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EARLY LIFE HISTORY OF THE BLUE CRAB *CALLINECTES SAPIDUS*: A REVIEW

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ABSTRACT The blue crab *Callinectes sapidus* Rathbun has been the subject of scientific investigation for more than 100 years. The crab is a key predator in shallow estuarine and coastal environments, and supports a large commercial fishery along the Atlantic and Gulf Coasts of the United States. Much of the initial research on *C. sapidus* was purely descriptive and provided only a patchwork perspective on the natural history of the crab. This is in contrast to more modern work that has defined a clear, interrelated series of processes that underlie the early life history of the species. The intent of the present review was to discuss contemporary understanding of the early life history of blue crabs in the context of a coherent time line of development. The review begins with a short section on general aspects of the life history, which provides a background for the overall discussion. This is followed by a segment on courtship and mating, with particular emphasis on chemical communication between mating pairs. Three subsequent sections then deal, respectively, with spawning migrations within the estuary, larval release in the adjacent coastal ocean, and transport of larvae on the inner continental shelf. A following segment, describes settlement of the larvae in the lower estuary and eventual transport of early juvenile stages to estuarine nursery areas. The final section provides a summary and conclusions. Points of emphasis in the review include the following: (1) the role of pheromones in courtship and mating; (2) the discovery of two distinct phases in the spawning migration; (3) the importance of chemical cues in assuring synchronized hatching of eggs; (4) the predominant effect of wind- and buoyancy-driven processes in controlling larval transport in the coastal ocean; (5) the development of mathematical models that allow critical analysis of transport processes; and (6) the combined physical and behavioral processes that facilitate transport of megalopa larvae from the estuarine mouth to nursery habitat in the lower estuary.

KEY WORDS: blue crab, *Callinectes sapidus*, mating, larvae, juveniles, behavior, transport, review

INTRODUCTION

Breeding populations of the blue crab *Callinectes sapidus* (Rathbun) extend from southern New England to Argentina (Williams 1974, 2007). The crab is an important predator in shallow estuarine and coastal waters throughout its range (Hines 2007), and supports a large commercial fishery along the Atlantic and Gulf Coasts of the United States (Fogarty & Lipcius 2007, Kennedy et al. 2007). In many locations there are records of annual landings that extend nearly a century, and in some cases, yearly variations in stock size are routinely monitored, independent of the fishery (Jensen & Miller 2005, Jensen et al. 2005, Ralph & Lipcius 2014). In addition, the species has been subject to broad-based scientific study for at least 125 y, and general descriptions of its life history have been available since the early 20th century (Epifanio 2007). Succeeding years have witnessed a number of review articles citing hundreds of scholarly works (Tagatz & Hall 1971, Van Engel 1987, Epifanio 1995), crowned by an extensive, multiauthor synthesis that was published in book format in 2007 (Kennedy & Cronin 2007a). But regardless of the remarkable interest in the species, some very important aspects of its early life history have remained enigmatic.

The intent of the present review is to discuss contemporary understanding of the early life history of blue crabs in the context of a coherent time line of development, starting with courtship and mating of adult crabs, and extending through a number of subsequent steps to the eventual settlement and metamorphosis of larvae in juvenile habitat. The review begins with a short section on general aspects of the life history, which provides background for the overall discussion. This is followed by a segment on courtship and mating, with particular emphasis on chemical communication between mating pairs. Three subsequent sections then deal, respectively, with spawning migrations within the estuary, larval release in the adjacent coastal ocean, and transport of the larvae on the inner continental shelf. In a following segment, the settlement of larvae in the lower estuary and eventual transport of early juvenile stages to estuarine nursery areas is described. A final section provides a summary and conclusions.

GENERAL ASPECTS OF EARLY LIFE HISTORY

Reproduction in blue crabs includes an extensive, pheromone-mediated courtship, followed by copulation, storage of sperm, and internal fertilization of eggs (Jivoff et al. 2007). Mating occurs mostly in oligohaline and mesohaline regions of estuaries, and is followed by migration of females to the lower estuary and the adjacent coastal ocean, where eggs are brooded externally before hatching as planktonic zoea larvae. Larval development includes seven zoeal stages followed by a single megalopal stage (Kennedy 2007, Fig. 1). Zoeal development requires 3–4 wk under favorable conditions, whereas duration of the megalopal stage is more variable and depends on a number of chemical and physical factors (Epifanio 2007). Zoeae (larval stages) are strong swimmers compared with most zooplankton, which allows the maintenance a position high in the water column (Epifanio 1995). Development of zoeae occurs in the open coastal ocean, and recruitment to juvenile populations is dependent on advective transport of megalopae back to the estuary. Megalopae are particularly strong swimmers and undergo rhythmic vertical migrations that facilitate upstream transport within an estuary (Forward & Tankersley 2001). Once in the estuary, settlement and metamorphosis of the megalopae are stimulated by chemical cues associated with appropriate nursery habitat (Epifanio & Cohen 2016). Newly metamorphosed juveniles are a few mm in carapace width and remain in juvenile habitat for several months until they reach a width of 20–30 mm (Dittel et al. 2000, Epifanio et al. 2003).

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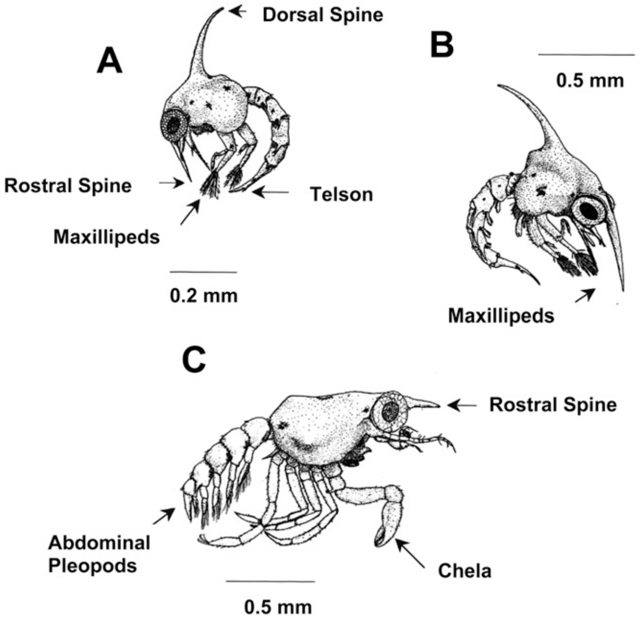

Figure 1. External anatomy of representative larval stages of the blue crab *Callinectes sapidus*. (A) Early zoeal stage: Note the maxillipeds used in swimming. (B) Advanced zoeal stage: Note the change in scale and the proportionally larger maxillipeds for swimming. (C) Megalopal stage: Note the abdominal pleopods used in swimming, the horizontal placement of the rostral spine, and the appearance of chelae. (Modified from Costlow & Bookhout 1959)

COURTSHIP AND MATING

Courtship

There are two basic categories of mating behavior in female brachyuran crabs based on the degree of calcification (i.e., hard versus soft integument) at the time of copulation (Norman 1996). The occurrence of these different types of copulation varies with habitat and taxonomy. For example, the hard-female pattern is common among intertidal and terrestrial species, regardless of taxonomy (Schubart et al. 2001, Brockerhoff & McLay 2005, Anderson & Epifanio 2010a), whereas the soft-female pattern is common in some families, regardless of habitat (Bamber & Naylor 1996, Jivoff & Hines 1998, Wolcott et al. 2005). Blue crabs are classified in the family Portunidae and exhibit an archetypal pattern of soft-female mating behavior (Jivoff et al. 2007).

Blue crab females reach maximum size (>130 mm carapace width) and sexual maturity after 17–19 postlarval molts (Williams 1974, Uphoff 1998), and do not undergo additional molting during their remaining life history (Newcombe et al. 1949, Van Engel 1958, but see Havens & McConaugha). The final ecdysis is termed the *pubertal molt*, and it results in a major change in the morphology of the female abdomen that provides greater surface area for brooding eggs (Kennedy & Cronin 2007b). The occurrence of a terminal molt stage in female crabs is associated with degeneration of the *Y*-organs, which are glands that produce molt-stimulating hormones, and continued functioning of the *X*-organs, which are glands that produce molt-inhibiting hormones (Carlisle 1957, Skinner et al. 1985, Jivoff et al. 2007).

Copulation in female blue crabs occurs during the soft stage immediately following the pubertal molt, and the females are incapable of additional copulations once the integument becomes calcified (Van Engel 1958, Millikin & Williams 1980). By contrast, males are fully calcified at the time of copulation and are promiscuous (Kendall & Wolcott 1999, Kendall et al. 2001). The whole courtship and mating process may involve as many as 17 explicit behaviors that serve to protect vulnerable females from predators and to facilitate exclusive copulatory access by respective males (Jivoff et al. 2007). Pair formation is prompted by urinary-borne pheromones (see the following paragraphs) released by mature males and prepubertal females (Gleeson 1980), and there is some indication that nonurinary pheromones may be important as well (Bushman 1999). In either case, the chemical cues are perceived by chemosensory structures (*aesthetasc sensilla*) that are concentrated on the outer flagella of the first antennules of the crabs (Hallberg & Skog 2011, Schmidt & Mellon 2011).[1]

Visual signals are also involved, and recent work indicates that courtship behavior can be provoked by visual stimulation alone (Baldwin & Johnsen 2009). In either instance, the elicited behaviors result in the following: (1) precopulatory mate guarding, wherein the male physically carries the female beneath his abdomen for several days before female ecdysis; (2) actual copulation immediately following ecdysis; and (3) postcopulatory guarding until the female integument is sufficiently calcified (Fig. 2).

The visual signals are conveyed in concert with the release of pheromones and include changes in posture and movement, as well as conspicuous display of sexually dimorphic patterns of coloration (Baldwin & Johnsen 2009). Early investigation of courtship pheromones suggested that crustacean molting hormone (or a similar molecule) might serve as a cue for mating behavior in crabs (Kittredge et al. 1971, Kittredge & Takahashi 1972, Shorey 1976), but subsequent studies of partially purified pheromones from blue crabs have shown no structural similarity to crustecdysone molecules (Gleeson et al. 1984). More recent investigation has focused on other putative pheromones released in the urine of prepubertal females (Kaimo 2009, Kaimo & Derby 2011) and has identified one active component as a small molecule (<1,000 Da) that consistently elicits courtship behavior in mature males (Kaimo et al. 2014, Kaimo et al. 2017). Additional analysis (nuclear magnetic resonance, mass spectrometry, and HPLC) has identified the molecule as *N*-acetylglucosamino-1,5-lactone, which is probably produced from *N*-acetylglucosamine (a monomer of chitin) by enzymatically catalyzed oxidation. Results of concurrent physiological and behavioral experiments have shown that the pheromone is detected by the chemosensory system of males and is probably one component of a mixture of active molecules in the female urine (Kaimo et al. 2014). Behavioral studies indicate that mature male crabs also release water-soluble pheromones that in this case attract prepubertal females (Gleeson 1991, Bushman 1999), but the active molecule in the pheromone has not been characterized (Jivoff et al. 2007).

Mating and Insemination

Copulation itself is initiated within minutes of the pubertal molt and relies on sequential pairs of male anatomical

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[1] In this article, the terms *pheromone* and *chemical cue* are used synonymously. For discussion, see Wyatt (2011).

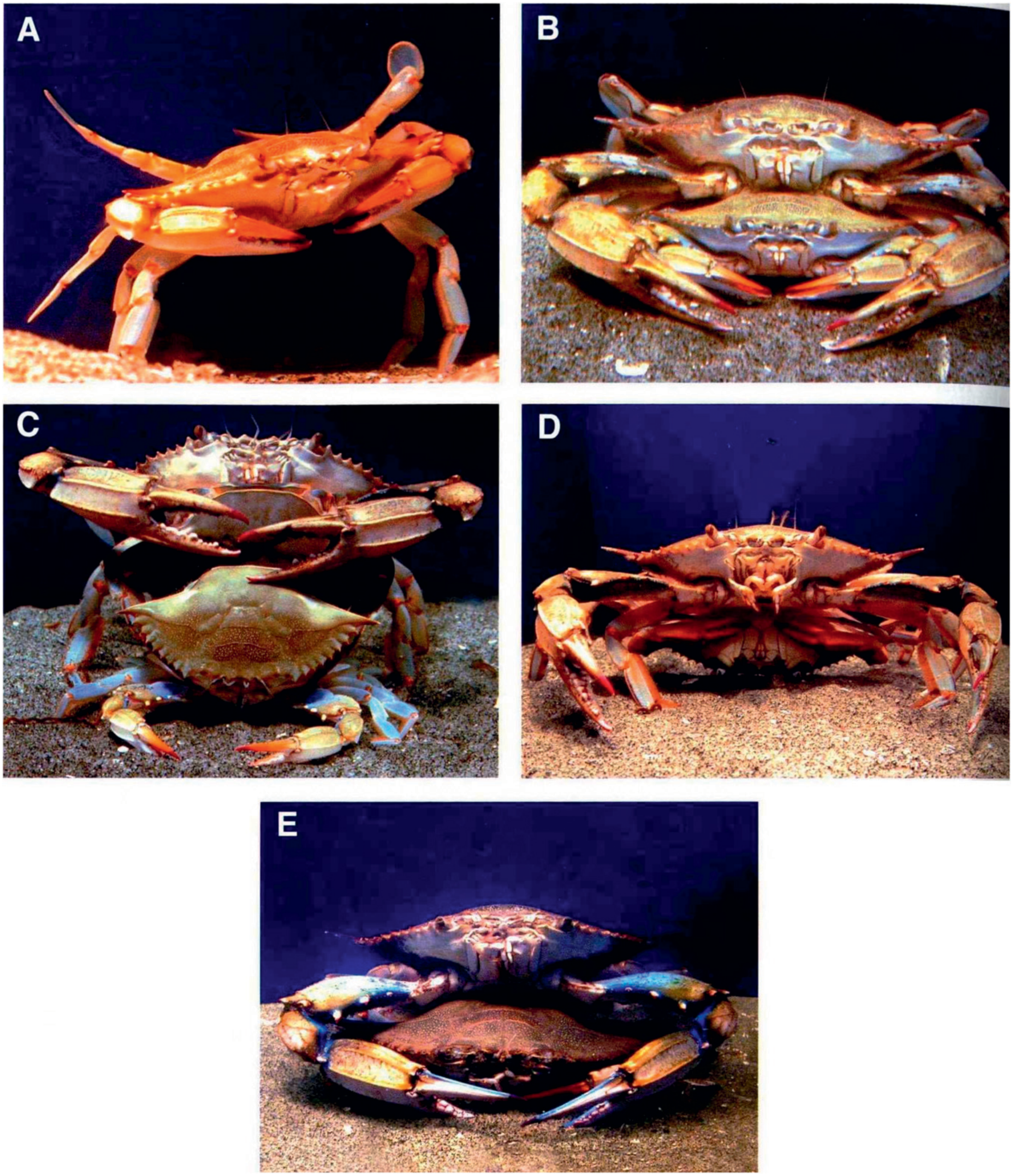

Figure 2. Mating behavior in the blue crab *Callinectes sapidus*. (A) Male mating display. (B) Precopulatory guarding. (C) Female undergoing pubertal molt. (D) Copulation. (E) Postcopulatory guarding. (From Jivoff et al. 2007)

structures (*vas deferentia*, *penes*, *2° pleopods*, and *1° pleopods*) to transfer the ejaculate to the female (Jivoff et al. 2007). The ejaculate consists of seminal fluid and packages of sperm called *spermatophores*. The ejaculate is introduced to the female (via the 1° *pleopods*), through a pair of genital pores on the ventral surface of the female abdomen. In turn, the pores are connected by vaginal ducts to respectively paired structures known as *seminal receptacles* or *spermathecae*. Each spermatheca is joined by a duct to one of the ovaries, which in time allows eggs to pass from the ovaries to the spermathecae where fertilization occurs.

Oocytes within the ovaries are undifferentiated at the time of copulation, and spermatophores are stored in the spermathecae during the months-long process of egg maturation before they are eventually used in the fertilization of the eggs (Hopkins 2002, Hines et al. 2003). Newly fertilized eggs are then extruded from the spermathecae through the vaginal ducts and genital pores to the ventral surface of the abdomen, where they are attached to abdominal appendages (*pleopods*) and brooded until hatching. Connection to the pleopods depends on the formation of external egg membranes and their associated attachment stalks. Details of the attachment process are poorly understood but it appears to require a sandy or muddy substratum (Sulkin et al. 1976, Jivoff et al. 2007).

Although female blue crabs do not provide nutritional sustenance to the developing eggs, the size, aggressive behavior, and full calcification of the ovigerous females serve to deter macrofaunal predators. In addition, brooding females devote considerable time to grooming the egg masses with their walking legs, which aerates the broods and may remove parasites and inviable eggs (Kuris 1991, Levi et al. 1999, Oh & Hartnoll 1999). Nevertheless, the developing egg mass may be subject to fungal infection (Bland & Amerson 1974) or infestation by nemertean worms that prey on the eggs (Milliken & Williams 1980, Overstreet 1982). The effects of these conditions on proportional egg survival within an egg mass are not well known (Jivoff et al. 2007).

In any event, blue crabs are highly fecund, and a typical female produces more than 2 million eggs in her first brood (Prager et al. 1990). This high fecundity is related to the small size of the individual eggs, the large internal space available for developing ovaries, and the extensive abdominal area suitable for external brooding (Hines 1982, 1988, 1991). The number of eggs decreases in subsequent broods but is still high compared with most other crab species (Hines 2003), and considering that an individual female may produce three or more broods over her life time, the overall fecundity is remarkable (Jivoff et al. 2007).

SPAWNING MIGRATIONS

General Aspects

There are 16 species in the genus *Callinectes*, and all of them inhabit warm, high-salinity coastal waters during at least part of their respective life histories (Williams 2007). The blue crab *Callinectes sapidus* differs from most of its congeners in the extension of its geographical range into temperate regions (where winter temperatures at the water/sediment interface reach near freezing) and in exploitation of the full scope of estuarine salinities available throughout that range (Williams 1984, Table 1). This broad variety of habitats is permitted by well-developed osmoregulatory capabilities, combined with wide thermal tolerance in adults and older juveniles (Tankersley & Forward 2007, Towle & Burnett 2007). By contrast, the larval and early juvenile stages require relatively high salinities and temperatures characteristic of coastal surface waters during the warm season (Costlow & Bookhout 1959, Costlow 1967, Rosenberg & Costlow 1976). In a typical temperate estuary, mature males are most common in low- to mid-salinity areas, and ovigerous, mature females are predominant in high-salinity habitats near the estuarine mouth or in the adjacent coastal ocean (Tankersley & Forward 2007, Table 2). Likewise, early juveniles of both sexes are common in the lower estuary (Orth & van Montfrans 1987, Lipcius et al. 1990), whereas advanced juveniles cohabit the middle and upper estuary along with mature males (Hines 2007).

TABLE 1.

Salinity and temperature requirements for the various life-history stages of the blue crab *Callinectes sapidus*.

Stage	Salinity	Temperature
Embryo	Stenohaline ↑	Stenothermal ↑
Early zoea	Stenohaline ↑	Stenothermal ↑
Late zoea	Stenohaline ↑	Stenothermal ↑
Megalopa	Stenohaline ↑	Stenothermal ↑
Early juvenile	Stenohaline ↑	Stenothermal ↑
Late juvenile	Euryhaline ↕	Eurythermal ↕
Adult	Euryhaline ↕	Eurythermal ↕

Direction of arrows indicates tolerance of high (>20; >20°C) and/or low (<20; <20°C) levels of the respective variables. See Tankersley and Forward (2007) for source data and discussion.

Courtship and mating in blue crabs occur mainly in the warm season in oligo- and mesohaline regions of estuaries, where salinities are often below the tolerance limits for larvae and early juveniles (Van Engel 1958, Schaffner & Diaz 1988, Ramach et al. 2009). Thus, newly inseminated females must migrate from the mating grounds in the upper and middle estuary to areas near the estuarine mouth to assure suitable conditions for brooding of eggs and release of larvae. This migration occurs in two phases (Milliken & Williams 1980, Tankersley et al. 1998, Carr et al. 2004) and in large estuaries may cover a distance greater than 200 km (Fig. 3). The timing of the migration varies with water temperature and occurs earlier in the year at lower latitudes (Tagatz 1968). But in any case, the first phase of migration is preceded by a refractory period, when inseminated females recover from molting and achieve full calcification, which allows normal feeding and accumulation of nutritional reserves (Jivoff et al. 2007).

Phase I Migration

The inseminated females begin the initial phase of the migration in the first autumn following mating, in presumed response to falling water temperatures and shortening day length (Turner et al. 2003, Aguilar et al. 2005). Like the adult form of most species in the family Portunidae, *Callinectes sapidus* is a capable swimmer, but the relative importance of swimming and walking in the initial phase of migration is not clear (Jivoff et al. 2007).

The phase I migration in large estuaries has been studied most thoroughly in Chesapeake Bay (along the east coast of North America), where the chief migration corridor is located along the edges of the deep channel that marks the main stem of the bay (Aguilar et al. 2005). Migration in this corridor begins in early autumn and includes overwintering of large groups of inseminated females along the migratory route (Lipcius et al. 2003, Turner et al. 2003). There is little known about Phase I migration in small estuaries, where the average depth of the main stem is much shallower and the distance from mating grounds to brooding grounds is much shorter (Tankersley et al. 1998, Darnell et al. 2012, Eggleston et al. 2015). But in any event, the extent of seaward displacement of the migrating crabs

TABLE 2.

Spatial and temporal distribution of the respective life-history stages of the blue crab *Callinectes sapidus* in temperate estuaries.

Location	Stage	Season
Tidal river (fresh water)	Adult males	Summer
	Late juveniles	Summer
Upper estuary (oligohaline)	Adult males	Summer
	Juvenile males	Summer
	Prepubertal females	Summer
	Inseminated females	Summer
Mid-estuary (mesohaline)	Phase I migrating females	Autumn
	Overwintering Phase I females	Winter
Lower estuary (polyhaline)	Brooding females	Summer
	Settling megalopae	Summer/autumn
	Nursery juveniles	Summer/autumn
Coastal ocean (euhaline)	Zoeae	Summer
	Megalopae	Summer
	Phase II migrating females	Summer

Phase I refers to inseminated (but nonovigerous), adult females. *Phase II* refers to ovigerous adult females.

depends on variation in autumn water temperature, and at levels less than 10°C the crabs cease moving and bury a few centimeters into the sediment (Hines et al. 2003). The females resume their migration concurrent with rising water temperatures in spring and, by early to midsummer, reach high-salinity areas near the estuarine mouth where final maturation and fertilization of eggs occur.[2] Newly fertilized eggs are then extruded from the gonopores on the ventral surface of the abdomen (see aforementioned) and are attached to hairs on the abdominal pleopods. The eggs are then brooded under the abdomen of ovigerous females for 2–3 wk until they are ready to hatch (Fig. 4).

Phase II Migration

Phase II of the migration involves the movement of ovigerous females from the lower estuary to the adjacent coastal ocean, where eggs hatch and larvae are released into the water column (Tilburg et al. 2008). Investigations of Phase II have shown that seaward displacement of ovigerous females is based on a temporal pattern of swimming known as *selective tidal stream transport* (Forward et al. 2003b). In this pattern of movement (which can be divided into *flood-tide transport* and *ebb-tide transport*), the crabs enter the water column during one tidal phase (either ebb or flood), but remain on the bottom during the other. For example, Tankersley et al. (1998) conducted high-frequency sampling of blue crabs swimming at night near the mouth of a small estuary in North Carolina and found that most crabs collected during the ebb phase were ovigerous females with late-stage eggs that were ready to hatch. By contrast, crabs collected during the flood phase were mostly non-ovigerous females that showed morphological signs of recent spawning. It was concluded that late-stage, ovigerous females use ebb-tide transport when migrating to spawning sites in the coastal ocean and use flood-tide transport to reenter the estuary after their larvae have been released (Forward et al. 2003b). Results of a follow-up laboratory study showed that ovigerous females with late-stage eggs display an endogenous, circatidal rhythm in swimming activity (see the following paragraphs) that underlies the pattern of nocturnal ebb-tide transport observed in the field (Forward et al. 2003a). Additional laboratory work showed that the circatidal rhythm also occurred in crabs with mid-stage embryos and was unaffected by the light/dark cycle (Forward & Cohen 2004). Thus, it was concluded that migrating crabs also may use ebb-tide transport during daylight hours but at a deeper depth.

Subsequent field work with acoustically tagged, ovigerous crabs has corroborated the use of ebb-tide transport in Phase II migration (Carr et al. 2004). For example, tethered crabs that were rigged with miniature pressure sensors showed an ebb-tide pattern of vertical swimming, regardless of embryo stage (Hench et al. 2004). These results were supported by yet another investigation, which also demonstrated ebb-tide transport in ovigerous females regardless of the stage of embryonic development and also in nonovigerous females shortly after larval release (Forward et al. 2005). A more recent laboratory investigation has generally supported these results and has shown that behaviors underlying ebb-tide transport are not expressed in inseminated females until oviposition of the first brood of eggs (Darnell et al. 2010). These findings were supported by a final tethering study that compared patterns of swimming in various habitats characterized by different tidal regimes (Darnell et al. 2012). The results of that investigation showed that swimming did not occur in nontidal habitats and that some tidal habitats served as migration corridors, whereas others functioned as foraging stopovers.

LARVAL RELEASE

Spatial Aspects

Release of larvae occurs in the estuarine mouth and in the adjacent coastal ocean, and there appears to be a latitudinal difference in the across-shelf distribution of hatching grounds. In the Middle Atlantic Bight (MAB), along the east coast of North America, hatching ensues in the estuarine mouth itself or immediately outside the estuary and along the contiguous coast

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[2] Note that the sperm used to fertilize these eggs has been stored in the spermathecae of the females since the previous summer.

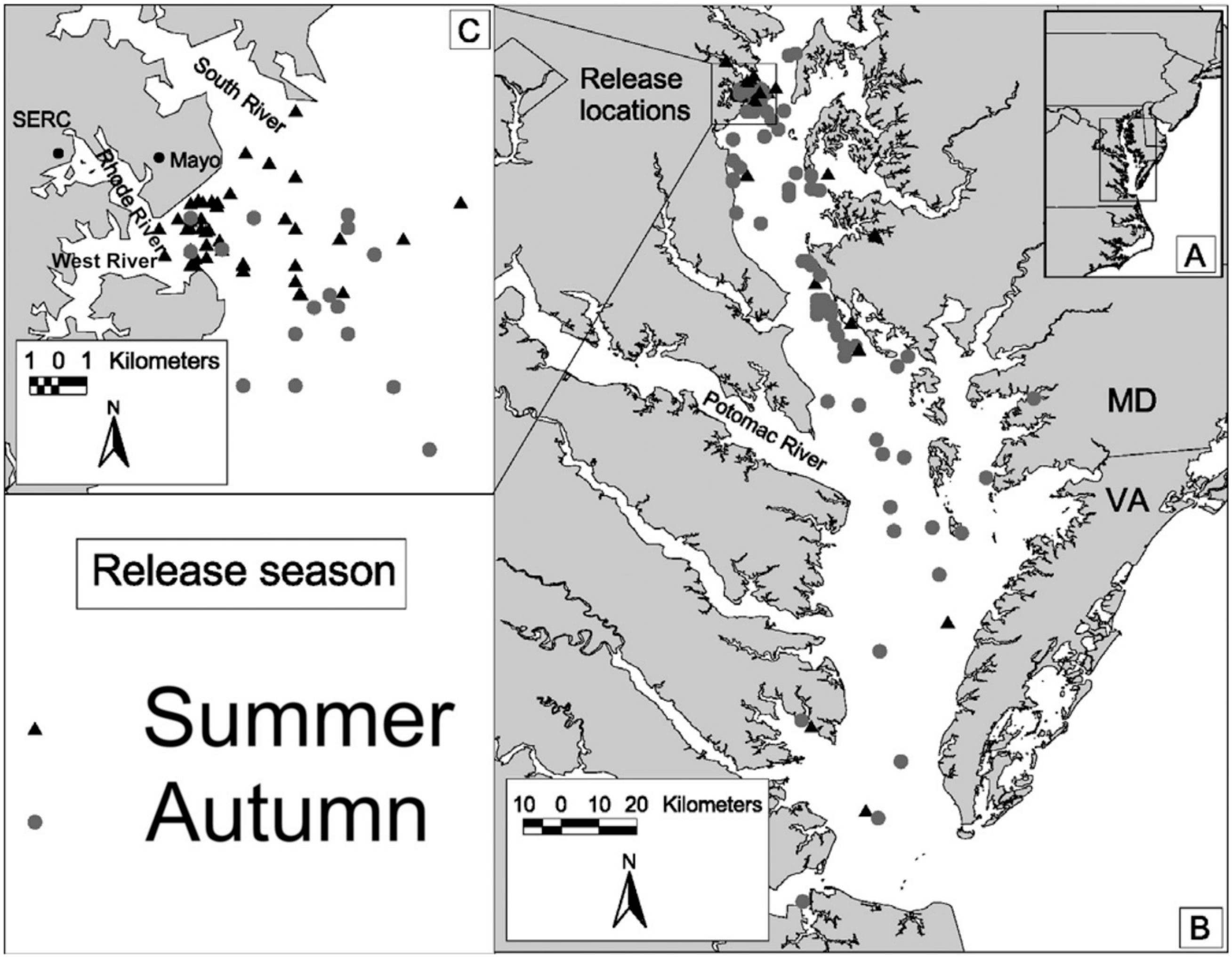

Figure 3. Recapture locations of mature female blue crabs *Callinectes sapidus* that were tagged and released near the mouth of the Rhode River in Chesapeake Bay along the east coast of the United States (1999–2002). Triangles represent crabs released in summer (June–August); circles represent crabs released in autumn (September–October). Note the down-estuary movement of crabs tagged in autumn. (A) The coastal region from Long Island to South Carolina. (B) The southern Chesapeake Bay. (C) The tag-and-release region in the mouth of the Rhode River. (From Aguilar et al. 2005)

(Provenzano et al. 1983, Roman & Boicourt 1999, Tilburg et al. 2009). By contrast, hatching grounds farther south (in the South Atlantic Bight and northern Gulf of Mexico) occur as much as 50 km offshore, and areas closer to shore function as migration corridors (Gelpi et al. 2009, Gelpi et al. 2013, Ogburn & Habeffer 2015). Reasons for this difference are not clear, but results of modeling studies show strong effects of hatching location on subsequent transport of larvae (Tilburg et al. 2007). Moreover, hatching grounds greater than 5 km offshore are outside the jurisdiction of individual states, which complicates management and conservation of the stocks (Gelpi et al. 2009, Ogburn & Habeffer 2015).

Temporal Synchrony

Regardless of location, hatching in blue crabs occurs as a short, synchronous event, where all eggs in the broods of neighboring females are released near the time of early morning high tide (Tankersley et al. 2002). This synchrony is important in the generation of large surface patches that characterize the spatial distribution of blue crab larvae on the continental shelf (Natunewicz & Epifanio 2001). The synchronous aspect of larval release is controlled by endogenous tidal and diel clocks and is facilitated by chemical communication between females and brooding embryos (Tankersley et al. 2002, Rittschof & Cohen 2004). Until recently, it was assumed that the circadian rhythm is entrained in the embryos independent of the brooding female and that the ambient light/dark cycle is the agent that sets the rhythm (*zeitgeber*). Thus, the circadian rhythm would be inculcated in the embryo as soon as the developing eyes could distinguish light and dark, which occurs well-before hatching (Forward et al. 2014). More recent work with other subtidal crab species, however, has shown that ovigerous females actually entrain the circadian rhythm in the brooded embryos via water-soluble, chemical cues (Epifanio & Cohen 2016, Forward et al. 2016).

Hatching itself involves initial uptake of water into the egg, which ruptures the outer embryonic membrane (Davis 1965) and releases waterborne pheromones that elicit simultaneous hatching behavior within a given brood and presumably in the

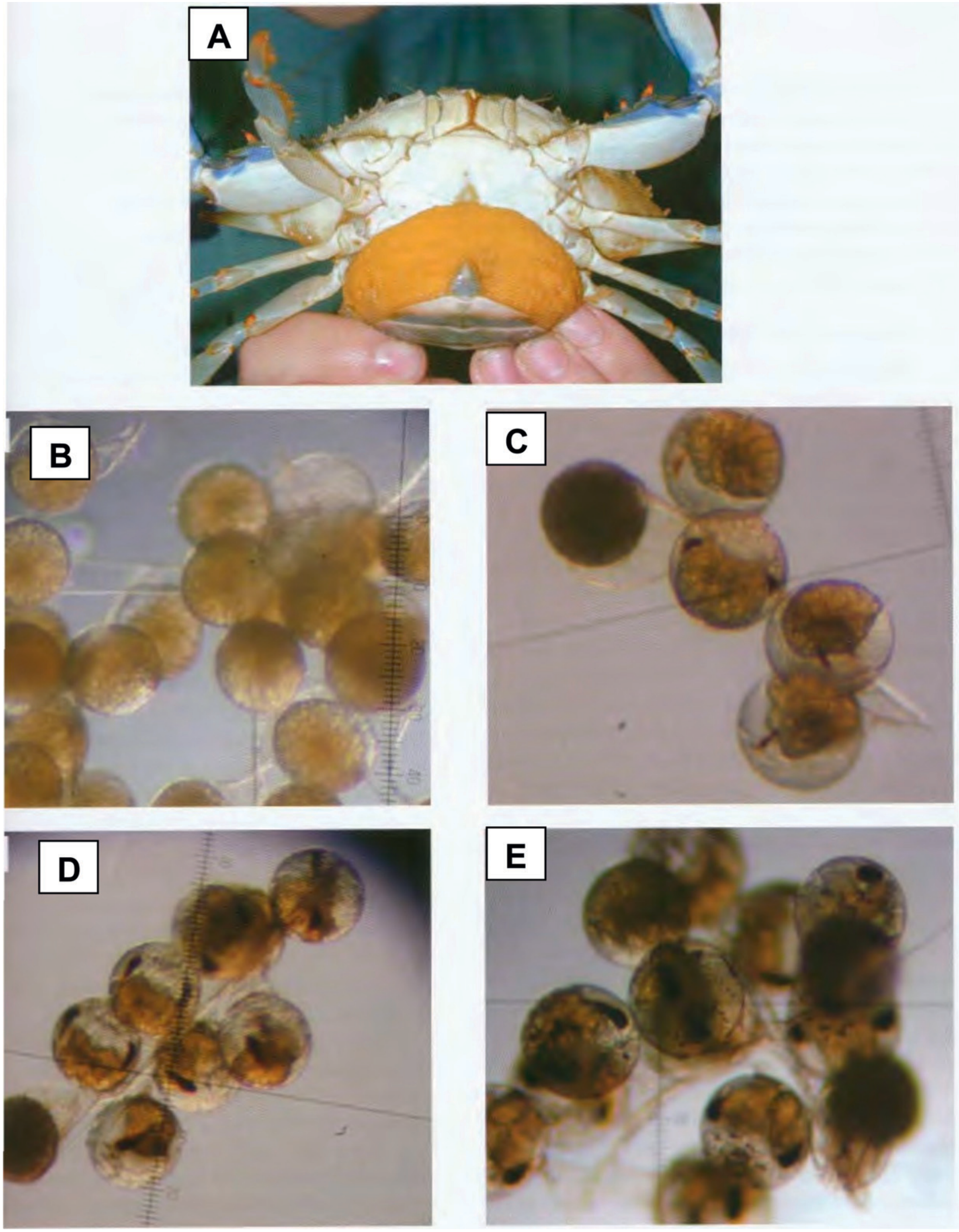

Figure 4. Embryonic development of blue crab eggs. (A) Ventral view of an ovigerous female and egg mass. (B) 5-day-old embryos with egg attachment stalks visible. (C) 9-day-old embryo with developing eye pigment. (D) 11-day-old embryos with visible abdomen and eyes. (E) 12-day-old eggs ready to hatch. (From Jivoff et al. 2007)

broods of neighboring females (Tankersley et al. 2002, Darnell & Rittschof 2010). These pheromones are small peptides (<500 Da) with one or more neutral amino acids preceding arginine or lysine at the carboxyl terminus and are probably generated by proteolytic cleavage of proteins in the egg membrane (Rittschof & Cohen 2004). The hatching behavior in ovigerous females consists of sustained flexing of the abdomen, which apparently plays a role in release of larvae from the eggs.

According to Darnell and Rittschof (2010), late-stage ovigerous females swim upward in the water column immediately before egg hatching, and actual release of larvae occurs at the surface; however, quantitative documentation of this behavior has not been provided.

LARVAL TRANSPORT

Historical Perspective

Early work on transport of blue crab larvae concluded that hatching occurs near the estuarine mouth and that larvae are retained in the lower estuary throughout zoeal and megalopal development. Because blue crab zoeae require high-salinity water for maximum growth and survival (Costlow & Bookhout 1959, Costlow 1967, Rosenberg & Costlow 1976), the lower estuary was perceived as a critical nursery habitat that expands and contracts in concert with interannual variation in rainfall (Van Engel 1958). Thus, years with low precipitation would foster maximum nursery size and elevated larval survival. By contrast, years with high precipitation would result in minimum nursery size and depressed survival. A codicil to this hypothesis was the idea that blue crab populations would experience little exchange of larvae among estuaries and that each estuary would contain a separate stock. This concept was challenged by more recent work on migration of ovigerous females (Carr et al. 2004, Hench et al. 2004, Forward et al. 2005 and see aforementioned) and on the observed distribution of zoea larvae in the field (Dittel & Epifanio 1982, Epifanio et al. 1989, Epifanio 1995). These lines of inquiry showed that larval release and subsequent development occur mostly in the open waters of the continental shelf and that recruitment to juvenile populations requires movement of megalopae back to the estuary (Natunewicz & Epifanio 2001, Tilburg et al. 2006, Epifanio & Tilburg 2008).

Role of Swimming in the Larval Transport

As with most brachyuran crabs, the first zoeal stage of the blue crab lacks abdominal appendages, and the larvae swim via natatorial motion of two pairs of cephalic appendages (*maxillipeds*) and their associated setae (Fig. 1).[3] Swimming speed in blue crab zoeae varies with developmental stage and ranges from 0.5 to 2.0 cm sec^{-1} (Sulkin et al. 1980, Forward 1986, 1990), which is slower than typical surface currents on the inner continental shelf (Garvine 1991, Epifanio & Garvine 2001, Whitney & Garvine 2005). Thus, blue crab zoeae are unable to influence their transport by horizontal swimming. Sustained vertical swimming, however, allows zoeae to maintain a position high in the water column, which has important consequences for horizontal transport (Epifanio 1995, 2007). On molting to the megalopal stage, blue crab larvae have well-developed abdominal pleopods (Fig. 1) that are used to swim at sustained speeds approaching 5.0 cm sec^{-1} (Luckenbach & Orth 1992). This rate of movement is closer to the speed of ambient currents and may be important in controlling horizontal displacement on a small spatial scale during the actual settlement process (Anderson & Epifanio 2010b).

Studies of vertical swimming in crab larvae have focused on responses to cues in the environment, including temperature, salinity, hydrostatic pressure, gravity, and various aspects of light (Epifanio & Cohen 2016). Responses to these cues may occur as a change in orientation of swimming (*taxis*), a change in frequency or speed of swimming (*kinesis*), or both. Moreover, the responses may include a temporal pattern that requires continuing exposure to a recurring cue (*exogenous rhythm*) or in contrast persists through time in the absence of continued stimulation (*endogenous rhythm*).

Initial laboratory work on blue crabs indicated that zoea larvae have a kinetic response to increasing hydrostatic pressure (*barokinesis*) regardless of developmental stage (Table 3). Early-stage larvae, however, showed upward orientation in the water column (*negative geotaxis*), whereas advanced larvae exhibited downward orientation (*positive geotaxis*). Together, these results predict a near-surface distribution of early-stage zoeae and a deeper position as larval development progresses (Sulkin et al. 1980, Sulkin & Van Heukelem 1982). But once larvae have molted to the megalopal stage, they resume negative geotaxis (in the laboratory) and also display an endogenous swimming rhythm with maximum activity during the diurnal phase of the light/dark cycle. This combination of responses predicts a surface aggregation of megalopae during diurnal hours and a somewhat deeper distribution at night (Tankersley & Forward 1994, Forward et al. 1997).

Results of field observations (via plankton tows) have provided partial corroboration of these laboratory-based predictions. For example, surveys at different locations on the continental shelf have shown a consistent surface occurrence of early-stage zoea larvae (Steppe & Epifanio 2006, Epifanio & Tilburg 2008, Tilburg et al. 2008). In contrast to laboratory predictions, however, field studies also have shown an enhanced surface abundance of late-stage zoeae, and reasons for this disparity are not understood (Epifanio 2007).

In addition, laboratory findings have anticipated a reverse diel migration (daytime upward/nighttime downward) of megalopae

TABLE 3.

Vertical displacement of blue crab larvae and juveniles in response to environmental factors.

Stage	Factor	Displacement
Zoea	Downward light	↑
	Increasing salinity	↑
	Increasing pressure	↑
	Gravity	↑
Shelf megalopa	Diurnal phase (day)	↑
	Diurnal phase (night)	↓
	Increasing pressure	↑
Estuary megalopa	Diurnal phase (day)	↓
	Diurnal phase (night)	↑
	Increasing salinity	↑
	Increasing pressure	↑
	Increasing turbulence	↑
	Decreasing turbulence	↓
Early juvenile	Nocturnal phase (night)	↑

The displacement column describes the vertical movement of larvae or juveniles in the water column in response to each factor. Direction of arrows indicates net displacement toward or away from the surface. See text for discussion of vertical swimming behavior and consequent displacement. (Modified from Epifanio 2007)

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[3] Note that zoeal maxillipeds are also important in the capture and manipulation of prey organisms.

on the continental shelf, and there is evidence for diurnal surface occurrence of megalopae from daytime sampling in surface waters near the mouths of estuaries (Johnson 1985, McConaugha 1988, Epifanio et al. 1989). More recent work, however, has included both diurnal and nocturnal sampling, and has found only weak evidence for vertical migration on the shelf (Biermann et al. 2016). Accordingly, it has been concluded that onshore transport of blue crab megalopae in the coastal ocean is unrelated to vertical migration and is instead controlled by wind- and buoyancy-driven processes (see the following paragraphs).

The consensus view of the laboratory and field studies described previously envisages a surface distribution of both zoeae and megalopae during development in the coastal ocean. Thus, the circulation of surface water controls the transport of all stages of blue crab larvae while in the coastal ocean. This circulation is impelled by a combination of wind- and buoyancy-driven forces impacting the coastal region and occurs at frequencies that are lower than the frequency of tidal oscillation (Garvine 1991, Epifanio & Garvine 2001, Epifanio & Tilburg 2008). Accordingly, the temporal frequency and spatial scale of plankton net sampling has to be matched to the frequency of the physical forcing factors to allow sensible inference concerning the distribution of blue crab larvae in the coastal ocean (Epifanio & Garvine 2001 and see discussion below).

Details of Circulation on the Inner Shelf

Breeding populations of *Callinectes sapidus* in the United States extend from Long Island, NY, to the northern Gulf of Mexico. This range encompasses three major coastal regions (the MAB; the South Atlantic Bight; and the Gulf Coast), each with its own characteristic circulation. Among these regions, the southern expanse of the MAB has received the most study concerning the relationship between surface flow and transport of larval forms (Epifanio 1995, Epifanio & Garvine 2001, Epifanio 2007). The southern MAB is an area of broad continental shelf that extends 700 km southwestward from Long Island to Cape Hatteras, NC. Typical shelf width is 100 km, and depth at the shelf break varies from 50 to 100 m.

Details of shelf circulation in the southern MAB were poorly understood when work on coastal transport of blue crab larvae was initiated in the early 1980s (Epifanio 1995). Available data showed predominant subtidal flow from north to south, with some evidence of occasional reversals (Bumpus 1965, Beardsley et al. 1976, Norcross & Shaw 1984). The seasonality and strength of the reversed flow, however, were not well described (Bumpus 1965, Boicourt 1973, 1982), and the relevance to larval transport was not clear (Sulkin & Epifanio 1986). Data concerning across-shelf flow were also scarce but included observational, analytical, and modeling approaches to the problem (Beardsley & Hart 1978, Wang & Elliott 1978, Pape & Garvine 1982).

Interest in the physical oceanography of coastal regions generally increased in the 1990s, and there was extensive investigation of circulation in the southern MAB (Garvine 1995, Wiseman & Garvine 1995, LeVine et al. 1998). Related studies have continued into the 21st century and provide a physical basis for the present understanding of blue crab larval transport in the region (Yankovsky et al. 2000, Whitney & Garvine 2005, Tilburg et al. 2007).

The modern consensus is that low-frequency circulation on the inner shelf is controlled by variation in buoyant outflow from estuaries interacting with wind-driven circulation associated with regional weather patterns and events (Epifanio & Garvine 2001). Of particular consequence are the discrete coastal currents exiting the three large estuaries of the southern MAB (Fig. 5). Each of these currents is the strongest just south of its estuarine source, but down-shelf flow may continue for distances greater than 100 km (Münchow & Garvine 1993, Sanders & Garvine 1996). In all the three systems, flow intensifies in late spring, coincident with maximum river output, and the currents are weaker during the remainder of the year. Prevailing winds in summer blow from southwest to northeast and drive a persistent northward flow adjacent to the offshore edges of the respective coastal currents. This circulation includes an across-shelf, upwelling phenomenon that mixes water from the coastal currents offshore to the mid-shelf region (Epifanio & Garvine 2001). By contrast, onshore movement of surface water occurs when winds blow from northeast to southwest, often as a result of the passage of low-pressure atmospheric systems along the coast. These events drive downwelling circulation with an increase in subtidal sea level along the coast and consequent flow into the estuaries from the shelf (Wong & Garvine 1984). In both scenarios, it is primarily the along-shore component of the wind (which varies on a time scale of days to a week) that drives the across-shelf flow (Garvine et al. 1997). Less dynamic across-shelf circulation also occurs near the mouths of the MAB estuaries in association with their gravitational circulation (Beardsley & Hart 1978, Pape & Garvine 1982).

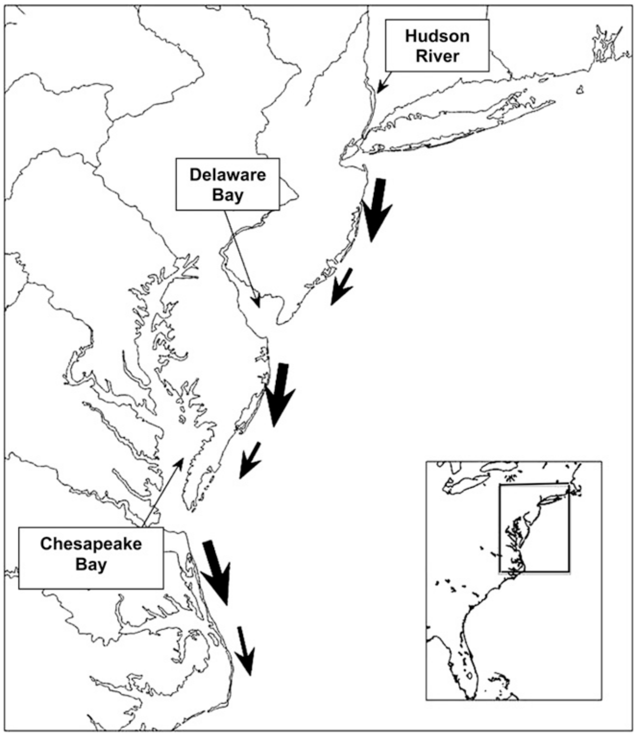

Figure 5. Map of the southern MAB. Black arrows show the general locations of the three coastal currents. Relative size of the arrows indicates maximum flow near the estuarine sources and decrease in flow at locations remote from each source. The inset shows the location of the MAB along the east coast of the United States. (Modified from Epifanio & Tilburg 2008)

The principal tidal signal in the southern MAB is the semi-diurnal M_2 tide. Tidal ellipses are mainly oriented in an across-shelf direction, and tidal residuals are weak (Pietrafesa et al. 1985). Accordingly, the net effect of tides on long-term transport of blue crab larvae while in the coastal ocean is small (Epifanio & Garvine 2001).

Surface circulation in other parts of the blue crab's range is broadly similar to the southern MAB and appears to have similar consequences for larval transport (Perry et al. 1995, Ogburn & Forward 2009, Jones et al. 2015). Nevertheless, there are considerable differences in the details of circulation. Although the southern MAB is dominated by the outflow of three large rivers, the South Atlantic Bight receives the discharge from a larger number of much smaller rivers, for example, Cape Fear, Cooper, Santee, Savannah, etc. This results in a narrow coastal current flowing southwestward along the coast (Blanton et al. 1989) and interacting with the upwelling/downwelling circulation that is driven by alongshore winds (Blanton et al. 1995). Mid-shelf circulation appears to be mostly wind-driven during the blue crab spawning season with surface flow mainly toward the northeast (Lee et al. 1982). By contrast, coastal circulation in the northern Gulf of Mexico is dominated by the westward-flowing Louisiana coastal current, which is driven by the outflow of the Mississippi and Atchafalaya rivers (Wiseman & Kelly 1994). As in the South Atlantic Bight, mid-shelf circulation is responsive to wind forcing and is characterized by weak along-shelf flow (Wiseman & Dinnel 1988) and more vigorous across-shelf flow associated with episodic wind events (Wiseman et al. 1988).

Early Conceptual Models of Larval Transport

Initial work in the mouths of Delaware Bay and Chesapeake Bay reported surface aggregations of newly hatched blue crab larvae in midsummer (Fig. 6), followed by similar pulses of megalopae in late summer and early autumn (Dittel & Epifanio 1982, McConaugha et al. 1983, Provenzano et al. 1983). Additional survey work in mid-shelf regions near the Chesapeake Bay also found concentrations of advanced zoeal stages in surface waters (Smyth 1980), and later work 30 km off Delaware Bay showed no evidence of vertical migration of blue crab zoeae regardless of time of day or stage of development (Epifanio 1988). Taken as a whole, these findings supported the idea that newly hatched blue crab larvae are exported from the estuary and that development through the subsequent zoeal stages occurs on the adjacent continental shelf.

As described previously, circulation in the southern MAB was poorly understood in the 1970s, and if surface flow were predominantly southward (as was thought at the time), then blue crab zoeae would be transported away from the natal estuaries and perhaps lost entirely to the MAB during the month-long duration of larval development. Convincing evidence for northward return flow, however, was developed in the late 1980s in a study that included simultaneous measurements of larval distribution and surface circulation near the mouth of Delaware Bay (Epifanio et al. 1989, Fig. 7). Results of current meter deployments provided strong evidence of wind-driven, northward-flowing surface water in late summer, and the intensity of that flow was sufficient to retain blue crab larvae

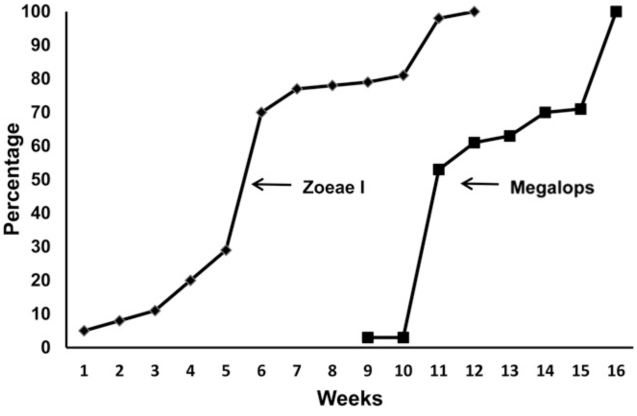

Figure 6. Cumulative percentage of the respective total numbers of Stage I blue crab zoeae and megalopae collected at a station located in the mouth of Delaware Bay during the 1979 spawning season. Sampling was conducted weekly and began in late June. Numbers on the *X* axis represent weeks of sampling. Note that megalopae occurred at the station 4–5 wk after Stage I larvae. This lag corresponds well to the duration of zoeal development of blue crabs in this geographical region. (Modified from Epifanio et al. 1984)

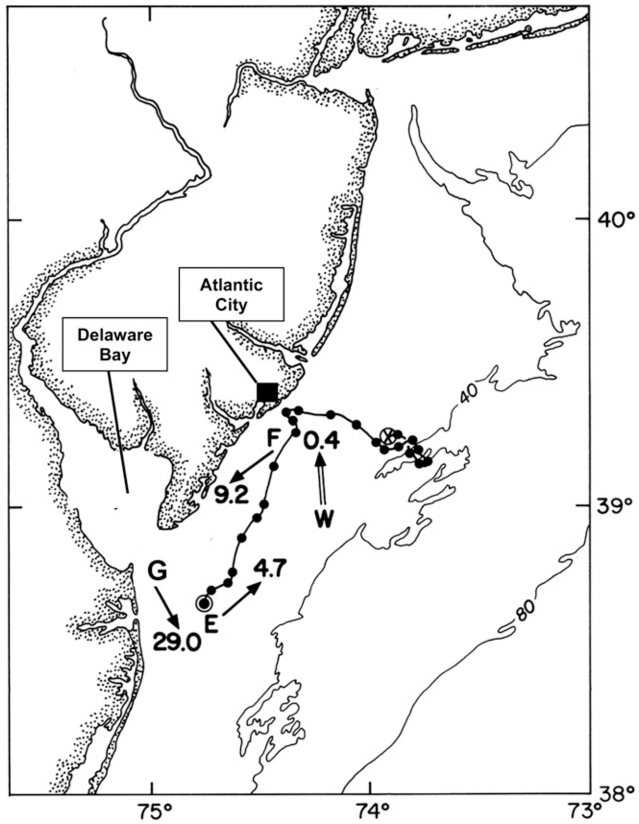

Figure 7. Progressive vector diagram for low-pass filtered surface current records from the summer of 1984 at Mooring E on the inner continental shelf off Delaware Bay, United States. Closed circles along each diagram represent 1-day increments in time. Mean current vectors for the entire sampling period are shown at Moorings E, F, and G with wind directions along the arrow and speed (cm sec^{-1}) given at the arrow point. The mean wind vector (W), measured at Atlantic City (filled square), is also shown with wind speed (m sec^{-1}) at the point of the arrow. Isobaths are in meters. (From Epifanio et al. 1989)

within the southern MAB and in many cases in the vicinity of the parent estuary itself (Garvine et al. 1997).

Although those studies demonstrated a clear mechanism for northward, along-shelf transport of zoeae, there still remained the issue of across-shelf transport of megalopae. Available data at that time included results of an extensive survey of megalopal abundance in the coastal ocean off Chesapeake Bay, which found a surface distribution of blue crab megalopae in the mid-shelf region along with a small but increasing number of megalopae deeper in the water column at stations closer to the bay mouth (Johnson 1985). Subsequently, Sulkin and Epifanio (1986) published a conceptual model that attempted to reconcile this observed distribution of megalopae with the potential transport mechanisms that were known for the region. The model proposed that surface-dwelling megalopae would be transported into the estuary as pulses associated with southward wind events, whereas those deeper in the water column would move shoreward along with the deep gravitational circulation. The model, however, had serious flaws associated with the sluggish flow of the gravitational circulation (Pape & Garvine 1982) and the low temperature of the near-bottom water, which was less than the thermal tolerance of blue crab megalopae (Epifanio 1988). Thus, subsequent work on across-shelf transport has concentrated almost entirely on the wind- and buoyancy-driven mechanisms that drive surface flow in the coastal ocean. For example, Goodrich et al. (1989) conducted high-frequency plankton sampling over periods as long as a week and correlated the episodic settlement of blue crab megalopae in lower Chesapeake Bay with the nearly simultaneous occurrence of southward wind events along the adjacent continental shelf. Little and Epifanio (1991) used similar techniques in the mouth of the Delaware Bay and reported comparable results. It has been agreed that downwelling circulation driven by southward wind events was the likely mechanism of across-shelf transport of blue crab megalopae from the coastal ocean into estuaries.

In addition, the development of moored collecting devices for megalopae in the 1990s allowed daily measurement of settlement in putative nursery habitat in the lower estuary (van Montfrans et al. 1995). Because of the matched temporal frequencies of megalopal sampling and the relevant physical processes, these data permitted a time series analysis of the interaction between larval settlement and wind-driven transport. Studies using these devices showed that settlement occurs as an aperiodic series of discrete events, rather than as a constant or cyclical supply of megalopae to the settlement site (Fig. 8), and further demonstrated strong association between settlement pulses and episodes of downwelling circulation (Jones & Epifanio 1995).

Present Conceptual Model of Transport

The results of the aforementioned body of research were encapsulated in the mid 1990s in a detailed conceptual model of blue crab transport in the southern MAB that has survived more than two decades of scientific scrutiny (Epifanio 1995, Epifanio & Garvine 2001, Epifanio 2007, Epifanio & Tilburg 2008, Ogburn et al. 2009, Ogburn & Forward 2012, Epifanio & Cohen 2016). In this three-part model, larvae are released on the continental shelf adjacent to the estuarine mouth and carried southward in the associated coastal current (Fig. 9). Advanced-stage zoeae are subsequently mixed offshore of the coastal current by upwelling circulation and are entrained in a northward-flowing current in the mid-shelf region. Megalopae are eventually transported across-shelf and back to the estuary as part of downwelling circulation associated with southward wind events that impact the continental shelf in late summer and autumn.

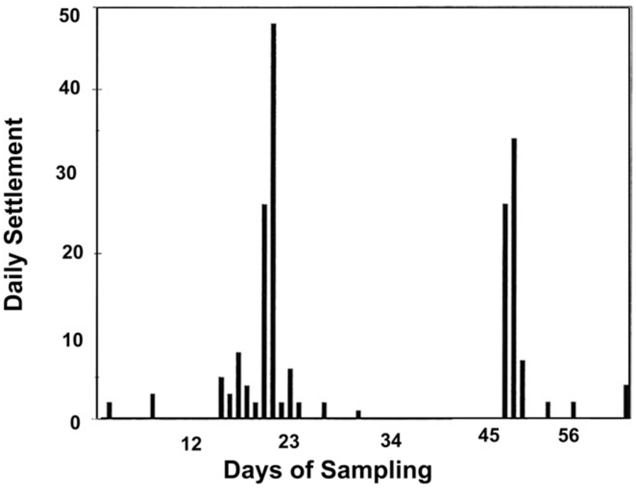

Figure 8. Daily settlement of blue crab megalopae in juvenile habitats near the mouth of Delaware Bay in the southern MAB. Sampling began on September 1, 1991. Values on the Y axis are the number of settling megalopae collected each day. Note that peaks in settlement occurred during southward wind events. (Modified from Jones &Epifanio 1995)

This conceptual model provides plausible mechanisms for the transport of blue crab larvae that are coherent with the life history of the species and with the present understanding of shelf circulation. But transport in the real world depends on the co-occurrence of patches of larvae with the onset of relevant physical processes. So an appreciation of the spatial distribution of larvae in the coastal ocean is important to the analysis of the transport problem (Epifanio & Garvine 2001).

Horizontal Distribution in Patches

Early surveys of blue crab zoeae provided some indication of spatial patchiness (Dittel & Epifanio 1982). The spatial and temporal aspects of sampling in that era, however, were inadequate for the characterization of the patches. For example, Epifanio et al. (1989) collected blue crab zoeae at a weekly frequency on the continental shelf adjacent to the mouth of the Delaware Bay and were able to determine the seasonality of occurrence and broad-scale spatial distribution of larvae. The fine-scale structure and temporal character of patches, however, remained enigmatic.

More recent work has used high-frequency plankton sampling on a fine spatial scale, combined with moored current meters and satellite-tracking protocols. These techniques have allowed spatial and temporal characterization of the patches (Epifanio 2007). Results have shown that patches of blue crab larvae are elliptical in shape with linear dimensions ranging from 500 to 2,500 m (Fig. 10). Initial formation of patches depends on synchronized spawning of a large number of females (Petrone et al. 2005), and distribution of patches in the coastal ocean is related to the location of larval release sites (Tilburg

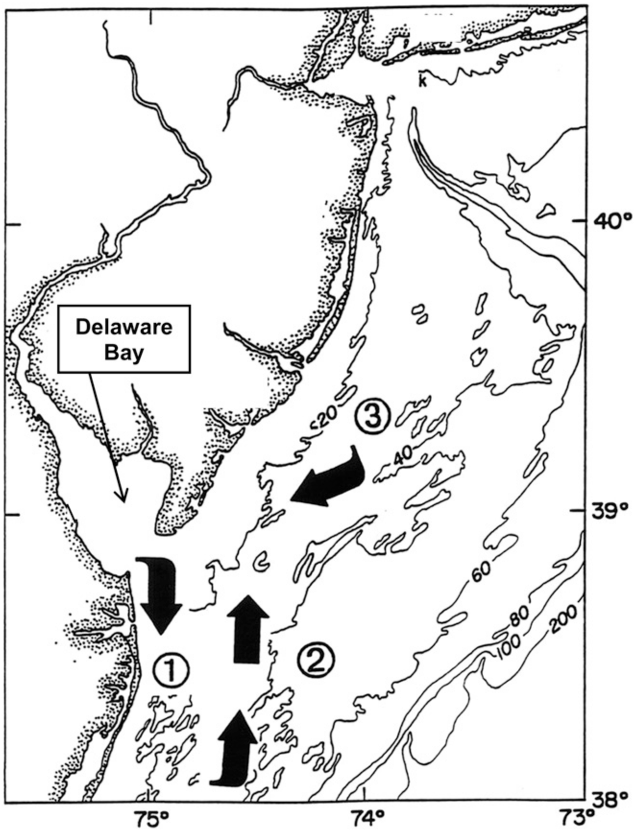

Figure 9. Bathymetric map of the Delaware Bay region in the southern MAB, illustrating the conceptual model for transport of blue crab larvae in summer and early autumn. 1. Midsummer southward transport in the buoyancy-driven flow originating in Delaware Bay. 2. Offshore transport in wind-driven upwelling circulation with associated northward transport. 3. Onshore and southward transport as part of downwelling circulation driven by southward wind events in late summer and autumn. (From Epifanio & Garvine 2001)

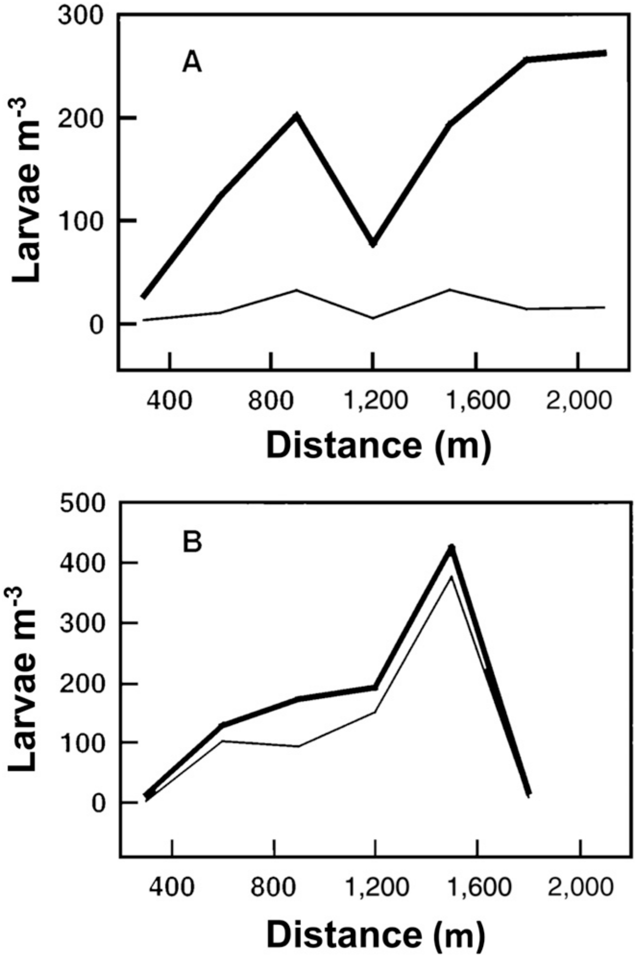

Figure 10. Dimensions of two representative patches of blue crab larvae (*Callinectes sapidus*) in the coastal ocean adjacent to Delaware Bay in the southern MAB. Abundance of Stage I (bold line) and Stage II (thin line) zoeae along a transect within a tagged patch. (A) August 10, 1998. Densities of the two stages are significantly correlated in space, but note the small percentage of Stage II. (B) August 13, 1998. Densities of the two stages are significantly correlated in space, but note the relatively high percentage of Stage II. (From Natunewicz & Epifanio 2001)

et al. 2006). For example, patches released in the coastal current are advected away from the release site, whereas those released in the coastal null zone (outside of the coastal current) are retained near the natal estuary (Steppe & Epifanio 2006, Tilburg et al. 2007). Moreover, satellite tracking of specific aggregations of zoeae showed that patch structure is maintained by physical processes in the water column (Natunewicz & Epifanio 2001, Natunewicz et al. 2001, Tilburg et al. 2006) and that trajectories of these patches over a period of few days were coherent with model simulations driven by physical data collected during actual tracking periods (Garvine et al. 1997, Natunewicz et al. 2001, Tilburg et al. 2006).

Most work on patchiness in blue crab larvae has concerned early-stage zoeae (Natunewicz & Epifanio 2001, Tilburg et al. 2006, Epifanio 2007), but there is additional evidence that advanced zoeal stages also are distributed in discrete aggregations (Petrone et al. 2005, Steppe & Epifanio 2006, Tilburg et al. 2009). Likewise, it is well established that settlement of blue crab megalopae occurs as distinct temporal pulses (Jones & Epifanio 1995, van Montfrans et al. 1995, Ogburn & Forward 2009), and these results have been interpreted as evidence that megalopae are distributed in spatial patches as well (Epifanio 1995). This idea was corroborated in a study that used high-frequency plankton sampling and moored current meters to characterize the length scales of megalopal patches at the mouth of the Delaware Bay (Jones & Epifanio 2005). The results from that study have provided strong evidence that blue crab megalopae are distributed in well-defined patches, which may partially explain the episodic pattern of settlement in nursery habitats near the estuarine mouth (Ogburn & Forward 2009, Ogburn et al. 2009).

Mathematical Models of Transport

The use of mathematical models provides a powerful tool for isolating effects of factors that govern larval transport in complicated flow regimes (Metaxas & Saunders 2009, Corell et al. 2012; Drake et al. 2013). For example, realistic simulation models allow researchers to turn off one physical process (e.g., tidal circulation) to focus on the effects of some other process (e.g., buoyancy-driven flow or wind-driven flow). Likewise, an investigator can run a model simulation with or without larval swimming behavior to isolate the effect of a biological process, such as diel vertical migration. Generally, the availability of mathematical models allows researchers to conduct experiments or observations in the virtual world that would be impossible in the real world (Tilburg et al. 2008). In addition, these models allow generation of surrogate data sets that link available real-world field observations.

There are two kinds of transport models, empirical models (Hill 1990, Garvine et al. 1997) and numerical prediction models (North et al. 2008). Empirical models are based on observed relationships between forcing factors (e.g., tide, wind, or river discharge) and current velocity. So to develop predictive algorithms, empirical models require extensive sets of coincident data concerning forcing factors and currents. By contrast, numerical prediction models are based on the fundamental (i.e., first-principle) equations that govern the physical flow fields, including the response to factors such as wind stress and topography. In practical use, the results of hydrodynamic simulations are linked to particle transport models that create trajectories of simulated larvae in the flow field (Tilburg et al. 2007, North et al. 2008, Jones et al. 2015). This type of coupled model can track large numbers of larvae released simultaneously or sequentially at different locations in the model domain (Tilburg et al. 2005, Banas et al. 2009).

Early modeling work on transport of blue crab larvae in the southern MAB used a two-dimensional, empirical model that assumed a near-surface distribution of zoeae on the inner continental shelf (Garvine et al. 1997). In this study, virtual zoeae were released in the coastal ocean near the mouth of the Delaware Bay, and eventual transport of megalopae back to Delaware Bay was defined as recruitment. This empirical model was designed to test the tenets of the conceptual model described previously (Epifanio 1995) and allowed investigators to compare trajectories of simulated and actual patches of zoeae (Natunewicz & Epifanio 2001). These data, in turn, allowed the researchers to compare simulated and actual settlement of megalopae in juvenile habitat (Garvine et al. 1997). In both cases the mathematical model provided reasonable support for the conceptual model.

Subsequent work on the transport of blue crab larvae has used a three-dimensional, numerical prediction model (ECOM3d) linked to a particle transport model to simulate larval trajectories (Blumberg & Mellor 1987, Tilburg et al. 2006). This approach has allowed investigators to address a number of issues, including settlement of megalopae in juvenile habitat (Tilburg et al. 2005), dynamics of larval patches (Tilburg et al. 2006), retention of larvae in coastal null zones, and convergent fronts (Tilburg et al. 2006, 2007, Epifanio et al. 2013), and effects of temporal patterns in larval release (Tilburg et al. 2008).

Additional work with blue crabs has used a numerical prediction model farther south along the Atlantic coast of the United States in Pamlico Sound (Reyns et al. 2007). Model simulations in this study incorporated known patterns of megalopal swimming behavior along with relevant physical processes in the study area (Forward et al. 1997). Results showed that simulated horizontal distribution of megalopae and early juveniles corresponded well to field observations, when both wind and tides were included in the model runs, but the relationship was incoherent when simulations included only wind or only tide.

SETTLEMENT AND METAMORPHOSIS

Types of Nursery Habitat

Blue crabs use several types of structured bottom habitats as nursery areas for juveniles (for detailed review see Hines 2007). These habitats include seagrass beds, macroalgal patches, marsh fringes, and oyster reefs. Nursery areas such as these provide settlement substrata for megalopae, as well as refuge from predation (Orth & van Montfrans 1987, Hovel & Lipcius 2001, Hovel & Fonseca 2005) and abundant prey organisms for juveniles (Beck et al. 2001, Seitz et al. 2011, Litvin et al. 2018). A given nursery site typically hosts a few distinct cohorts of juveniles each spawning season as a function of the episodic supply of megalopae (Jones & Epifanio 1995, Epifanio et al. 2003). This reduces intercohort cannibalism within the nursery. Once juveniles have reached a carapace width of 20–30 mm, they begin to leave the nurseries and move to open or less structured bottom habitat (Orth & van Montfrans 1987, Epifanio et al. 2003, Lipcius et al. 2007). This exodus may be triggered by a reduction in the refuge value of the nursery, that is, the crabs may simply outgrow the hiding places afforded by a structured bottom (Eggleston & Lipcius 1992, Lipcius et al. 2007, Johnston & Lipcius 2012). Alternatively (or perhaps in concert), the emigration may be driven by a trade-off between the increased predation risk for juvenile crabs foraging on open bottom and the augmented efficiency for juveniles in locating prey in unstructured habitat (Bromilow & Lipcius 2017). In any case, the relocation is facilitated by significantly lower rates of predation on juveniles once they have reached a carapace with greater than 15 mm (Pile et al. 1996, Hovel & Lipcius 2001, Orth & van Montfrans 2002).

The role of seagrass beds as nurseries has received particularly intense study throughout the North American range of the blue crab (Hines 2007). At least four species of seagrass serve this function, with eel grass *Zostera marina* predominant from New Jersey to North Carolina, shoal grass *Halodule wrightii* and turtle grass *Thalassia testudinium* more common farther south, and wigeon grass *Ruppia maritima* prevalent in very shallow water. Abundance of newly settled juveniles sometimes exceeds 100 crabs m^{-2} in seagrass beds (Heck & Thoman 1984, Orth & van Montfrans 1990, Wilson et al. 1990b, Etherington & Eggleston 2000, Rakocinski et al. 2003), but abundance generally decreases because of predation and emigration as the crabs pass through succeeding molt stages (Heck et al. 1995, Orth & van Montfrans 2002, Etherington & Eggleston 2003, Lipcius et al. 2005).

The abundance of seagrass is declining in some areas, however, and open bottom associated with this decline is sometimes colonized by benthic macroalgae (Orth & Moore 1983, Timmons & Price 1996, Moore et al. 2000). Although this habitat has not received a great deal of study, available evidence indicates that algal beds constitute critical nursery habitat for blue crabs in areas devoid of seagrasses (Wilson et al. 1990a, 1990b, Sogard & Able 1991, Epifanio et al. 2003). For example, abundance approaching 100 juveniles m^{-2} has been observed in beds of green *Ulva lactuca* and red *Gracilaria* spp. algae in a small lagoonal estuary near the mouth of Delaware Bay, and there appears to be a direct trophic link between amphipods that graze on the algae and juvenile crabs that prey on the amphipods (Epifanio et al. 2003). Moreover, algal beds at similar locations farther north along the coast of New Jersey appear to provide refuge from predation comparable with nearby seagrass habitat (Wilson et al. 1990a).

Blue crabs also use salt marshes as a nursery habitat (Tupper & Able 2000, Lipcius et al. 2005, Seitz et al. 2005), but the abundance in marshes is often lower than in seagrass or algal beds, and utilization by newly settled juveniles may be restricted to marsh fringe and tidal creeks (Mense & Wenner 1989, Fitz & Wiegert 1991, Jivoff & Able 2003). A few nonvegetated habitats are also used as nurseries by juvenile blue crabs. These include oyster reefs (Coen et al. 1999, Posey et al. 1999, Lehnert & Allen 2002) and coarse woody debris found in shallow areas adjacent to forested shorelines (Everett & Ruiz 1993). The abundance of juveniles in these habitats is generally low compared with seagrass or algal beds (Coen et al. 1999, Lehnert & Allen 2002).

Role of Larval Swimming in Finding Nursery Habitat

Both laboratory and field data indicate that blue crab megalopae undergo a change in behavior once they enter the estuary (Table 4). This new pattern of behavior is a type of vertical migration, wherein megalopae swim upward in the water column during nocturnal flood tides and remain deeper during ebb tides and diurnal flood tides (Epifanio et al. 1984, DeVries et al. 1994, Olmi 1994, Forward et al. 2007). The stimuli for upward swimming include increasing levels of salinity and hydrostatic pressure that are associated with rising tides (Tankersley et al. 1995). This response appears to be muted during daylight tides by a chemical cue in estuarine water (Forward & Rittschof 1994, Forward et al. 1996, Forward et al. 2005).

Upward swimming during nocturnal flood tides is augmented by a kinetic response to turbulent flow associated with the main current. In laboratory studies, megalopae continued to swim in the water column when turbulent kinetic energy was greater than a certain threshold (Welch et al. 1999). When turbulence dropped below the threshold, however, the megalopae sank to the bottom, where they remained until a combination of turbulence, increasing salinity, and darkness stimulated the recurrence of vertical swimming. This response provides a mechanism for upward swimming exclusively during nocturnal flood tides, followed by sinking and near-bottom distribution during other diel/tidal phases (Tankersley et al. 1995). This type of movement (*flood-tide transport*) is controlled by vertical shear in estuarine tidal currents, where maximum flow occurs at the surface and minimum flow occurs at the bottom (Epifanio & Garvine 2001). The effect of this behavior is rapid transport (at tidal frequency) from the estuarine mouth to nursery areas in the lower estuary (Forward et al. 2003b).

TABLE 4.

Transport of respective life-history stages of the blue crab *Callinectes sapidus* by currents in estuaries and on the adjacent continental shelf in the southern MAB.

Stage	Current	Frequency	Speed
Zoea	Coastal current	Subtidal	↑↑↑
	Northward shelf current	Subtidal	↑↑
	Upwelling circulation	Subtidal	↑↑
	Coastal null zone	Subtidal	↑
Shelf megalopa	Coastal current	Subtidal	↑↑↑
	Northward shelf current	Subtidal	↑↑
	Downwelling circulation	Subtidal	↑↑
	Coastal null zone	Subtidal	↑
Estuary megalopa	Nocturnal flood tide	Tidal	↑↑↑↑↑
Early juvenile	Nocturnal flood tide	Tidal	↑↑↑↑↑
	Nocturnal ebb eide	Tidal	↑↑↑↑↑
	Nocturnal wind-driven	Subtidal	↑↑↑
Phase I female	???	???	???
Phase II female	Nocturnal ebb tide	Tidal	↑↑↑↑↑

Relative speed of the currents and consequent transport is represented by different numbers of arrows. See text for a discussion of tidal-frequency and subtidal-frequency currents.

Primary Settlement and Secondary Dispersal

As discussed above, the advent of moored collectors in the 1990s allowed time series analysis of megalopal settlement on artificial substratum in a number of estuaries in the Middle Atlantic and South Atlantic Bights. Analysis of settlement at a daily frequency has documented a strong positive correlation between settlement peaks and episodes of wind-driven, onshore flow, and more than 50% of annual settlement at a given site was often explained by the combined settlement during just a few of these episodes (Jones & Epifanio 1995, Ogburn et al. 2009, 2012). Likewise, analysis at hourly frequency has shown a strongly episodic nature of settlement with a primary peak at high slack water and a secondary peak at slack water before flood (Tankersley et al. 2002). These results are coherent with laboratory data showing a cessation of upward swimming of megalopae when turbulent kinetic energy in the water column is low (Welch et al. 1999).

In large estuaries with weak tidal circulation, primary settlement of megalopae is limited to nursery habitats located close to ocean inlets, and secondary dispersal to structured habitat farther up the estuary (away from the inlets) is dependent on wind-driven transport of newly metamorphosed juveniles (Forward et al. 1995, Etherington & Eggleston 2000, 2003, Reyns & Eggleston 2004, Reyns et al. 2007, Eggleston et al. 2010). This process requires upward swimming into the water column by the juvenile crabs, which has been corroborated by field observations in the Albemarle-Pamlico Estuarine System along the Atlantic coast of North Carolina (Blackmon & Eggleston 2001, Etherington & Eggleston 2003, Forward et al. 2004). Companion laboratory studies of early-stage juvenile crabs from this system have demonstrated a pattern, wherein the juvenile crabs swim up in the water column during the time of darkness in the field, regardless of tidal phase (Forward et al. 1995, 2004, 2005). Thus, a simple circadian rhythm in swimming activity provides the behavioral basis for nocturnal, secondary dispersal of early juvenile blue crabs in weakly tidal systems. This process, however, has yet to be studied in large, strongly tidal estuaries such as the Chesapeake or Delaware Bay (Reyns et al. 2007).

Role of Chemical Cues in Finding Nursery Habitat

Because of the patchy spatial distribution of estuarine nursery habitats, it is not surprising that chemical cues are involved in the settlement process (Eggleston et al. 1998). Like other brachyuran crabs, blue crab larvae eventually reach a point at which they are competent to undergo metamorphosis (Epifanio & Cohen 2016). This transition occurs during the megalopal stage and is marked by a progression in the molt cycle from intermolt to premolt stage (Forward et al. 2001). During this period of competency, megalopae respond to environmental cues that accelerate or retard the process of metamorphosis, and the effect of any putative cue can be quantified as the amount of time between initiation of competency and the actual metamorphic molt.

Early study of effects of chemical cues on metamorphosis in blue crabs used field-caught megalopae. For example, Wolcott and De Vries (1994) collected megalopae from the inner shelf near the mouth of Chesapeake Bay and found that exposure to estuarine water accelerated metamorphosis compared with water from the site of collection. Forward et al. (1994) corroborated these results and again found that estuarine water stimulated metamorphosis compared with shelf water and that the addition of the eelgrass *Zostera marina* yielded further acceleration of the molting process. Exposure to odors from adult blue crabs, however, had no effect compared with shelf water alone, and this result has been attributed to the widespread distribution of adult blue crabs in the estuary compared with the patchy distribution of nursery habitat, that is, there is no selective advantage to settling near adults. In fact, there may be a major disadvantage to settling near adults and older juveniles because of the high incidence of intercohort cannibalism in this species (Moksnes et al. 1997, Hines 2007, Bromilow & Lipciius 2017). In follow-up studies, Forward et al. (1996) again found that metamorphosis was accelerated in estuarine water and determined that one of the active cues was a small molecule (<10 kDa) in the humic acid family. Further investigation indicated that exposure to natural humic acids extracted from estuarine water had a significant effect on metamorphosis, and a similar effect was obtained from commercial humic acid (Forward et al. 1997).

Additional laboratory study of habitat-specific cues tested effects of seagrass and benthic algae on metamorphosis (Brumbaugh & McConnaugha 1995, Forward et al. 1996). The results showed that water-soluble compounds produced by seagrasses accelerated metamorphosis as effectively as exposure to the grass itself and also found that abiotic mimics of the seagrasses had no effect at all. Moreover, the influence of benthic algae varied strongly among species, with some taxa producing a significant effect on metamorphosis and others having no activity whatsoever. A related field investigation of settlement in blue crabs showed similar results in which megalopae settled preferentially on artificial substratum that contained seagrass blades but not on substratum that contained salt-marsh cordgrass (Welch et al. 1997). The findings of that study also showed that settlement was reduced significantly on substratum that contained potential predators, and related laboratory trials demonstrated that megalopae avoided water that contained predator odors. These results were corroborated by additional work, which showed strong preference by blue crab megalopae for seagrass in field-deployed mesocosms and cages (van Montfrans et al. 2003, Moksnes & Heck 2006).

Additional laboratory studies used flume techniques to investigate the role of directional swimming in finding a suitable nursery habitat (Diaz et al. 1999, Forward et al. 2003a). Results of these studies showed an increase in upstream swimming in response to rising concentrations of seagrass odor. By contrast, there was an increase in downstream swimming in response to chemical cues produced by potential predators.

SUMMARY AND CONCLUSIONS

The intent of the present review has been to discuss contemporary understanding of the early life history of blue crabs in the context of a coherent time line of development, beginning with courtship and mating of adult crabs, and extending through a number of subsequent steps to the eventual settlement and metamorphosis of megalopae in juvenile nursery habitat. The summary presented in the following paragraphs is a condensation and critical evaluation of that discussion and is organized along similar lines.

Courtship and Mating

Female blue crabs reach sexual maturity after 17–19 postlarval molts and do not undergo additional molting during their remaining life history (Williams 1974). Copulation in female blue crabs occurs during the soft stage immediately following the final (pubertal) molt, and females are incapable of additional copulations once the integument becomes calcified (Milliken & Williams 1980). By contrast, males are fully calcified at the time of copulation and are promiscuous (Kendall et al. 2001). Precoital pair formation is prompted by pheromones released by mature males and prepubertal females. Recent work has chemically characterized one of the pheromones found in female urine (Kaimo et al. 2017).

Copulation itself is initiated within minutes of the pubertal molt. Male ejaculate consists discrete packages of sperm (spermatophores) immersed in seminal fluid. Oocytes are undifferentiated at the time of copulation, and spermatophores are held for several months in female storage structures (spermathecae) during the process of egg maturation (Jivoff et al. 2007). Fertilization eventually occurs in the spermathecae, and newly fertilized eggs are extruded through the genital pores to the ventral surface of the abdomen and brooded until hatching. Blue crabs are highly fecund, and a typical female produces more than 2 million eggs in her first brood (Prager et al. 1990).

Spawning Migrations

Mating in blue crabs occurs during the warm season in oligo- and mesohaline regions of estuaries, where salinities are often below the tolerance limits for larvae and early juveniles (Epifanio 2007). Consequently, inseminated females migrate from mating grounds in the upper and middle estuary to areas near the estuarine mouth, where eggs are brooded and hatched. The migration occurs in two phases and in large estuaries may cover a distance greater than 200 km (Aguilar et al. 2005). The initiation of migration is preceded by an extended refractory period during which inseminated females remain in the mating grounds to recover from molting and copulation (Jivoff et al. 2007). The first phase of migration occurs along the edges of the deep channel that marks the main stem of most estuaries. Migration in this corridor begins in the first autumn after copulation and includes overwintering of large groups of inseminated females along the migratory route (Turner et al. 2003). The females resume their migration in the following spring and, by midsummer, reach high-salinity areas near the estuarine mouth, where fertilization of the eggs occurs (Jivoff et al. 2007).

The second phase of migration involves the movement of ovigerous females from the lower estuary to the adjacent coastal ocean, where eggs hatch and larvae are released. In this part of the migration, ovigerous females swim upward into the water column during ebb tidal flow and drop to the bottom during flood tides, which facilitates seaward transport of the crabs (Forward et al. 2003b).

Larval Release

The release of larvae occurs in the estuarine mouth and in the adjacent coastal ocean, and there is a latitudinal difference in the across-shelf distribution of hatching grounds (Gelpi et al. 2013). Hatching occurs as a short, synchronous event, where all eggs in the broods of neighboring females are released near the time of early morning high tide (Tankersley et al. 2002). This is important in the generation of large surface patches that characterize the spatial distribution of blue crab larvae on the continental shelf (Natunewicz & Epifanio 2001). The synchronous aspect of larval release is controlled by endogenous tidal and diel clocks and is facilitated by chemical communication between females and brooding embryos (Rittschof & Cohen 2004).

Larval Transport

Larval development in blue crabs includes seven zoeal stages followed by a single megalopal stage. Zoeal development requires 3–4 wk under favorable conditions, whereas duration of the megalopal stage is more variable. The swimming speed of blue crab larvae is slower than the speed of surface currents on the inner continental shelf, and larvae are unable to modulate their movement on the shelf by horizontal swimming (Epifanio & Garvine 2001). Instead, larval transport is controlled by the interaction between sustained vertical swimming and circulation of the surface water (Epifanio 2007). Important aspects of surface flow include the interaction of buoyant outflow from estuaries and wind-driven circulation associated with regional weather patterns and events (Epifanio & Garvine 2001). Of particular consequence are the buoyant coastal currents exiting large estuaries along the coast and their interaction with the upwelling/downwelling circulation that characterizes the inner shelf during the blue crab spawning season (Epifanio & Garvine 2001). Recent work on the transport of blue crab larvae has been aided by development and application of mathematical models (Tilburg et al. 2008).

Settlement and Metamorphosis

Blue crabs use several types of structured benthic habitat as nursery areas for juveniles. These areas provide settlement substrata for megalopae, as well as refuge from predation and abundant prey organisms for the juveniles (Hines 2007). Once juveniles have reached a carapace width of 20–30 mm, they begin to leave the nurseries and move to open or less structured bottom habitat (Epifanio et al. 2003). The role of seagrass beds as nurseries has received particularly intense study, and abundance of newly settled juveniles sometimes exceeds 100 crabs m^{-2} in this habitat (Lipcius et al. 2005).

Transport of megalopae to nursery habitat involves a change in swimming behavior after the megalopae have moved from the coastal ocean back into the estuary (Forward et al. 2005, 2007). In this new behavioral pattern, the megalopae swim upward in the water column during nocturnal flood tides and remain deeper during ebb tides and diurnal flood tides. The stimuli for upward swimming include increasing levels of salinity and hydrostatic pressure that are associated with rising tides, augmented by a kinetic response to turbulent flow associated with the main current (Forward et al. 2005). This overall response provides a mechanism for upward swimming exclusively during nocturnal flood tides, followed by sinking and near-bottom distribution during other diel/tidal phases (Tankersley et al. 2005). The effect of this behavior is rapid transport from the estuarine mouth to nursery areas in the lower estuary (Forward et al. 2003). In estuaries with weak tidal circulation, however, primary settlement of megalopae is limited to nursery habitat located very close to ocean inlets, and secondary dispersal to structured habitat farther up the estuary is dependent on wind-driven transport of newly metamorphosed juveniles, aided by a circadian rhythm in upward swimming activity (Eggleston et al. 2010).

Selection of appropriate settlement sites by blue crab megalopae involves the reception of chemical cues emanating from nursery habitat. Early study of effects of chemical cues found that estuarine water accelerated metamorphosis compared with shelf water and attributed the effect to a small molecule in the humic acid family that is typically found in estuarine water (Forward et al. 1996). Additional investigation over the following decade pointed to seagrasses and seagrass odors as one of the signature characteristics of appropriate juvenile habitat (van Montfrans et al. 2003). Work with other crab species, however, indicates that these odors are not detectable beyond a few meters distance (Anderson & Epifanio 2010a). Accordingly, the broad-scale transport of megalopae to nursery habitat is not mediated by chemical cues *per se*. Rather, megalopae use characteristic odors to discriminate between suitable and adverse settlement sites only after they have arrived at putative nursery habitat, and the transport process itself is dominated by physical processes in the water column (Epifanio & Cohen 2016).

CONCLUSIONS

The synthesis presented in this review is based on a large body of research on blue crabs stretching back to the late 19th century. Much of the early work was purely descriptive and provided a patchwork perspective on the natural history of blue crabs. This is in contrast to more modern work that has taken an integrated approach intended to provide a coherent time line of processes important in the early life history of the species. For example, recent investigation of courtship and mating has emphasized the role of chemical cues and has characterized the chemical structure of at least one of the important pheromones. Likewise, contemporary work on the female spawning migration has shown that the journey consists of two distinct phases and that the second phase is based on an endogenous tidal rhythm of vertical swimming by the ovigerous females. Further study of this process has shown that hatching of eggs occurs in the coastal ocean—not in the estuary as previously thought—and that release of larvae occurs as a short, synchronous event, which is important in the generation of large surface patches that characterize the spatial distribution of blue crab larvae on the continental shelf. Additional modern study of hatching has shown that the synchronous aspect of larval release is controlled by endogenous tidal and diel clocks, and is facilitated by chemical communication between females and brooding embryos. Perhaps the most important contribution of the past few decades has been the discovery that larval development in blue crabs occurs mainly in surface waters of the inner continental shelf—not in the estuary—and that larval transport on the shelf is controlled by the interaction between buoyant discharge from the estuary and wind patterns over the coastal ocean. Accordingly, the recruitment of blue crab larvae to estuarine nursery habitat is influenced largely by physical processes until the larvae leave the coastal ocean and reenter the estuary, after which a suite of larval behaviors becomes additionally important. The present understanding of these processes has been greatly facilitated by recent development of mathematical models that have allowed researchers to conduct experiments or observations in the virtual world that would be impossible in the real world.

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