria in water column	6.7
Heterotrophic microflagellates	5.4
Microzooplankton	8.2
Zooplankton	4.9
Ctenophores	1.3
Sea nettles	0.1
Other suspension feeders	7.2
Mya arenaria	2.9
Oysters	0.3
Other polychaetes	22.5
Nereis spp.	8.8
Macoma spp.	56.6
Meiofauna	6.3
Crustacean deposit feeders	12.4
Blue crab	3.8
Bay anchovy	0.3
Dissolved organic carbon	6.7
Suspended particulate carbon	67.4
Sediment particulate organic carbon	90.9
Sum	439.7

if careful attention is given to small-scale spatial and temporal comparisons that are important in niche differentiation. In upper Chesapeake Bay, blue crabs and epibenthic fishes (particularly spot, Atlantic croaker, and hogchoker) comprise a guild of predators that forage on soft-bottom invertebrates during warm months (Hines et al. 1990) (Fig. 9). Diet of large blue crabs exhibited high overlap (54% to 61%) compared with other members of the guild combined, especially in early summer when most species fed on polychaetes and amphipods that were abundant at the sediment surface (Hines et al. 1990). However, diet overlap with individual fish species was only 4% to 36%, depending on type of substrate and time of season (Hines et al. 1990). In other habitats, interspecific competition with blue crabs can be deduced from observations of species with similar habitat use and feeding modes of digging infaunal bivalve prey. Such probable competitors include horseshoe crabs (Woodin 1981) and possibly some benthic-feeding rays and sharks, such as cownose rays (Orth 1977). In oyster and mussel aggregations, blue crabs and xanthid crabs may compete for food resources such as oyster spat and mussels (Galtsoff 1964; Seed 1980; Eggleston 1990a, b). Blue crabs exhibited considerable spatial, dietary, and sometimes temporal overlap with lady crab *Ovalipes ocellatus* and Atlantic rock crab *Cancer irroratus* in the Hudson-Raritan estuary (Stehlik et al. 2004). Blue crabs and lady crabs exhibited the greatest overlap in summer. In the same study, xanthid crabs formed the major diet component of blue crabs (20% by volume), indicating that blue crabs out-compete mud crabs by preying on them (Stehlik et al. 2004).

Clearly, other species of *Callinectes* may exhibit the greatest potential for competitive interactions, although comparative studies remain limited. *Callinectes similis* and *C. sapidus* had high dietary overlap and similar habitat use in Mobile Bay, Alabama, although these resources were partitioned partially by size of crabs (Hsueh et al. 1992a, b). Similarly, *C. sapidus, C. similis,* and *C. ornatus* often overlap in habitat use and diet (with a major bivalve component) in lagoon systems in Florida, Caribbean islands, and Bermuda (Haefner 1990a; Stoner and Buchanan 1990; pers. obs.). In Caribbean estuaries, several species of *Callinectes* appear to have strong potential for competitive interactions and partition the habitat along the salinity gradient based on adult size and aggressive behavior in combination with tolerance of low salinities (Norse 1975, 1977, 1978a, b; Norse and Estevez 1977; Norse and Fox-Norse 1982; Buchanan and Stoner 1988). *Callinectes toxotes* and *C. arcuatus* also interact aggressively and partition the salinity zone of Pacific coast estuaries

(Norse 1978a, b). The outcome of interspecific agonism also depends on body size, such that the species in lower salinities are larger than the high salinity species (Norse 1978b). However, for *C. sapidus*, intraspecific habitat partitioning by size is a bit more complex, with depth zonation as well as salinity zonation (Hines and Ruiz 1995). (Also see Interspecific Variation in Diet above.)

In contrast to the ambiguities of interspecific competition, intraspecific competition seems evident for blue crabs, despite the obviously extensive and fine-grained partitioning of resources by life stages throughout their life cycle. Cannibalism upon juveniles and molting crabs by larger intermolt blue crabs is one important form of intraspecific competition (Ruiz et al. 1993; Dittel et al. 1995; Hines and Ruiz 1995). Laboratory experiments indicate agonistic interference competition among large crabs that reduces their foraging for clams (Mansour and Lipcius 1991; Moody 1994, 2001, 2003). Density-dependent foraging rates on Baltic macoma in the laboratory differed between treatments with one versus two crabs, and the presence of a second crab increased foraging time at low prey densities (Kuhlmann and Hines 2005). Aggressive interactions among competing large crabs also affected their foraging rates on bivalve prey in rigorous field experiments using biotelemetry in upper Chesapeake Bay (Clark et al. 1999a, b, 2000) (Fig. 15). These studies indicated that crabs foraging on small (0.25 m^2) experimental patches of clams were able to detect and respond to other crabs as potential aggressive competitors as far as 5 m away. In large (400 m^2) field enclosures, the frequency of a crab's meral-spread threat displays and movement increased significantly and the per capita foraging rate decreased significantly and disproportionately with increasing blue crab density. Furthermore, distributing prey between two patches instead of one resulted in disproportionately decreased agonistic interactions and increased clam consumption. These experiments all indicate clear intraspecific competition for bivalve prey resources. (See also the next section.)

PREDATORS, CANNIBALISM, AND AGONISTIC INTERACTION

Just as blue crabs are important predators in estuarine food webs, they are subject to predation by many estuarine species, as well as to intense cannibalism. Inter- and intra-specific predators of blue crabs change during the crabs' ontogeny, reflecting shifts in vulnerability to predators and to agonistic interactions as functions of the crabs' size and molt stage, and of their habitat use.

Inter-Specific Predation upon Blue Crabs

A diverse array of at least 101 species have been documented to prey upon blue crabs, including fishes, reptiles, birds, small mammals, some invertebrates, and blue crabs themselves (Table 3). The effect of predation appears to vary greatly among predators (Guillory and Elliot 2001), but there have been surprisingly few quantitative comparisons.

Although several species of invertebrates may eat blue crabs (Table 3), there are almost no quantitative estimates of this predation. Auster and DeGoursey (1994) reported that up to 81% of torpid blue crabs were preyed upon by the seastar *Asterias forbesi* as winter water temperatures dropped below 5°C in Connecticut. Interspecific predation among species of *Callinectes* may be important in regulating the distribution of blue crabs zoned along the salinity gradient of Caribbean estuaries (Norse 1975, 1977, 1978a, b; Norse and Estevez 1977; Norse and Fox-Norse 1982; Buchanan and Stoner 1988; Haefner 1990a; Stoner and Buchanan 1990). However, effects of interspecific invertebrate predators other than *Callinectes* spp. seem to be small.

Consumption of blue crabs by reptiles is poorly quantified, and probably does not produce major population effects. However, alligators *Alligator mississippiensis* may feed heavily on blue crabs in some locations (Valentine et al. 1972), and Kemp's Ridley sea turtles *Lepidochelys kempii* feed exclusively on blue crabs in lower Chesapeake Bay (Van Engel 1987). Sub-adult loggerhead sea turtles

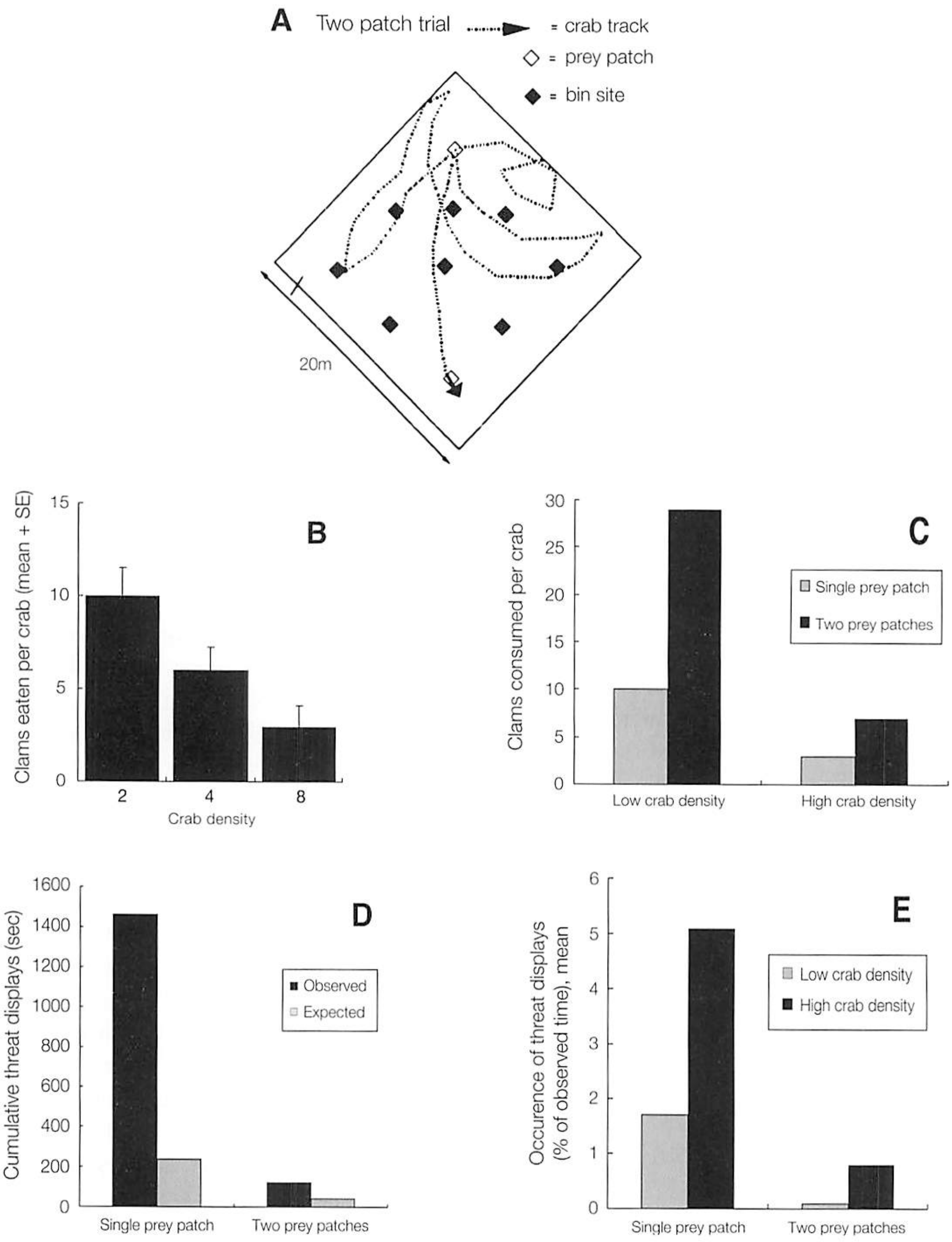

Figure 15. Competitive interference among foraging blue crabs: effect of prey patch distribution and crab density on foraging rate and agonistic interactions of blue crabs in large experimental enclosures. (A) Design of 20 m x 20 m fenced enclosure with a grid of bin sites for small (0.25 m^2) patches of clams *Macoma balthica*, allowing deployment of one or two clam patches as prey for two, four, or eight large male crabs introduced into the enclosure. One of the experimental crabs was fitted with a dual channel biotelemetry tag (see Figs. 5B, 6B), allowing its movement, feeding, and threat displays to be tracked within the enclosure. An example of one track is shown. (B) Per capita consumption of clams declined with increasing crab density. (C) Clam consumption increased at low crab density and especially when clams were provided in two prey patches. (D) Agonism (threat displays) increased markedly when clams were provided in single prey patches. (E) Threat displays also increased markedly at high crab density. From Clark et al. (1999a, 2000).

Table 3. Predator species of juvenile and adult blue crabs.

Predator Species	References
	Crustacea
Callinectes sapidus (blue crab)	Darnell (1958), Heck & Spitzer (2001); Hines & Ruiz (1995) Hovel & Lipcius (2001), Laughlin (1982), Moksnes et al. (1997), Moody (2001, 2003), Peery (1989), Ryer et al. (1997)
Crangon septemspinosa (sand shrimp)	Olmi & Lipcius (1991)
Menippe adina (western gulf stone crab)	Powell & Gunter (1968)
Mithrax spinosissimus (Caribbean king crab)	Winfree & Weinstein (1989)
Palaemonetes pugio (grass shrimp)	Olmi & Lipcius (1991)
	Echinodermata
Asterias forbesi (starfish)	Auster & DeGoursey (1994)
	Pisces
Albula vulpes (bonefish) .	Bruger (1974)
Ancylopsetta quadrocellata (ocellated flounder)	Stickney et al. (1975)
Anguilla rostrata (American eel)	Shirley et al. (1990), Wenner & Musick (1975)
Aplodinotus grunniens (freshwater drum)	Darnell (1958)
Archosargus probatocephalus (sheepshead)	Darnell (1958), Fontenot & Rogillio (1970) in Guillory & Elliot (2001), Gunter (1945), Overstreet & Heard (1982), Overstreet (unpubl.) in Guillory & Elliot (2001)
Arius bonillai (new granada sea catfish)	Norse (1975)
Arius felis (hardhead catfish)	Darnell (1958)
Bagre marinus (gafftopsail catfish)	Gunter (1945)
Bairdiella chrysoura (silver perch)	Brooks et al. (1982), Darnell (1958), Thomas (1971)
Brevoortia tyrannus (Atlantic menaden)	McHugh (1967)
Caranx hippos (crevalle jack)	Overstreet (unpubl.) and Heard (unpubl.) in Steele & Perry (1990)
Carcharhinus leucas (bull shark)	Darnell (1958), Heard (unpubl.) in Steele & Perry (1990, Sadowsky (1971)
Carcharhinus obscurus (dusky shark)	Kemp (1949) in Guillory & Elliot (2001)
Carcharhinus plumbeus (sandbar shark)	Ellis (2003), Medved et al. (1985), Medved & Marshall (1981)
Centropristis philadelphica (rock sea bass)	Brooks et al. (1982)
Centropristis striatus (black sea bass)	Brooks et al. (1982)
Citharichthys spilopterus (bay whiff)	Stickney et al. (1975)
Cynoscion arenarius (sand seatrout)	Krasprzak and Guillory (1984), Overstreet (unpubl.) in Steele & Perry (1990), Overstreet & Heard (1982)
Cynoscion nebulosus (spotted seatrout)	Darnell (1958), Gunter (1945), Overstreet & Heard (1982), Overstreet (unpubl.) in Steele & Perry (1990)
Cynoscion regalis (weakfish)	Brooks et al. (1982), Lascara (1981), Merriner (1975), Thomas (1971)
Dasyatis americanus (southern stingray)	Dahlberg & Heard (1969)
Dasyatis centroura (roughtail stingray)	Hess (1961)
Dasyatis sabina (Atlantic stingray)	Darnell (1958)
Dasyatis sayi (bluntnose stingray)	Heard (unpubl.) in Steele & Perry (1990), Hess (1961)
Elops saurus (ladyfish)	Austin & Austin (1971)
Epinephelus itajara (goliath gouper)	Kemp (1949) in Guillory & Elliot (2001), Pew (1954)
Fundulus diaphanus (banded killifish)	Rogers (1982)

Table 3. continued.

Predator Species	References
	Pisces, continued
Fundulus grandis (gulf killifish)	Levine (1980) in Guillory & Elliot (2001)
Galeocerdo cuvier (tiger shark)	Kemp (1949) in Guillory & Elliot (2001)
Ictalurus catus (white catfish)	Heard (1973) in Guillory & Elliot (2001), Van Engel & Joseph (1968) in Guillory et al. (2001)
Ictalurus furcatus (blue catfish)	Darnell (1958), Lambou (1961)
Ictalurus punctatus (channel catfish)	Menzel (1943)
Lagodon rhomboides (pinfish)	Darnell (1958)
Leiostomus xanthurus (spot)	Brooks et al. (1982), Levine (1980) in Guillory & Elliot (2001)
Lepisosteus oculatus (spotted gar)	Darnell (1958), Goodyear (1967), Lambou (1961)
Lepisosteus osseus (longnose gar)	Stuttkus (1963) in Guillory & Elliot (2001)
Lepisosteus spatula (alligator gar)	Darnell (1958), Lambou (1961)
Lobotes surinamensis (tripletail)	Gunter (1945)
Lutjanus apodus (schoolmaster)	Austin & Austin (1971)
Lutjanus campechanus (red snapper)	Felder (1971)
Lutjanus griseus (gray snapper)	Starck (1971)
Megalops atlanticus (tarpon)	Hildebrand (1963) in Guillory & Elliot (2001)
Menidia beryllina (inland silverside)	Levine (1980) in Guillory (2001)
Micropogonias undulatus (Atlantic croaker)	Darnell (1958), Fontenot & Rogillio (1970) in Guillory & Elliot (2001), Merriner (1975), Orth et al. (1999), Overstreet & Heard (1978a), Stickney et al. (1975), Thomas (1971) in Guillory et al. (2001), van Montfrans (unpubl.) in Dybas (2002)
Micropterus salmoides (largemouth bass)	Darnell (1958), Lambou (1961)
Morone americana (white perch)	Brooks et al. (1982), Lambou (1961)
Morone mississippiensis (aka *M. interrupta*) (yellow bass)	Darnell (1958)
Morone saxatilis (striped bass/rockfish)	Austin (1993), Darnell (1958), Manooch (1973), Orth et al. (1999), Truitt & Vladykov (1937), Tupper & Able (2000), van Montfrans (unpubl.) in Dybas (2002)
Mustelus canis (smooth dogfish)	Bigelow & Schroeder (1953)
Opsanus beta (gulf toadfish)	Heard (unpubl.) in Steele & Perry (1990)
Opsanus tau (oyster toadfish)	Abbe & Breitburg (1992), Bisker et al. (1989), Schwartz & Dutcher (1963)
Paralichthys albigutta (gulf flounder)	Stokes (1977) in Guillory & Elliot (2001)
Paralichthys dentatus (summer flounder)	Manderson et al. (2000), Moody (1994, 2001, 2003)
Paralichthys lethostigma (southern flounder)	Darnell (1958), Overstreet (unpubl.) in Steele & Perry (1990)
Pogonias cromis (black drum)	Fontenot & Rogillio (1970) in Guillory & Elliot (2001), Gunter (1945), Overstreet (unpubl.) in Steele & Perry (1990), Overstreet & Heard (1982), Van Engel & Joseph (1968) in Guillory et al. (2001)
Pomatomus saltatrix (bluefish)	Brooks et al. (1982), Lascara (1981)
Prionitus tribulus (bighead searobin)	Diener et al. (1974)
Rachycentrum canadum (cobia)	Arendt et al. (2001), Meyer & Franks (1996), Overstreet (unpubl.) in Steele & Perry (1990)
Raja eglanteria (clearnose skate)	Hildebrand & Schroeder (1928)
Sciaenops ocellatus (red drum)	Bass & Avault (1975), Boothby & Avault (1971), Darnell (1958), Fontenot & Rogillio (1970) in Guillory & Elliot (2001), Guillory &

Table 3. continued.

Predator Species	References
Pisces, continued	
	Prejean (2001), Gunter (1945), Orth et al. (1999), Overstreet & Heard (1978b), Scharf & Schlicht (2000), Simmons (1957) in Guillory et al. (2001), van Montfrans (unpubl.) in Dybas (2002)
Scomberomorus cavalla (king mackerel)	Hovel & Lipcius (2001)
Sphoeroides maculatus (northern puffer)	Moody (1994, 2001, 2003), Hovel & Lipcius (2001)
Sphoeroides nephelus (southern puffer)	Reid (1954)
Sphyrna tiburo (bonnethead)	Gunter (1945), Hoese & Moore (1958), Woodbury (1986)
Strongylura marina (Atlantic needlefish)	Brooks et al. (1982) in Guillory & Elliot (2001)
Sygnathus fuscus (pipefish)	Ryer (1988)
Tautoga onitis (tautog)	Moody (1994, 2003)
Tylosurus acus (agujon)	Brooks et al. (1982) in Guillory and Elliot (2001)
Urophycis regius (spotted hake)	Sikora & Heard (1972)
Reptilia	
Alligator mississippiensis (American alligator)	Valentine et al. (1972)
Caretta caretta (loggerhead sea turtle)	Van Engel (1987)
Lepidochelys kempii (Atlantic or Kemp's Ridley)	Van Engel (1987)
Aves	
Ardea alba (=*Casmerodius albus*) (great egret)	Bailey (1971) in Guillory & Elliot (2001)
Ardea herodias (great blue heron)	Steele & Perry (1990), Wolcott (pers. comm.) in Micheli (1997b); Hines (unpubl. obs.)
Egretta (=*Florida*) *caerulea* (little blue heron)	Rogers (1982)
Eudocimus albus (=*Guana alba*) (white ibis)	Bildstein (1993), Hammat (1981)
Grus americana (whooping crane)	Hedgpeth (1950), Lewis (1995)
Larus atricilla (laughing gull)	Barass & Kitting (1982), Bass & Avault (1975)
Larus argentatus (herring gull)	Micheli (1997b), Prescott (1990)
Larus delawarensis (ring-billed gull)	Micheli (1997b), Prescott (1990)
Larus spp. (gulls)	Day et al. (1973) in Guillory & Elliot (2001)
Lophodytes cucullatus (hooded merganser)	Steele & Perry (1990)
Mergus merganser americanus (common merganser)	Steele & Perry (1990), Stieglitz (1966)
Nycticorax nycticorax (black-crowned night heron)	Allen (1938)
Nyctanassa violacea (yellow-crowned night-heron)	Watts (1995)
Rallus longirostris (clapper rail)	Bateman (1965), Steele & Perry (1990)
Somateria mollissima (common eider)	Burnett & Snyder (1954)
Sterna spp. (terns)	Barass & Kitting (1982), Micheli (1997b)
Mammalia	
Canis rufus (red wolf)	Guillory & Elliot (2001)
Lutra canadensis (river otter)	Chabreck et al. (1982)
Procyon lotor (raccoon)	Steele & Perry (1990)

Caretta caretta also feed on blue crabs (Van Engel 1987).

Among mammals, racoons *Procyon lotor* and perhaps river otters *Lutra canadensis* and red wolf *Canis rufus* are capable of eating blue crabs opportunistically along estuarine shorelines and marshes (Table 3). Like birds, their effects are probably low as a result of their relatively low densities.

Blue crabs are an important component of the diet of at least 15 species of birds, plus two groups of birds in the genera of gulls (*Larus* spp.) and terns (*Sterna* spp.) (Table 3). The bird species include the great blue heron *Ardea herodias* (Steele and Perry 1990; Hines, unpubl. obs.) and the endangered whooping crane *Grus americana* (Hedgpeth 1950; Lewis 1995). For whooping cranes, habitat quality and food availability are very dependent on the availability of blue crabs in the birds' over-wintering habitats along the coastal marshes of the Gulf of Mexico (Lewis 1995). Some species of wading birds were very numerous historically, and may have imposed important effects on crab abundance; however, recent densities of these avian predators are generally low, so that population effects on blue crabs are probably not large. Other birds (e.g., gulls, rails, mergansers) appear to take blue crabs opportunistically in very shallow water. Seasonal variation in risk of predation by terns and gulls in North Carolina affected foraging behavior and effects of blue crabs on sand flats and salt marshes, although experimental crabs were not consumed by the avian predators (Micheli 1997b).

Predation upon juvenile or adult blue crabs has been documented for 70 species of fish (Table 3) and appears to be significant from the perspective of providing important food resources to many nearshore and estuarine species. Although some of these are records of incidental consumption of blue crabs, blue crabs serve as important prey for several sport and commercial fish species, including several sciaenids (red drum *Sciaenops ocellatus*, Atlantic croaker, black drum *Pogonias cromis*, and spotted sea trout *Cynoscion nebulosus*); sheepshead *Archosargus probatocephalus*; bass (striped bass or rockfish, yellow-bass *Morone interrupta*, largemouth bass *Micropterus salmoides*); flatfish (southern flounder *Paralichthys lethostigma*); cobia *Rachycentron canadum*; American eel; and blue catfish *Ictalurus furcatus*. For cobia in Chesapeake Bay, blue crabs comprised 57%-59% of the diet (Arendt et al. 2001). Along the Gulf Coast, red drum appear to be the important piscine predator, with an average frequency of occurrence of blue crabs in their stomachs of 32% (range: 2%-62%) and a predation index (predator diet weighted by predator abundance) that was 4.8 times greater than the next highest ranked species (Guillory and Elliot 2001; Guillory and Prejean 2001). Other predators in the Gulf of Mexico with diets that were relatively high in blue crab contents included hardhead catfish *Arius felis* (23%), black drum (7%), sheepshead (7%), gafftopsail catfish *Bagre marinus* (7%) and spotted sea trout (5%). It remains unquantified and unclear, however, whether this predation has important effects on blue crab populations along the Gulf Coast.

Cannibalism

Cannibalism by large crabs attacking small crabs, and by hard, intermolt crabs attacking soft molting crabs is a major source of mortality for blue crabs, as mentioned earlier. Analysis of stomach contents shows that crabs comprise significant portions of the diet of large blue crabs (Laughlin 1982; Hines et al. 1990; Mansour 1992). Laboratory experiments provide indications of effects of size, density, and habitat on cannibalism (e.g., Peery 1989; Mansour and Lipcius 1991). Much of the quantitative evidence for cannibalism comes from use of tethering techniques in which crabs are fitted with fishing leader tied or glued to their dorsal carapace and then staked out in particular habitats in the field (Heck and Thoman 1981; Wilson et al. 1987, 1990a, b; Ruiz et al. 1993; Dittel et al. 1995; Hines and Ruiz 1995; Pile et al. 1996). Tethered crabs are free to move within the radius of their tether, and they are checked periodically for injury and survival. Although tethering can cause artifacts and biases about sources of mortality and altered behaviors (Barshaw and Able 1990; Peterson and Black 1994; Zimmer-Faust et al. 1994; Smith 1995), these problems do not appear to be serious for blue crabs as a relative measure of predation rate, especially where cannibalism is the major single source of mortality (Hines and Ruiz 1995). Analysis of the damaged remains of tethered intermolt crabs and of predators caught on tethered crabs indicates that cannibalism rates are high and account for 75 to 97% of mortality in juvenile blue crabs in some estuarine habitats of Chesapeake Bay (Hines and Ruiz 1995). Molting blue crabs also suffer high mortality rates, often attributable to cannibalism, but experimental artifacts of tethering techniques may be more pronounced, because molting crabs must be held in mesh bags to secure them (Shirley et al. 1990; Ryer et al. 1997).

Juvenile intermolt blue crabs tethered in non-vegetated habitats suffered high mortality rates. Rates include 40 to 90% of 30 to 70 mm crabs being killed per day mostly by cannibalism in water >70 cm deep in a central Chesapeake subestuary during summer (Hines and Ruiz 1995); 11 to 45% for 10 to 60 mm crabs in New Jersey (Wilson et al. 1987, 1990a, b; Heck and Coen 1995); 15 to 40% for 12 to 64 mm crabs in New Jersey (Wilson et al. 1990a, b); 25% for 20 mm crabs in lower Chesapeake Bay (Pile et al. 1996); 14 to 86% for 18 to 25 mm crabs in Florida (Heck and Thoman 1981), and 85 to 91% for 5 to 20 mm crabs in Alabama (Heck and Coen 1995). Tethered juvenile blue crabs suffered higher rates of predation by adult blue crabs than did juvenile lady crabs because the blue crabs did not bury as deeply in sediments as did lady crabs (Barshaw and Able 1990).

Relative Effects of Cannibalism versus Inter-Specific Predation on Blue Crabs

Instances of predation by fish markedly reducing blue crab abundance have been quantified only in particular habitats and primarily for early post-settlement juveniles <10 mm CW. In seagrass habitats along the Gulf of Mexico, very intense predation on early post-settlement juvenile blue crabs (<10 mm CW) by pinfish *Lagodon rhomboides*, pipefish (*Sygnathus* spp.), and numerous other species rapidly limits the abundance of juveniles entering these nursery habitats (Heck and Coen 1995; Morgan et al. 1996; Heck et al. 2001; Spitzer et al. 2003). In seagrass habitats of Mobile Bay, Alabama, for example, episodic settlement events did not result in increased juvenile abundance, because cohorts of new recruits were consumed in less than 14 d after settlement, with predation causing as much as 95% mortality d^{-1}, such that juvenile densities rapidly returned to pre-settlement "background" levels (Heck et al. 2001).

In video-taped tethering experiments in lower Chesapeake Bay (Moody 1994, 2003), large blue crabs and several fish species (spot, Atlantic croaker, summer flounder *Paralichthys dentatus*, northern puffer *Sphoeroides maculatus*, hogchoker, and tautog *Tautoga onitis*) made attempts to attack juvenile crabs (10-30 mm CW). Although 84% of attacks by summer flounder and 100% by blue crabs were successful, only 9% of attacks by spot resulted in effective predation. Northern puffers also can be effective predators on blue crabs by foraging synergistically in "gangs." Moody's (1994, 2003) underwater remote videotaping of tethered crabs in the field and laboratory experiments showed that individual puffers distracted adult crabs from the anterior while others attacked from the side or rear to remove legs and then consume the crab body. Attacks by other species in his video records were not successful.

In Chesapeake Bay there is a major controversy about the effect of fish predators in regulating blue crab populations because the abundances of striped bass and perhaps some sciaenid species increased markedly while blue crabs declined coincidentally during the 1990s. This correlation could indicate that fish predation contributed significantly to the decline in blue crab abundance. On the other hand, blue crabs and fish apparently coexisted in abundance before human populations were a factor, and fishery data indicate that much of the decline in blue crabs can be attributed to intense fishing pressure, with up to 70% of the legal population of Chesapeake blue crabs caught each year by humans (Miller and Houde 1998; Sharov et al. 2003).

Nevertheless, evidence for fish predation on blue crabs merits careful consideration. Stomach contents of fish often include blue crabs, but the percentage that blue crabs comprise of fish stomach contents is usually low and only occasionally high (Guillory and Elliot 2001; Guillory and Prejean

2001). Although anecdotal reports from fishermen note instances of striped bass stomachs full of small blue crabs (pers. obs.), Austin and Walter (1998) found that when they analyzed larger (>45 cm) striped bass (N= 2009 fish) collected from fish processing houses and by a variety of fishery-independent sampling gear, blue crabs occurred in only 9.4% of fish with stomach contents. The crabs in these stomach contents averaged 41 mm CW (range 11-150 mm).

Two detailed studies of blue crab consumption by fishes in lower Chesapeake Bay seagrass beds indicate that juvenile blue crabs may be abundant in stomachs of some species, but predation by these fishes probably has relatively small effects on juvenile blue crab populations. In one study, abundance and stomach contents of fish were measured simultaneously over two 12-h periods to estimate predator effect (Orth et al. 1999; van Montfrans cited in Dybas 2002). Gut analysis showed that 100% of red drum had eaten an average of 4.5 juvenile blue crabs, whereas 60.5% of striped bass contained 2.3 crabs and 35.7% of croaker consumed 1.4 crabs on average. The size of blue crabs in the fish stomachs averaged 23 mm for striped bass and 22 mm for red drum. Of the remaining striped bass and croaker that did not consume blue crabs, 14.5% and 39.3%, respectively, had empty stomachs, and 13.2% and 25%, respectively, contained only food items other than crabs. By integrating diet and fish abundance with seagrass aerial cover, predation effects were estimated for the 1.6 billion blue crabs within this habitat as 7.35 x 10^7 crabs (4.6%) by striped bass, 3.06 x 10^5 crabs (0.42%) for croaker, and 1.20 x 10^4 crabs (0.017%) by red drum. However, only one sampling period captured these large numbers of fish feeding upon blue crabs, whereas other sampling did not capture fish. Thus, in combination, fish predators could be estimated as consuming as much as 5% of the local blue crab population per 12 h period, but when averaged over several sampling periods, this percentage would be much lower. In a second, similar study (van Montfrans et al. 2005), overall fish predation on crabs was low, with striped bass having the greatest level of consumption (2.12-3.39% of total crabs available during spring and fall, respectively), followed by Atlantic croaker (0.33% and 0.13% of spring and fall totals, respectively), red drum (<0.00% and 0.13%, respectively) and weakfish (0.18% of fall total only). Thus, although it is clear that blue crabs may be important in the diet of some fish and other vertebrates, and that some species are effective predators on blue crabs, there are few quantitative data demonstrating rigorously that predation by fish or other vertebrates directly regulates blue crab populations at life stages >20 mm CW.

In contrast, in a subestuary of central Chesapeake Bay, tethering experiments over a 16-y period (1989-2005) recorded no instances of fish predation on tethered blue crabs, whereas more than 92% of the mortality was attributed to cannibalism (Ruiz et al. 1993; Dittel et al. 1995; Hines and Ruiz 1995; Hines, unpubl. data). The long-term decline in tether mortality during the decline of crab abundance and the increase in abundance of potential fish predators like striped bass is consistent with the hypothesis that large blue crabs are important predators whereas striped bass are not. Otherwise, increases in the fish predators would have produced higher mortality of juvenile crabs, and tethering studies would have detected frequent incidences of successful predation by fish. Although fish predators attacked juvenile crabs with fractional success at sites in the lower Bay, 100% of video-taped attacks by cannibalistic *C. sapidus* were successful (Moody 1994, 2003). Further, in several habitats (seagrass, salt marsh creek) of lower Chesapeake Bay, cannibalism was the only identifiable source of mortality in experimentally tethered crabs (Ryer et al. 1997), and cannibalized blue crabs in stomach contents of large crabs (>134 mm) in Virginia tributaries reached 45% (Mansour 1992).

Substantial spatial and temporal variation in consumption of blue crabs results from opportunistic foraging by some of the key predatory fishes, as well as by blue crabs themselves (see above section on Diet). For example, the diet of striped bass varied spatially within tidal creeks of New Jersey salt marshes, such that blue crabs comprised a major portion of fish stomach contents, with crabs forming as much as 50% occurrence and 60% of weight of stomachs in one creek and zero occurrence in another creek (Tupper and Able 2000). In upper Chesapeake Bay, the diet of large blue crabs shifts over the summer from only trace occurrence of small crabs in crab stomach contents early in the season to 15%-20% of stomach contents by September when infaunal prey have been depleted (Hines et al. 1990). Thus, both fish predation and crab cannibalism appear to be important sources of mortality for blue crabs.

The scale of studies on predator effects has yet to be expanded. Cannibalism by large blue crabs upon smaller crabs and molting crabs appears to be a major source of mortality that is common throughout most estuarine habitats, which often shapes the distribution of blue crabs among microhabitats by size, sex, and molt stage (see below). Of course, human effects also may be very large, affecting abundance, population size structure, sex ratio, and habitat distribution (see also Fogarty and Lipcius, Chapter 16 on population dynamics).

Vulnerability by Size, Molt Stage, Sex, and Morphological Variation

Vulnerability of blue crabs to predation varies greatly by size and molt stage. Generally, small crabs are subject to a wider range of predators and predator effects, and several studies have shown that crab vulnerability to predation decreases markedly with increasing size (Moody 1994, 2001, 2003; Dittel et al. 1995; Hines and Ruiz 1995). Tethering experiments and other studies in seagrass habitats along the Gulf of Mexico indicate very intense predation (averaging 85% mortality d^{-1} across sites, and with many sites >95% mortality d^{-1}) on early post-settlement juvenile blue crabs (5-20 mm CW) (Heck et al. 2001). In seagrass habitats of Mobile Bay, Alabama, for example, episodic settlement events did not result in increased juvenile abundance because cohorts of new recruits were consumed in <14 d after settlement, with predation causing as much as 95% mortality d^{-1}, such that juvenile densities rapidly returned to pre-settlement "background" levels (Heck et al. 2001). Tethering experiments in central Chesapeake Bay show that vulnerability to cannibalism decreases with size, allowing large crabs to move into deeper water with relative impunity compared to small crabs, which tend to be restricted to shallow (<40 cm deep) water along the shoreline (Terwin 1999; Hines, unpubl. data). These conclusions are supported by telemetry studies that contrasted movement of juveniles and adults in Chesapeake Bay: juveniles spent much more time in shallows (<1 m deep) along the shoreline whereas adults moved mainly in deeper channels (Hines et al. 1995).

Blue crabs are especially vulnerable at the time of ecdysis when they are soft and relatively immobile. Soft, post-molt crabs are often used for bait in sport fisheries, and soft crabs have been documented in the stomach contents of several fish species, including striped bass (Orth et al. 1999) and American eel (Shirley et al. 1990). Two experimental studies indicate that predation on soft postmolt crabs is much higher that on intermolt crabs (Shirley et al. 1990; Ryer et al. 1997). However, both studies used methods that involved tethering soft and hard crabs within mesh bags, which may affect their detection by predators.

Juvenile blue crabs may exhibit variation in lateral spine length, color, or other morphological features (Davis et al. 2004a, 2005a). Juveniles reared in experimental hatcheries appear to have shorter spines than wild crabs, but spine length grows quickly (within 2 molts) after exposure to field conditions, perhaps as a result of chemical cues from fish or other predators (Davis et al. 2005). However, mortality rates in the field do not appear to differ consistently as a function of spine length and source of the juveniles (Hines et al., unpubl. data). Color of juveniles is under hormonal control of chromatophores and varies within 1 to 2 h to match the background color and even fluctuates on tidal and diurnal rhythms (Fingerman 1955), so small crabs are able to match their background and achieve an adaptable camouflage from visual predators.

No studies to date indicate that predation rates differ by sex of blue crabs, although blue crabs do partition the habitat — and thus presumably exposure to predators — by sex (e.g., Hines et al. 1990). In the soft-crab fishery, molting male crabs suffer greater mortality, yet take lesser time to molt, than do females in shedding operations (Chaves and Eggleston 2003), but this is difficult to relate to natural mortality rates and vulnerability to predators in the field. As a part of mating behavior, female crabs undergoing their pubertal molt pair up with mature males for a period of both pre-copulatory and post-copulatory mate guarding that provides the female with protection from potential predation and cannibalism (Jivoff 1997a, b, 2003; Jivoff and Hines 1998a, b).

Refuges from Predation and Cannibalism

Blue crabs obtain refuge from predation by use of key habitats that provide structural complexity or are inaccessible to predators. Refuge habitats with structural complexity include seagrass, oyster reefs, emergent marsh vegetation, mangrove prop roots, and coarse woody debris from terrestrial trees. Habitats with structural refuges are especially important to small juveniles and molting blue crabs. Submerged aquatic vegetation beds have received extensive research, which found increased abundance and higher survival of juvenile and molting blue crabs in vegetated than in adjacent unvegetated habitat (Heck and Orth 1980a, b; Heck and Thoman 1981; Wilson et al. 1987, 1990b; Pile et al. 1996; Ryer et al. 1997) (Fig. 16). Indeed, an important component of the soft-crab fishery in Chesapeake Bay involves dredging for premolt crabs that use seagrass as a refuge (Oesterling 1995). Refuge value of seagrass patches for juvenile blue crabs depends upon the degree of fragmentation of the seagrass beds (Hovel and Lipcius 2001, 2002), distance from shoreline or other habitats such as salt marsh (Micheli and Peterson 1999), and aspects of the structure itself, such as the density and configuration of vegetation blades (Heck and Spitzer 2001; Hovel and Lipcius 2002; Orth and van Montfrans 2002). However, these effects of seagrass patch size and shoot density may vary seasonally because densities of predators and cannibalistic crabs fluctuate with recruitment into the patches, even to the point that predation rates on tethered juvenile crabs may be inversely related to shoot density as juvenile densities increase during fall after megalops' settlement (Hovel and Lipcius 2002). Effects of shoot density on habitat value for juvenile blue crabs may vary at different spatial scales (Worthington et al. 1992).

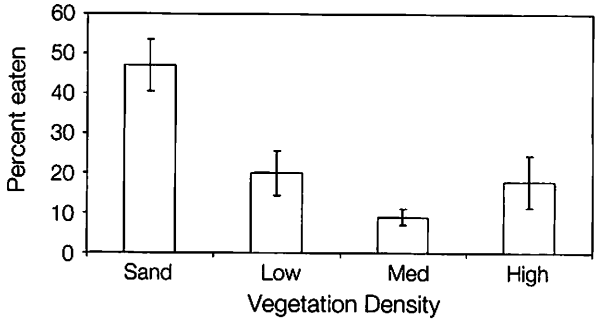

Figure 16. Effect of submerged aquatic vegetation on predation upon juvenile (30-70 mm CW) blue crabs tethered on bare sand and low, medium, and high densities of blades of eelgrass *Zostera marina*. Vertical bars indicate ± one standard error. From Wilson et al. (1987).

Blue crabs move onto marsh surfaces during flood tides, which allows them to escape from many predators, as well as to gain access to food resources (Orth and van Montfrans 1987; Lin 1989; Mense and Wenner 1989; Thomas et al. 1990; Fitz and Wiegert 1991b, 1992; Micheli 1997b; Tupper and Able 2000). In Chesapeake Bay, male crabs undergoing their pubertal molt move into tidal creeks in preparation for molting, which takes place along the fringing edge of emergent marsh vegetation (Hines et al. 1987; Shirley et al. 1990; Wolcott and Hines 1990). Salt marsh creeks also provide molting crabs with refuge from cannibalism (Ryer et al. 1997).

Similarly, juveniles associated with other structures gain refuge from predation. Juveniles in benthic or drift algae, e.g., *Ulva lactea* = *U. lactuca*, have reduced predation rates (Heck and Orth 1980a; Wilson et al. 1990a). Intermolt juveniles tethered near coarse woody debris have higher survivorship than those tethered on open sediment (Hines et al., in prep.), and molting juveniles in central Chesapeake Bay seek coarse woody debris for protection when they are soft (Everett and Ruiz 1993; Hines et al., in prep). Crabs tethered near oyster shell also obtain higher survivorship than those tethered on bare sediment (Hines et al., unpubl. obs.).

Shallow water, even in the absence of structure in the environment, is a crucial refuge habitat for 0+ age class juveniles (30-70 mm CW) in Chesapeake Bay (Ruiz et al. 1993; Dittel et al. 1995; Hines and Ruiz 1995) (Fig. 17). When approached from shore, escape orientation of blue crabs in the intertidal zone was consistently towards deeper water (Woodbury 1986). However, most predators appear to approach from deeper water, and juvenile blue crabs tethered experimentally during summer in a subestuary of central Chesapeake Bay suffered high mortality (40%-90% per day) in water deeper than 70 cm, whereas juveniles tethered in shallow water (40 cm deep) suffered less than half that mortality rate (15%-40% per day) (Hines and Ruiz 1995). The difference in relative morality of juveniles tethered in shallow versus deep water (Hines and Ruiz 1995) was greater than the difference in mortality of similarly tethered juveniles in vegetated versus non-vegetated habitats (Heck and Thoman 1981; Heck and Wilson 1987; Heck et al. 1995; Pile et al. 1996). Laboratory experiments using large tanks with depth gradients showed that juveniles (30-70 mm) shifted their depth utilization from deep and medium depths to shallow water in the presence of a large crab, but not in the absence of another crab or in the presence of another small crab (Dittel et al. 1995). Survival of juveniles preyed upon by large crabs was also significantly higher in tanks with depth gradients that provided shallow refuge than in tanks without depth gradients (Dittel et al. 1995).

Low salinity zones of river-dominated estuaries have fewer large crab and fish predators and afford reduced mortality (tested by tethering) than higher salinity zones (Posey et al. 2005). Similarly, upper, low-salinity ends of subestuaries of Chesapeake Bay afford lower mortality rates (also tested by tethering) to juveniles (Ruiz et al. 1993; Hines and Ruiz 1995; Seitz et al. 2003), especially in mud and sand flats associated with fringing salt marshes, including when compared to seagrass habitats at the lower end of the same tributaries (King et al. 2005; Lipcius et al. 2005; Seitz et al. 2005). Thus, low salinity zones may provide good nursery areas because of lower

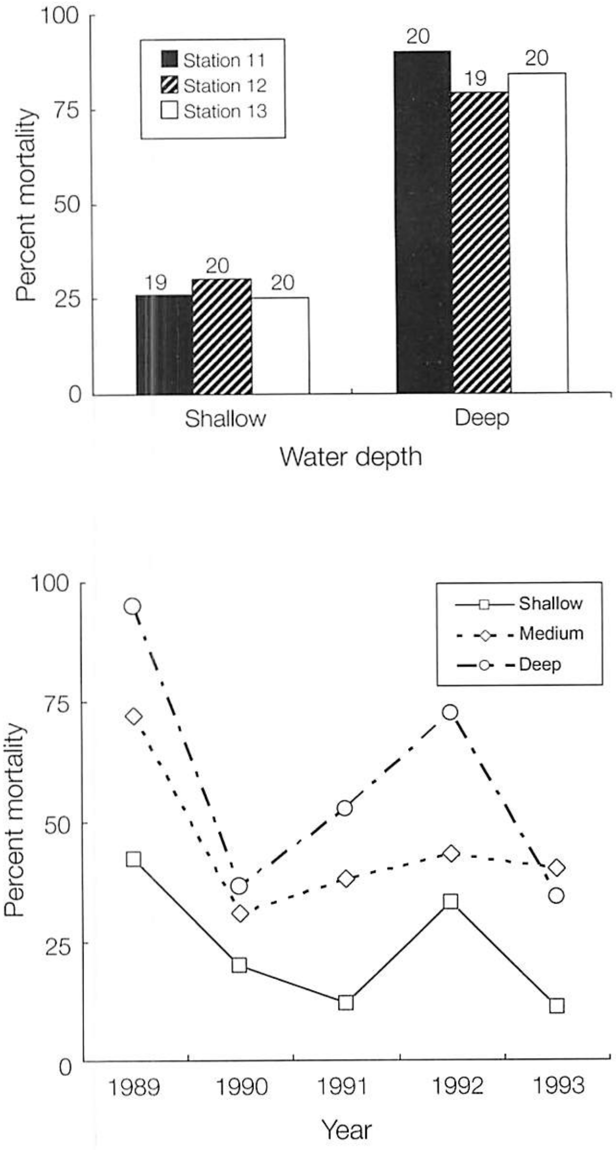

Figure 17. Shallow water as a refuge from predation upon juvenile (30-70 mm CW) blue crabs in Chesapeake Bay. Top panel shows mortality of juveniles tethered in shallow (15 cm) versus deep (80 cm) water on non-vegetated bottom at three shoreline stations along the Rhode River, a subestuary of Chesapeake Bay. Numbers at top of bars indicate sample sizes. Bottom panel shows annual variation in mortality of juveniles tethered in shallow (squares; 15 cm), medium (diamonds; 40 cm) and deep (circles; 80 cm) water on non-vegetated bottom of the nearshore waters of the Rhode River subestuary. From Hines and Ruiz (1995).

predator abundance and reduced mortality, as well as good food resources for juvenile blue crabs.

Juvenile crabs exhibit density-dependent mortality in muddy, non-vegetated nursery habitats of upper Chesapeake Bay, and experimental stocking in small coves resulted in higher survival at low than high juvenile densities (Davis et al. 2005). Low density may afford refuge to prey (such as bivalves) attacked by predators that exhibit density-dependent foraging (such as adult blue crabs) (Lipcius and Hines 1986; Eggleston et al. 1992; Seitz et al. 2001a). Low density of juvenile crabs in combination with shallow water allows a significant but only partial refuge from predation, especially cannibalism by large crabs (Dittel et al. 1995). Although the mechanism by which shallow water provides refuge from predation-cannibalism is not clear, the attack success of large blue crabs appears to be lower in shallow than deep water, as indicated by the damage:mortality ratios of tethered crabs (Hines and Ruiz 1995). Because large crab cannibalism on juveniles exhibits an inversely density-dependent functional response that characterizes unstable predator-prey interactions, large blue crabs may be able to drive juveniles locally extinct in many areas (Dittel et al. 1995). The effectiveness of the shallow-water refuge may vary with the steepness of the bottom slope, affecting the distance of forays made by large predators (Lin 1989). Human modification of the nearshore bathymetry by bulkheads, rip-rap, and dredging may have major effects on refuge value of the nearshore habitat by removing shallow depth habitat (Hines and Ruiz, unpubl. data).

Increased body size also affords blue crabs effective refuge from predation, which allows larger crabs to exploit certain habitats that have high risk of predation for smaller crabs. Survival of tethered early post-settlement juveniles increased with increasing size through the 5th instar and was not significantly different for crabs from 5th through 9th instars, indicating that relative refuge in size from predation is reached by the 5th instar (Pile et al. 1996). This behavior allows juveniles to disperse from the refuge afforded by seagrass beds and to move into other shallow habitats throughout the estuary. In central Chesapeake Bay, mortality of tethered crabs decreased markedly with increasing body size in the following categories: 30 to 50 mm >50 to 70 mm >90 to 110 mm >125+ mm (Hines and Ruiz 1995; Hines, unpubl. data). Tethered intermolt crabs >125 mm suffered no mortality in these experimental studies, indicating very low natural predation or cannibalism in marked contrast to high estimates of mortality attributed to fishing (60%-98% per year) (Sharov et al. 2003).

Vulnerability to predation or cannibalism does not appear to exhibit significant diel variation, as tethered juvenile crabs suffered similar mortality rates during day and night periods in central Chesapeake Bay (Hines and Ruiz 1995). The lack of diel variation is consistent with the conclusion that large crabs comprise the major source of juvenile mortality, because crabs are well adapted for chemotactile foraging in the absence of light and because they exhibit bimodal periods of morning and evening foraging activity that spans both day and night (Pearson and Olla 1977; Nye 1989; Clark et al. 1999b).

Agonistic Displays

Blue crabs may flee an attack by a predator or cannibal by walking or swimming away or digging, or they may perform aggressive behaviors that include displaying, fending, and striking (Wright 1968; Teytaud 1971; Jachowski 1974; Norse 1975, 1977). Blue crabs often exhibit a meral spread threat display (chelipeds extended laterally) during agonistic interactions with other crabs and potential predators (Jachowski 1974). During high intensity displays, the chelae may be extended to angles approaching 160°, but in lower levels of display the chelae may be angled slightly forward of the bent resting position (Wright 1968). When equipped with biotelemetry tags that transmit the crab's location and threat displays and feeding (Clark et al. 1999a, b), free-ranging adult crabs in Chesapeake Bay exhibited a bimodal pattern in the frequency of threat displays. The peaks in display activity lagged slightly after the bimodal peaks in morning and evening feeding activity, with crabs spending 10%-12% of their time in threat posture during peak periods (Clark et al. 1999a, b). Threat displays

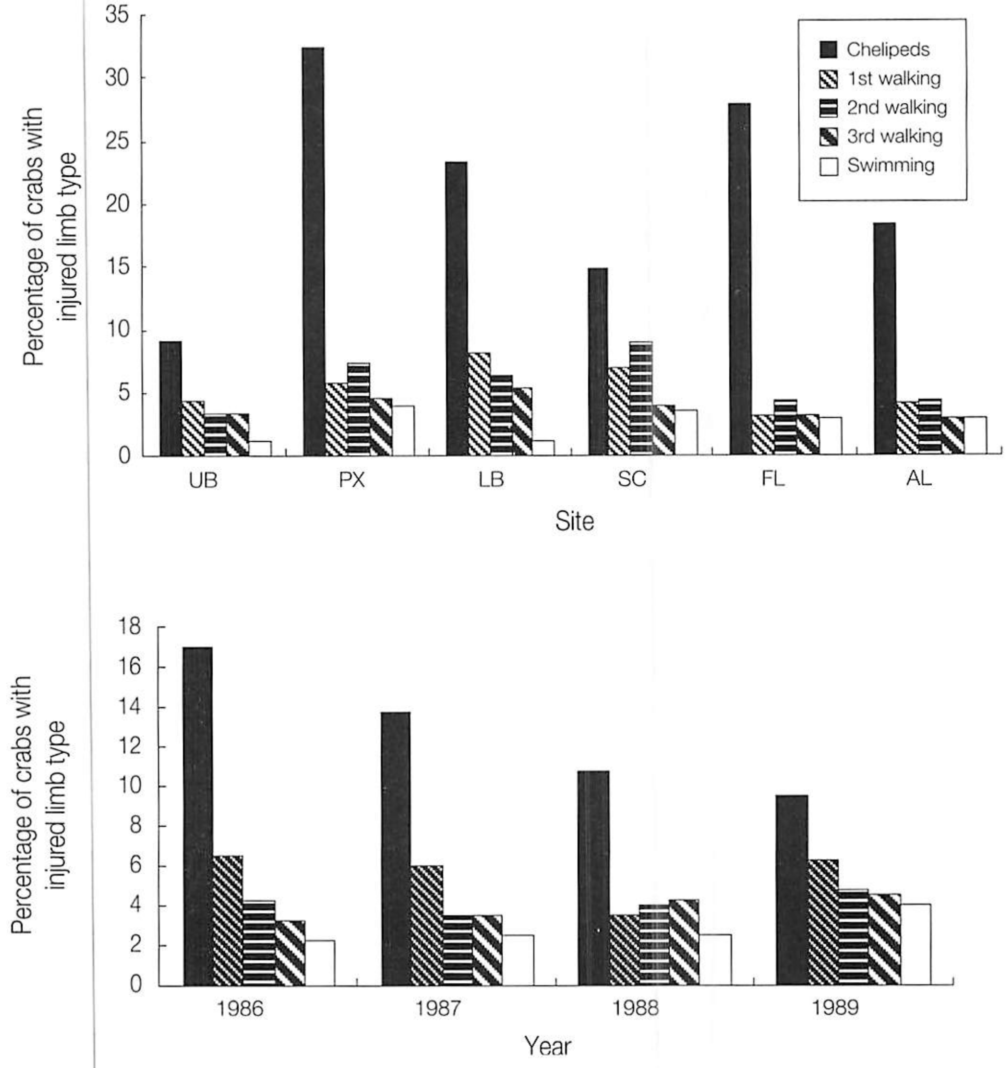

Figure 18. Variation in limb loss by limb type in blue crabs. Top shows spatial variation among three sites in Chesapeake Bay (UB = upper bay, PX = Patuxent River, LB = lower bay) and three sites along the East and Gulf coast (SC = South Carolina, FL = Florida, AL = Alabama) in 1989. Bottom shows temporal variation among years (1986 -1989) within the Rhode River subestuary of Chesapeake Bay, Maryland. From Smith and Hines (1991a).

occurred primarily at sites where crabs fed and increased with aggregation on prey patches and with increasing crab density (Clark et al. 1999a, b, 2000).

Autotomy

Autotomy is the reflex severance of an appendage, which provides adaptive advantages to limit damage and wounds (e.g., stops bleeding, avoids difficulty in future ecdysis of limb), as well as to avoid predators that are left holding the limb while the rest of the prey escapes. Most species of crabs, including blue crabs, are capable of autotomizing limbs (Juanes and Smith 1995). Blue crab populations often exhibit high but variable levels of limb autotomy, and the frequency of limb autotomy reflects variation in agonistic encounters, involving both other blue crabs and other potential predators (Smith 1990a). Autotomy frequency may be used as an indicator of intensity of predation and cannibalism within and among populations, although caution in interpretation is advised because autotomy really indicates non-lethal attacks.

In the most extensive and intensive survey of limb autotomy in arthropods to date, the frequency of blue crab autotomy varied temporally both within and among years, and over broad geographic scales from Chesapeake Bay, Maryland, to Mobile Bay, Alabama (Smith and Hines 1991a) (Fig. 18). Blue crab limb loss was substantial, ranging from 17% to 39% among sites, indicating that autotomy is an important mechanism for blue crab survival. Limb loss also varied significantly spatially among sites within Chesapeake Bay (19%-39%) but did not vary significantly among sites within a small subestuary of central Chesapeake Bay. Patterns of injury among limbs were remarkably consistent among all sites, such that chelipeds had the highest autotomy rate whereas swimming (5th) legs had the least, right and left limbs were lost with equal frequency, and severe autotomy of several multiple (four or more) limbs was rare (Smith and Hines 1991a). Loss of single chelipeds was common (4-17%) among sites, but loss of both chelipeds was rare (0-5%) (Smith and Hines 1991a). Frequency of limb loss was independent of sex and molt stage, but was positively correlated with crab size, perhaps because large crabs molt less often and accumulate injuries over long periods, or perhaps because agonistic interactions are more likely to result in death than autotomy for small crabs than for large crabs (Smith and Hines 1991a; Hines and Ruiz 1995). Within a subestuary of central Chesapeake Bay, limb loss varied significantly among 4 y, ranging from 17% to 25%, and autotomy frequency was density dependent, indicating that interactions among blue crabs may be a major cause of limb loss (Smith 1995).

Consequences and costs of limb autotomy in blue crabs vary by type and number of lost limbs, because each limb is specialized for particular functions. Further, blue crabs are heterochelous, typically with a right crusher claw and a left cutter claw, each with distinct morphology and mechanical advantage for handling prey (Hamilton et al. 1976; Blundon and Kennedy 1982a; Seed and Hughes 1997; see also Kennedy and Cronin, Chapter 3). Although blue crabs can regenerate autotomized limbs, lost crusher claws are replaced by cutter claws and up to three molts are required for regeneration of the full size of a limb (Govind and Blundon 1985; Smith 1990b). Loss of only a single limb had no apparent effect on crab growth, although severe multiple limb loss (four or more) significantly reduced molt increment and percent weight increase in the next molt (Smith 1990b). Foraging rate on soft clams did not differ significantly between blue crabs missing a single crusher cheliped and intact crabs, but crabs missing both chelipeds consumed significantly fewer clams than did intact crabs (Smith and Hines 1991b). However, the low incidence of crabs missing both chelipeds suggests that such injury does not affect crab predation on soft clams at the population level. Effect of limb autotomy (either with a single cheliped lost or with severe multiple loss of both chelipeds and two other legs) did not affect male crabs' abilities to mate with females, but both levels of autotomy reduced male crabs' abilities to compete for and defend females from "take-overs" by other intact males (Smith 1992). Effects of prior limb loss on escape from predators — especially of juveniles escaping cannibalism from large crabs — also depended upon number and type of limbs lost (Smith 1995). Juveniles with only a single missing leg remained fully effective at escaping attacks by large crabs, whereas juveniles with severe multiple limb loss changed their escape behavior, reducing activity levels and remaining buried, which reduced their encounters with cannibalistic large crabs.

OTHER SOURCES OF MORTALITY

Disease is an important source of blue crab mortality in many systems, with the blood disease (*Hematodinium* spp.) being particularly lethal at higher salinities, and high prevalence of the rhizochephalan *Loxothylacus texana* causing "reproductive death" by parasitic castration along the Gulf Coast (see Shields and Overstreet, Chapter 8). Analysis of disease effects on blue crabs needs much more study (Shields 2003).

Estuarine conditions may exceed physiological tolerances of blue crabs, resulting in mortality of appreciable fractions of local populations. Harsh winter conditions at combinations of low water temperatures <3° C in low salinity (<10) areas cause mortality in upper Chesapeake Bay and Delaware Bay, especially of large adults and very small juveniles (Kahn 1998; Sharov et al. 2003; Aguilar et al. 2005). Because *Callinectes sapidus* is a species with tropical evolutionary origin (Williams 1984), these winter effects may limit the northward geographic distribution of blue crabs along the East Coast. Although blue crabs generally avoid low oxygen conditions by moving to shallow habitats (Pihl et al. 1992; Diaz and Rosenberg 1995), mortality may result from large episodes of nocturnal anoxia or seiching of deep anoxic waters into shallow areas (see Tankersley and Forward, Chapter 10.) Further, modeling and empirical studies on the effects of low dissolved oxygen yield conflicting results of both increased crab catch (Eby and Crowder 2002) and reduced crab catch (Mistiaen et al. 2003), depending on the distribution of the fishing pressure and geomorphology of the estuary.

RESEARCH PROGRESS AND PRIORITIES

Research on the ecology of juvenile and adult blue crabs has progressed greatly over the past 20 y. The progress is due in part to the increased numbers of bright, energetic young scientists studying blue crabs as crucial predators in estuaries of the East Coast of North America — numbers of their publications have increased grandly, as the literature cited in this chapter shows. Progress comes, too, from new technology and tools, ranging from ultrasonic biotelemetry to global positioning systems, to remotely-sensed geographic information systems, and especially to ready access to powerful small computers. All these allow much more quantitative and sophisticated approaches to blue crab ecology. Biomolecular applications are just becoming readily accessible to marine ecologists, and these sophisticated tools will soon begin to allow new questions about recruitment dynamics, movement, demography, feeding interactions, and reproductive biology of blue crabs. However, we remain stymied by certain problems. For example, due to the obvious problem of working with animals that shed their exoskeletons in murky water, we know very little about predation and mortality rates in the field during molting, which we believe are much higher than during intermolt periods.

We now know a lot more about blue crabs in some locations like New Jersey marshes, Delaware Bay, Chesapeake Bay, the North Carolina sounds, South Carolina estuaries, Mobile Bay, and others. But there are many locations where we know little, including much of the coast of Central and South America and the Caribbean basin. Although the ecology of blue crabs is similar in many ways across sites, comparisons of East Coast and Gulf Coast systems indicate important differences between temperate and tropical systems, with regard to recruitment dynamics, competition with other predators, and major habitat changes (e.g., salt marshes drop out and mangroves become important). Some aspects of habitat use may differ as a result of differences in tidal regimes, such as "micro-tidal systems" of many areas such as Indian River Lagoon, Florida, or large areas of the Gulf Coast compared to "macro-tidal systems" of the East Coast estuaries where salt marshes regularly drain and flood on each cycle. Predation effects of blue crabs appear to vary widely with latitude, with clear dominance by blue crabs in many higher latitude estuaries but increasing complexity and diversity of the predator guild at lower latitudes. The relative roles of cannibalism and predation by fishes within and among estuaries are also not well understood.

Experimental ecologists have shown major interactive effects of crab density, prey resources, and habitat characteristics, so that multi-factorial experiments are now an essential element in blue crab research. Improved models are needed to integrate the complexity of these interactions and to scale up their application to large systems with extensive fisheries. It is apparent that effective protection of linked ecosystems is required for blue crab populations to complete the life cycle and sustain heavy fishing pressure on top of pollution and habitat destruction. Ecologists must provide the types of data that are essential for improved large scale models.

Unfortunately, progress also comes from the urgency of declining blue crab populations in many estuaries, especially Chesapeake Bay, which historically has been the most productive fishery. The scale of the fisheries is much greater than any of the research efforts underway, and this large-scale sampling by the fishery could be put to great scientific use to understand the complex ecology of the migratory life cycle of *Callinectes sapidus* moving large distances across many habitats. Yet use of much of this sampling effort by the fisheries is lost to science. Our knowledge of blue crab ecology could increase much more rapidly if scientists, fishery managers, and fishers could work more closely together to collect accurate, fine scale quantitative data on variation in crab abundance, distribution, and population structure.

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