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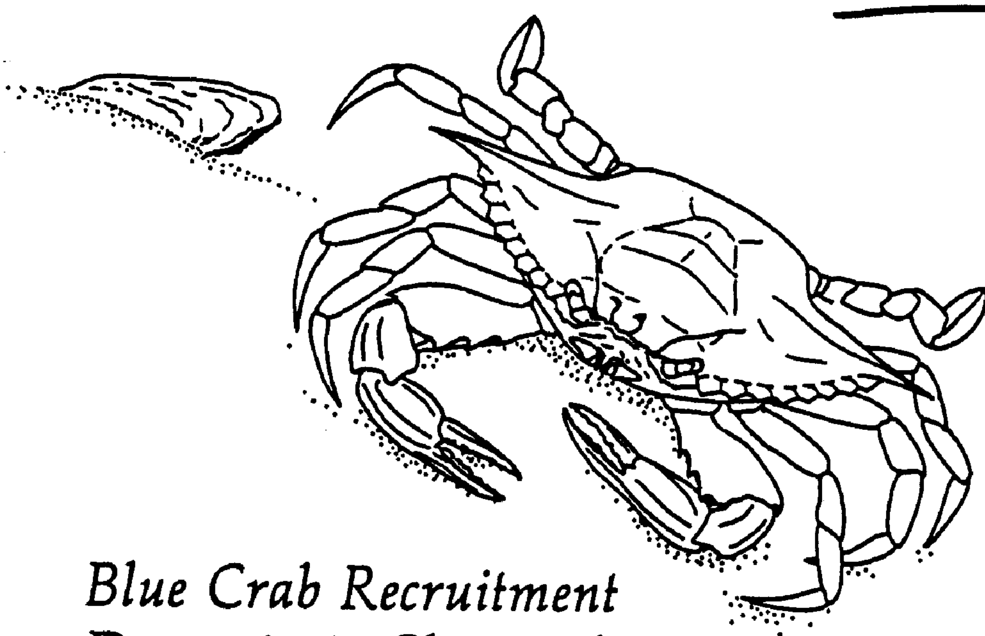

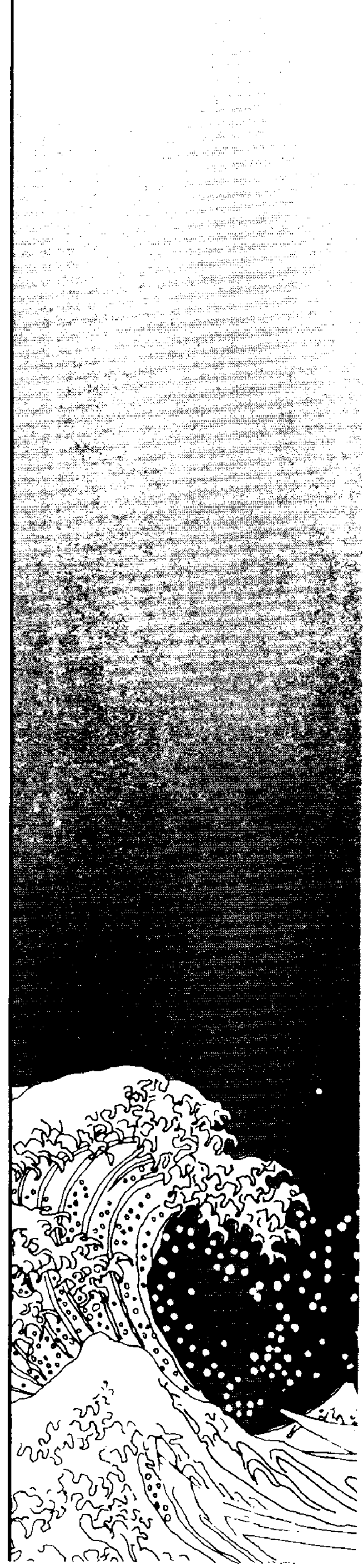

Blue Crab Recruitment Dynamics in Chesapeake Bay:

A REVIEW OF CURRENT KNOWLEDGE

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BLUE CRAB RECRUITMENT DYNAMICS IN CHESAPEAKE BAY: A REVIEW OF CURRENT KNOWLEDGE

David E. Smith and Mariana Knappenberger

To many people, Chesapeake Bay and the blue crab are synonymous; blue crabs have been harvested from the Bay for as long as anyone can remember. The bountiful harvests each year of this animal result in significant economic returns to the watermen, seafood processors and distributors of Virginia and Maryland. For example, the value of commercial hard shell blue crab landings in Virginia was over $10 million in 1987 alone. In addition, the blue crab is of great ecological importance as a major consumer and scavenger in the ecosystem. Yet, even with its associated economic and ecological importance, there are still major gaps in our scientific knowledge of the blue crab. These data gaps are particularly troublesome when scientists or resource managers try to quantitatively address the population dynamics of blue crab, including blue crab recruitment processes (i.e., the entry of new individuals into the Bay population). This brief synopsis is an effort to identify 1) what is known, and conversely unknown, about blue crab recruitment into Chesapeake Bay, and 2) the degree of scientific certainty, or uncertainty, regarding the current state-of-knowledge of blue crab recruitment processes in the Bay.

Mating and Fecundity -- The reproductive processes of the blue crab (Callinectes sapidus) are relatively well documented. In the Chesapeake Bay region, mating typically occurs during the months of May through October, with peak activity in late August through early September (Van Engel, 1958, 1987). Mating occurs immediately subsequent to the female crab molting, while the female is still in the soft-shell stage. During copulation, sperm is transferred by the attending male to the female where it is stored in seminal receptacles (Van Engel, 1958). Fertilization generally does not occur at the moment of mating; instead, the sperm remain viable for several months in these receptacles.

It is thought that males may mate several times during the year, while females apparently mate only once during their lives. According to conventional theory, females exhibit a "terminal molt", between the immature, per-pubertal female and mature adult stages, when successful mating must occur. Once the female molts into the mature adult stage the animal stops growing and molting. However, the data supporting this "terminal molt" hypothesis is not unequivocal. Recently, Havens and McConaugha (in press) summarized observations which tend to refute this hypothesis; however, their data are also circumstantial. Therefore the concept of a "terminal molt" in the female blue crab, and a single opportunity to mate, remains controversial.

Once females have successfully mated, they migrate toward the mouth of the Chesapeake Bay (Van Engel, 1958). Similar migrations have been observed in the estuaries of Louisiana (Darnell, 1959), North Carolina (Judy and Dudley, 1970), Florida (Tagatz, 1968) and South Carolina (Archambault <u>et al.</u>, in press).

In the vicinity of the Bay mouth an egg mass, or "sponge", is then extruded onto the animals pleopods, or abdominal appendages (Van Engel, 1958; Millikin and Williams, 1984;). Fertilization occurs as the eggs pass from the ovaries to the pleopods. Egg production peaks twice in the Chesapeake Bay region, once in May or June and again in August (Van Engel, 1958, 1987). Gross fecundity estimates have been published and generally range from less than 1,000,000 to 2,000,000 eggs (Churchill, 1919; Graham and Beaven, 1942; Pyle and Cronin, 1950; Van Engel 1958). However, with the exception of one account (Prager et al., in press), data relating fecundity to carapace length, width, or body weight are non-existent.

Duration of the egg stage generally varies between ten to seventeen days (McConaugha et al., 1983; Millikin and Williams, 1984; Van Engel, 1987). This variation is due in part to environmental influences, such as diffences in salinity and temperature, and may have a genetic component as well. Laboratory studies indicate that successful hatching occurs primarily in combination with environmental conditions (ie., salinity and temperature) typically found at the Bay mouth (Costlow and Bookhout, 1959; Davies, 1965). Circumstantial evidence implies a synchronized egg hatch which coincides with nightime ebb tide (Provenzano et al., 1983); however, there has been no direct observation of this phenomenon in the field.

Larval and Post-Larval Development -- After the eggs hatch, the first stage larvae, or first stage zoeae (Figure 1), swim toward

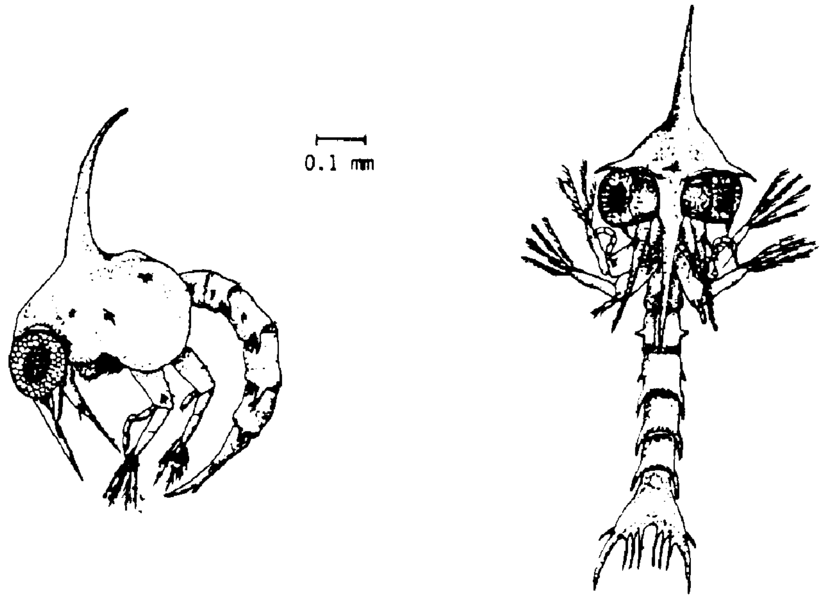

Figure 1 -- Gross morphology of first stage Callinectes sapidus zoeae (from Costlow and Bookhout, 1959).

the surface waters and into the neuston layer (McConaugha et al., 1981; Provenzano et al., 1983; Johnson, D. R., 1985). The field observation that zoeae are found in the surface water is consistent with laboratory data indicating that first stage zoeae are positively phototactic, negatively geotactic and display a high degree of barokinesis (Sulkin et al., 1980; Sulkin and Van Heukelem, 1982). Larval blue crabs pass through as many as eight zoeal stages, with seven stages being most commonly observed (Costlow and Bookhout, 1959; Epifanio et al., 1984; Van Engel, 1987). Laboratory studies of zoeal development indicate that zoeae survive and molt at salinities greater than 20°/oo and temperatures between 20-30° C. Beyond the first zoeal stage, optimum salinities for larval development increase; post-larval (megalopae) development is optimal at salinities above 30°/oo (Costlow and Bookhout, 1959). From laboratory experiments conducted at several salinities and temperatures, the duration of the zoeal stage ranges from approximately 30 - 60 days (Costlow and Bookhout, 1959; Sulkin and Van Heukelem, 1986). However, the authors note wide variation in the duration of any one particular zoeal stage.

Eventually the larval blue crabs molt into the post-larval, megalopal stage (Figure 2). Megalopae of C. sapidus, like the zoeae, have large variations in the length of their stage, ranging from thirty to ninety days under normal ambient conditions (Costlow, 1967), with an average duration of about forty days (Sulkin and Van Heukelem, 1986). Costlow (1967) and Sulkin and Van Heukelem (1986) have shown that temperature and salinity are important variables affecting megalopal duration,

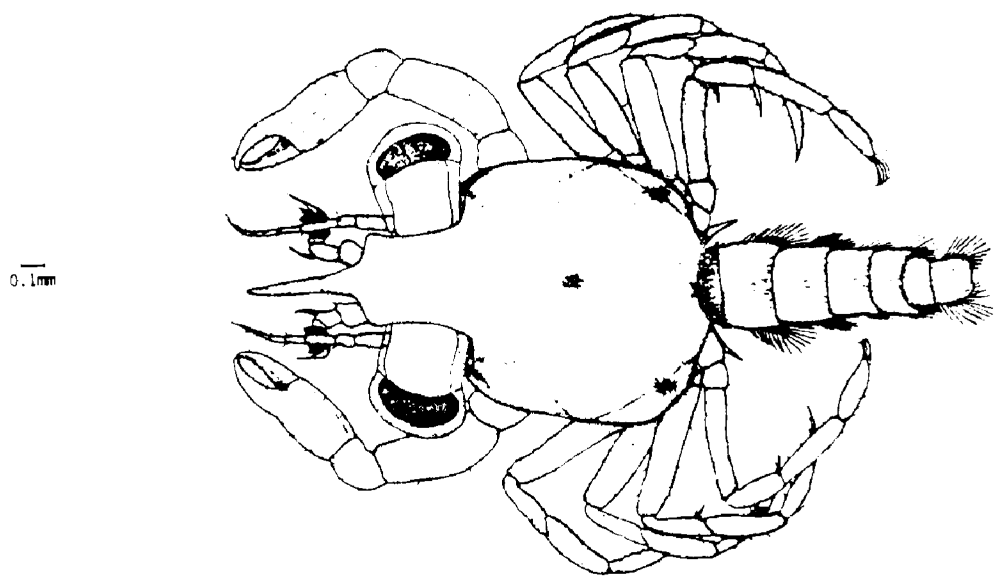

Figure 2 -- Gross morphology of Callinectes sapidus megalopae (from Costlow and Bookhout, 1959).

pointing out that this variation will affect potential recruitment success. Food quantity and quality are also important in determining life stage duration and have only recently become the focus of scientific inquiry.

Larval and Post-Larval Distribution and Behavior -- Ultimately, it is the behavior and survival of the pelagic zoeal and post-larval stages, and physical circulation at the Bay's mouth and on the adjacent continental shelf that will dictate to a great degree recruitment strength.

Some of the first accounts of zoeal distribution in the vicinity of the Chesapeake Bay mouth suggested that zoeal concentrations were highest between the two Virginia Capes and decreased both up the estuary and seaward (Van Engel, 1958). However, Sandifer (1973, 1975) reported that Callinectes larvae were more abundant just outside the Bay mouth than within the Bay, and were more concentrated in the surface waters than at depth. Field sampling in the early 1980's has documented high concentrations of zoeae offshore, over the continental shelf (McConaugha et al., 1981, 1983; Sulkin et al., 1982). These reports further indicate that only early stage zoeae are present in significant numbers in or near the Bay mouth, while later stage zoeae are most abundant further offshore (i.e., fifty or more kilometers east of the estuary). The zoeae sampled offshore were concentrated in the surface waters in general, and the neuston in particular (Figure 3). This field observation is not entirely consistent with the laboratory work of Sulkin et al.

(1980) which indicated that as the zoeae progressed through its various stages they became more positively geotactic, while their swimming rate decreased in response to higher salinities, resulting in a net downward movement in the water column. The observed distribution in the field is, however, accepted as correct.

This pattern of zoeal distribution creates an interesting situation for the larval crab; young crab larvae are being swept out of the Chesapeake onto the shelf and conceivably out of the Chesapeake Bay system. This prompted scientific inquiry into whether or not Chesapeake Bay-spawned crabs were being carried by the net southerly flow along the shelf to reinvade southern

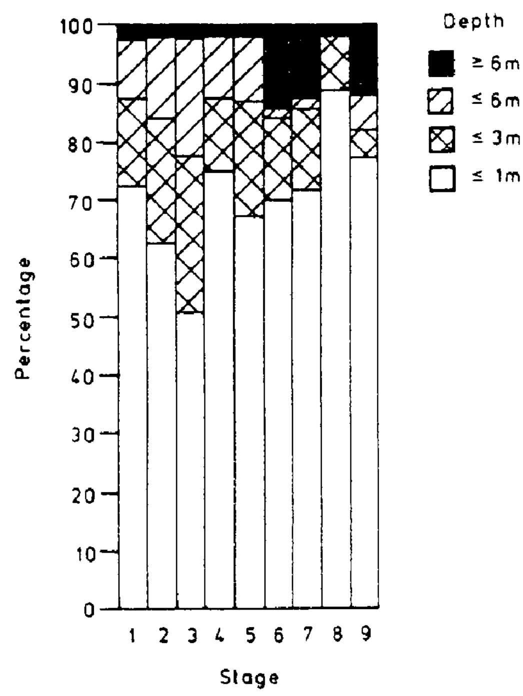

Figure 3 -- Typical depth distribution of <u>Callinectes sapidus</u> larvae over the inner shelf off Chesapeake Bay (from McConaugha, 1988).

estuaries (e.g. Pamlico/Albemarle Sound), or whether some mechanism existed to retain the larval and post-larval stages in the vicinity of the Bay mouth for potential reinvasion. A consensus response to this question has only recently begun to coalesce.

Surface waters, with associated biota including zoeae, leave the Bay mouth flowing in a southerly direction in a coastal plume (Boicourt, 1982). However, current meter measurements during the summer months have documented a net northern flow of surface water along the inner continental shelf (Boicourt, 1982). An examination of the magnitude of the local wind stress on the surface waters of the inner continental shelf also predicts a net northward flow (Johnson, D. R. et al., 1984; Johnson, D. R., 1985). This net flow occurs only on the inner shelf, independent of the southerly flowing coastal jet and surface water over the outer continental shelf (Figure 4). Because zoeae are primarily found in the surface waters and neuston over the shelf, as the coastal jet dissipates and loses its integrity, the zoeae become entrained in the northward-moving surface water along the inner shelf and are gradually swept back toward the Bay mouth. Reasonable estimates of flow rates, both measured and those calculated from surface wind intensities, predict that this process takes approximately one to two months, sufficient time for the larvae to transform into megalopae while being retained in the vicinity of the Bay mouth (McConaugha et al., 1983; Johnson, D. F., 1985).

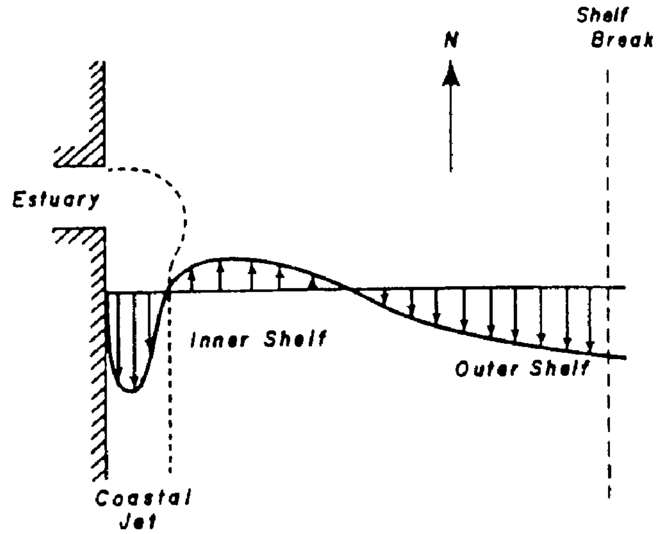

Figure 4 -- Diagram representing summer surface flow over the continental shelf in the Mid-Atlantic Bight (from Boicourt, 1982).

Megalopal crabs are found concentrated on the inner shelf adjacent to the Bay as well as farther offshore. McConaugha (1988) suggests a generalized distribution envelope for megalopae north of the preponderance of stage 1 zoeae (Figure 5). This distribution pattern is consistent with the gross physical circulation patterns previously described. Megalopae found far offshore, however, are probably lost to the recruiting population (McConaugha, 1988). These distribution patterns have led some researchers to postulate that the variability in duration of the larval and post-larval stages is an adaptation which helps assure that at least some progeny will be in close proximity to an appropriate estuarine nursery habitat when they metamorphose to first stage juvenile crabs (Sulkin and Van Heukelem, 1986).

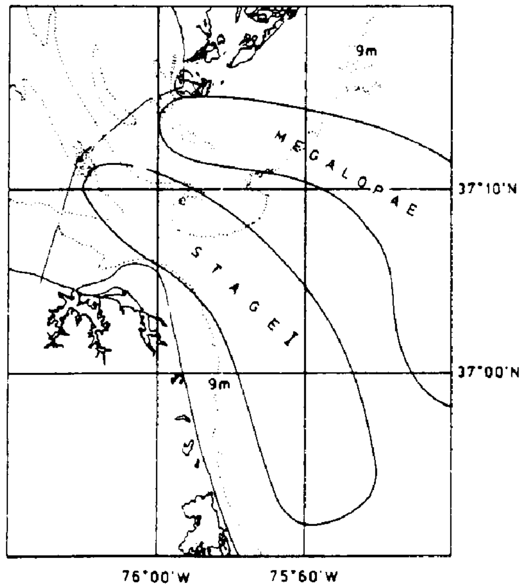

Figure 5 -- Generalized distributional envelopes of peak numbers of first stage zoeae and megalopae of Callinectes sapidus (from McConaugha, 1988).

While the above scenario provides a reasonable explanation for retaining Chesapeake Bay blue crab larvae and post-larvae in the vicinity of the Bay mouth, it does not offer a mechanism for reinvasion. In fact this step in the recruitment process is probably the least well understood.

Available data indicates that in offshore waters the megalopae, like the zoeae, are found in the neuston or surface layer (Johnson, D. R., 1985; McConaugha, 1988). Unfortunately, the number of samples taken near or in the Bay mouth is limited. Those samples that have been taken near or in the Bay mouth indicate significant variation over time in the vertical position of the megalopal population (McConaugha, 1988; Maris and McConaugha, 1988). The causes of these changes in vertical positioning are unknown. Significant concentrations of megalopae have also been observed in field samples from within the Bay itself. The small number of observations designed to assess the megalopae's vertical position in the Bay indicate that the primary center of abundance is in mid-depth to deep water (Maris and McConaugha, 1988), although some diel vertical migration appears to occur. However, Olmi (1989) has recorded high surface concentrations during nighttime flood tide in the York River. Environmental cues such as light, or tide, may effect the megalopaes vertical position, however the exact relationships and causes have not been elucidated. The concentrations of megalopae sampled in the Bay and over the continental shelf in the vicinity of the Bay mouth imply that the megalopae are the main reinvasive stage. But juvenile reinvasion may also be occurring to some degree (Sandifer, 1975; Johnson, 1985; Epifanio, 1988; McConaugha, 1988).

Post-Larval Reinvasion -- Assuming that the megalopae are the major reinvasive stage, a key recruitment question is how exactly do they reinvade? One theory is that megalopae take advantage of landward residual, non-tidal, currents (Sulkin and Van Heukelem, 1986). While the net flow from Chesapeake Bay is seaward, both the vertical and horizontal physical complexities of flow across the Bay mouth create reasonably predictable regions of residual net inflow of water. Megalopae located in these residual inflow areas will be transported into the Bay. A second proposed mechanism involves megalopae exploiting deep water, tidally-driven currents to invade the Bay. To take advantage of the tidal, landward currents, megalopae would have to swim up in the water column during flood tides, and sink in the water column on ebb tides thus producing a net landward movement (Epifanio _et al._, 1984). In other estuarine systems,such as Delaware Bay, megalopal migration into the surface waters during nighttime flood tides and back to the deeper waters during the day has been shown to be an effective mechanism for transporting the post-larval crab up the estuary (Meredith, 1982; Olmi, 1986; Epipanio, 1988). This behavior has not, however, been demonstrated to occur at the mouth of the Chesapeake Bay. In either case, the vertical position of the animal with respect to water flow is critical.

Another proposed mechanism for megalopal reinvasion centers on episodic, wind-induced water exchange events. Several researchers have suggested that during periods of strong and persistent easterly wind, shelf surface waters in the vicinity of the Bay mouth may be blown into the Bay, carrying with them megalopae residing in the surface waters (Johnson, D. R., 1985; Goodrich _et al._, 1988). Goodrich _et al._ (1988) noted a correlation between megalopal settlement on artifical substrates in the York River and the occurrence of positive Bay volume anomalies associated with major inflow events. While this concept is intriguing, causal relationships have yet to be demonstrated. Epifanio (1988) has also noted that in all "positive estuaries", such as Chesapeake Bay, the net flow of water is out of the estuary. Therefore, surface megalopal advection into the Bay via this mechanism could only occur during major atmospheric cyclonic disturbances.

Whatever the mechanism, or combination of mechanisms, the complex physical environment and the behavior of the crabs must interact to assure successful recruitment.

Once in the Bay, megalopae most probably utilize the tidal flood currents to move upstream to invade the shallow sub-estuaries and tributaries (Meredith, 1982; Olmi, 1986). During this journey, the megalopae will eventually settle and undergo metamorphosis to the first juvenile instar.

Post-Larval Settlement -- Recently, researchers have concluded four years of monitoring settlement in the York River using subsurface artifical substrate collectors (van Montfrans *et al.*, in press). Settlement typically occurs between the months of August and November in the Chesapeake Bay and is strongly episodic (Figure 6). Periodic pulses of megalopal settlement have been observed each year, but the timing and intensity of these pulses varies between years. The duration of these pulses is generally only a few days. These data, which have been analyzed for lunar and tidal correlational components, indicate significantly more megalopal settlement during periods surrounding the full moon. As one might expect, settlement was also correlated with periods of maximum tide resulting from the full moon, with a lag period of zero to two days (van Montfrans *et al.*, in press).

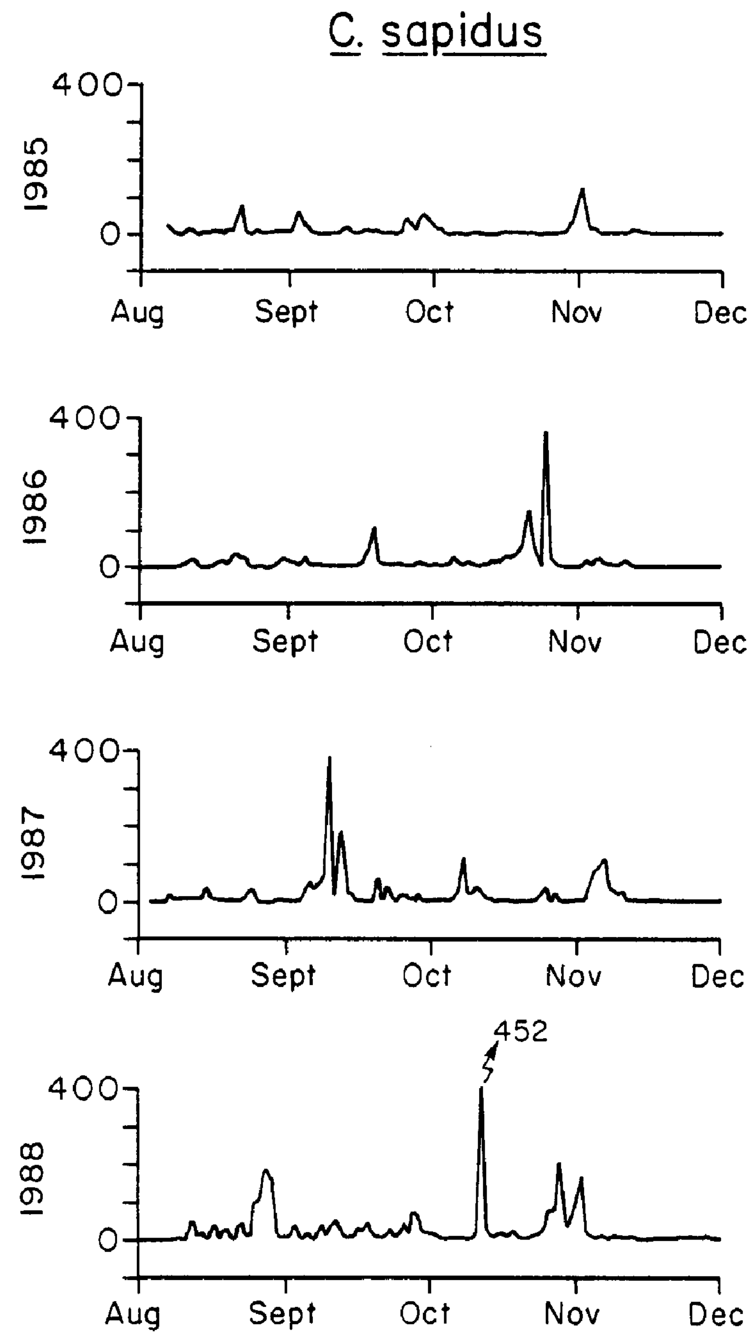

Figure 6 -- Daily settlement of blue crab megalopae on artificial collectors from August - December, 1985-88 (Courtesy of J. van Montfrans and R. Orth).

These observations are interesting and raise several scientific questions. First, are the data recovered from the York River site representative of the Bay in total? Second, are the settlement pulses purely the result of episodic settlement behavior, or are they a reflection of episodic reinvasion of the Bay by megalopae? In other words, how are larval availability and settlement patterns related in time and space? And lastly, what are the first-order processes or causes as opposed to correlations, which trigger the megalopae to metamorphose into juvenile crabs? These questions are the current focus of field and laboratory research in the Bay region.

To complete the recruitment picture, information regarding crab habitat preference is also being generated through additional research. Vegetated habitats support more juvenile crabs by an order of magnitude than adjacent unvegetated marsh creeks (Orth and van Montfrans, 1987). However, the exact environmental cues which stimulate megalopal settlement in one habitat over another have not been totally elucidated. Additionally, the ability of the megalopae to delay metamorphosis has been proposed as a mechanism important to successful recruitment by some researchers (e.g., McConaugha, 1988). While temperature affects the rate of metamorphosis, the exact role of many other water born environmental cues (e.g., chemical cues such as secondary metabolites released from aquatic plants) have yet to be definitively determined.

Figure 7 summarizes blue crab recruitment schematically. The matrix in Figure 8 attempts to put estimates on the degree of certainty to which information on blue crab ecology and recruitment dynamics is known. The assessments given in the matrix are those of the authors. Many other questions remain regarding blue crab recruitment into Chesapeake Bay which have not been addressed here. For example, while a physical/biological theory has been summarized which provides a mechanism for retaining exported Chesapeake Bay blue crab larvae within the Chesapeake system, how often, and to what degree, are larval and post-larval blue crab transported between major estuaries? How important is predation on the crab larvae and post-larvae to recruitment success, or lack of success? And what are the zoeal and megalopal feeding processes and dynamics? What are their nutritional requirements? These vital questions are now being investigated to varying degrees.

To answer these process-oriented questions and fill in the gaps in the matrix will require the joint expertise of biological and physical oceanographers, working together on similar spatial and temporal scales. Eventual fulfillment of this cooperative, interdiscplinary approach will yield the information necessary to construct, and validate, a comprehensive recruitment model for Chesapeake Bay blue crabs.

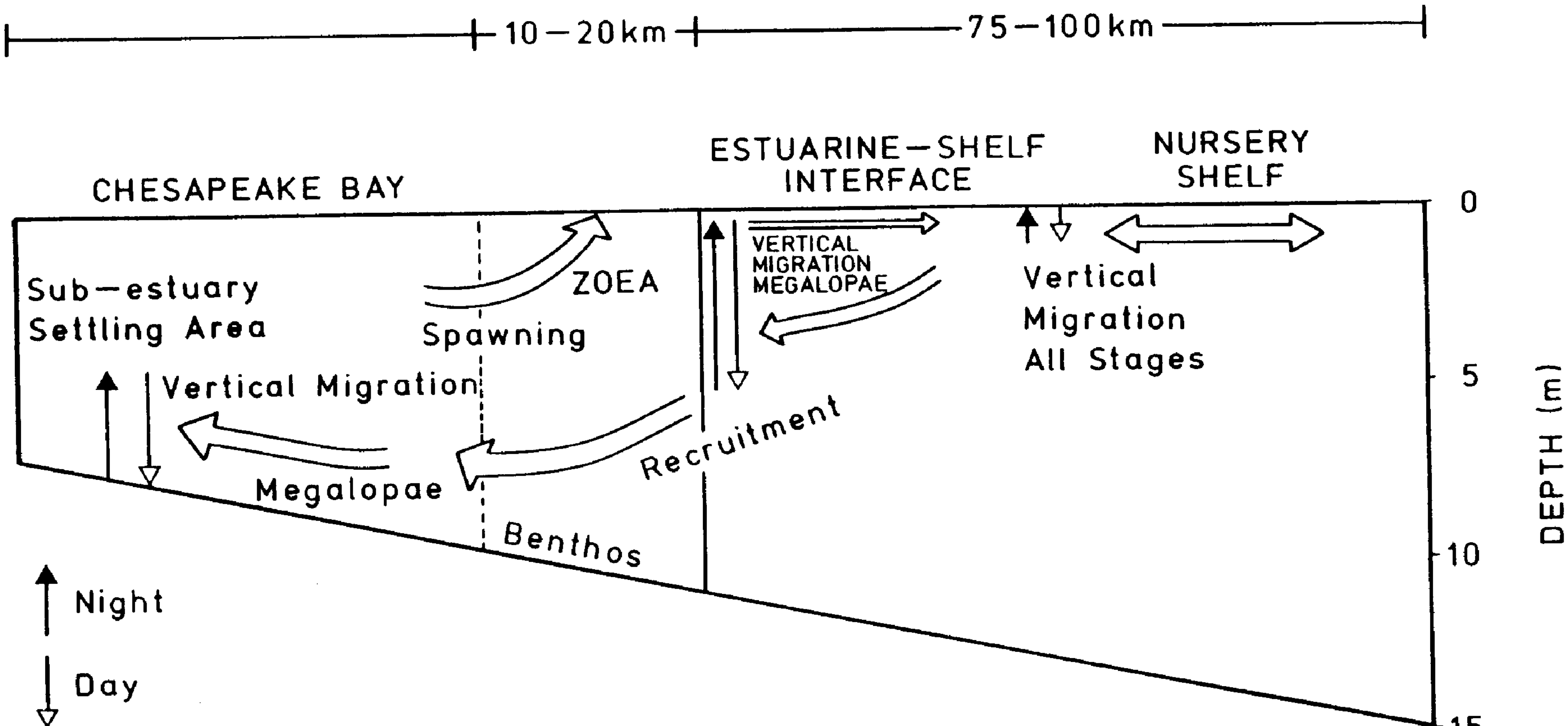

Figure 7 -- Schematic diagram of the recruitment path and processes responsible for blue crab recruitment into Chesapeake Bay. (Courtesy of J. McConaugha)

Figure 8 -- Degree of Understanding of the Recruitment Dynamics of Larval and Post-Larval Blue Crabs (*Callinectes sapidus*) in Chesapeake Bay

	Life History Stage			
	Mating	Egg Stage	Zoeal Stage	Megalopal Stage
Seasonality	●	●	●	●
Frequency	○[1]	-	-	-
Location Geographic	●	●	○[5]	○[5]
Fecundity	-	○[2]	-	-
Location Water Column	-	●	●	◒[7]
Envir. Requir. for Survival	-	●	◕[6]	○
Release Stimuli	-	○	-	-
Length of Stage	◕[3]	◕	◒[4]	◒[4]
Natural Mortality	-	○[10]	○[10]	○[10]
Settle. Stimuli	-	-	-	○[9]
Behavior	●	-	◕	◒[8]
Nutritional Requirements	-	-	○[11]	○[11]
Feeding Dynamics	-	-	◒[12]	◒[12]

Key: Well Known ● ◕ ◒ ○ Least Well Known

1/ Uncertainty regarding the existence of a "terminal molt" in the female blue crab results in significant uncertainty regarding the frequency of mating.
2/ While gross fecundity estimates exist, fecundity as related to body dimension and weight is not well defined.
3/ Sperm transferred to the female can remain viable for several months before being used to fertilize the eggs. Internal and external cues necessary to trigger spawning are not well defined.
4/ While the general duration of the stage(s) is known, the environmental factors (i.e., salinity, temperature, food quantity and quality, etc.) which dictate specific stage duration are unknown. The degree of genetic control of stage length is also

unknown although Sulkin and Van Heckelem (1986) documented significant variation in the length of the zoeal phase of sibling zoeae raised in the laboratory.

5/ While the general geographic region of distribution offshore is thought to be known (although the spatial and temporal coverage of field samples is very limited), the interaction of the physical environment (i.e., currents) with the individual animals is unknown. Currently, it is not possible to predict geographic distribution range or population center offshore for a given set of climate and hydrologic conditions.

6/ While a large amount of information exists regarding zoeal development under various environmental conditions (see Costlow and Bookhout, 1959; Costlow 1965), the matrix defining environmental conditions and development needs further definition.

7/ The limited number of field observations available indicate that offshore, megalopae are found in the surface water. However, water column location at the Bay mouth is not well defined (see note 8).

8/ In the vicinity of the Bay mouth, the vertical behavior of the megalopae and, more importantly, the environmental cues affecting behavior are unknown. Behavioral alterations due to developmental age of the megalopae are also unknown.

9/ Specific environmental cues for settlement, including chemical cues, are unknown.

10/ Total wastage due to starvation, predation and loss from the Chesapeake circulation system is unknown.

11/ An indepth comparison of optimal nutritional conditions verses what the animals experience in the field in terms of food types processed is not available.

12/ Quantified feeding dynamics, using ambient prey items and concentrations Have been investigated by McConaugha (pers. comm.).

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