THE BLUE CRAB:
A SURVEY WITH APPLICATION TO SAN ANTONIO BAY

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EXECUTIVE SUMMARY

The purpose of this report is to summarize the ecological attributes of the blue crab as manifested on, or relevant to the Texas coast, and specifically to San Antonio Bay. A literature survey of the biology and life stages of the blue crab is presented, with particular emphasis upon the Texas environment. Catch data from the Texas Parks and Wildlife Coastal Fisheries monitoring program is analyzed for San Antonio Bay.

The blue crab (*Callinectes sapidus* Rathbun) is a ubiquitous crustacean in San Antonio Bay, and on the Texas coast. It is ecologically important as both prey and predator, and is an important fishery resource for humans. The crab migrates between sea and estuary as part of its life cycle, the estuary serving as a nursery for the young. Knowledge of this organism is dominated by research on the mid-Atlantic coast, yet it has been known for many years that the blue crab life cycle on the Texas coast differs in some respects from that on the Atlantic. In general, the life cycle of the blue crab can be summarized as follows:

(1) Larvae (zoeae) are hatched in nearshore waters of the inner continental shelf. As plankton, they are carried about on the inner shelf by prevailing currents.
(2) Over a 1-2 month period, the larvae develop through seven zoeal stages, then metamorphose into postlarvae (megalops). Depending upon nearshore and shelf currents, zoeae and megalops can be dispersed many tens of kilometers along the coast, and from the coast out several tens of kilometers.
(3) Some of the postlarvae are transported by cross-shelf currents back into the nearshore zone, where a portion of these may be subject to transport into the mouths of estuaries.
(4) Postlarvae enter the estuary as irregularly timed pulses of high density. Once within an estuary, they are carried into nursery habitats, where they settle and metamorphose into the first juvenile crab stage. Despite their planktonic character, this is, at least in part, a directed migration, effected by a combination of deliberate vertical movement between seabed and water column, and horizontal transport by currents.

(5) During their early stages, some juveniles migrate further up the estuary, presumably by selectively entering the water column during favorable currents, where they populate additional nursery habitat.
(6) Crabs develop through approximately twenty juvenile stages, over one to three years depending upon conditions, during which they occupy deeper and less structured habitat, and migrate throughout the reaches of the estuary.
(7) Upon maturity, mating occurs, generally in the shallower reaches of the estuary. Females usually mate once, acquiring a lifetime supply of semen.
(8) The inseminated females begin a seaward migration, while males continue forage-meandering. This leads to a spatial partitioning between the two sexes in the estuary, the females increasing in abundance in the lower reaches of the estuary closer to the mouth, while in the upper reaches males become predominant.
(9) Ovigerous females migrate to the sea, where they spawn and ultimately hatch their broods, either in the estuary mouth or in the nearshore waters.

These stages of the life cycle apply generally throughout the range of the blue crab. However, the details of each vary with location.

The chief hydroclimatological variable that controls the blue crab life cycle is water temperature. Temperature influences mating, spawning, egg development, zoeal development, intermolt duration and growth rate, and a number of underlying metabolic functions. Apart from controlling the timing of major steps in the crab life cycle, one important influence of temperature is its enforcing of winter dormancy in the estuaries of the temperate latitudes (notably the mid-Atlantic).

There are three major differences apparent between the blue crab life-cycle on the mid-Atlantic coast and on the Texas coast, in San Antonio Bay in particular:

(1) The winter dormancy in the mid-Atlantic, when crabs burrow into the sediments and overwinter. During this period, growth ceases. There is no winter hiatus in Texas except during exceptionally cold winters.

(2) The shorter duration of the various life stage activities in the mid-Atlantic compared to Texas. For the mid-Atlantic, there is a cleaner separation between these stage-related activities (e.g., mating, spawning, immigration from the sea, juvenile grow-out), and a more step-like progression through the life-cycle stages, while on the Texas coast, all of the activities are underway nearly simultaneously.
(3) The shorter development to maturity on the Texas coast, completed in about a year, compared to over two years on the mid-Atlantic.

Part of the differences between these two geographical areas is due to the cooler temperatures on the mid-Atlantic, generally limiting the periods of biological activity. Part of it derives from the much larger size of the principal mid-Atlantic estuaries. On the Texas coast, crabs may migrate between the shallow inland marshes to the passes to the Gulf in a matter of days to a few weeks. On the mid-Atlantic, months are required for the same migration, which may be interrupted by the occurrence of winter.

The least understood phase of the blue crab life cycle is the period of larval development, which takes place on the inner continental shelf. Patches of blue-crab larvae created by hatching events are carried along the coast by seasonal currents. Along both mid-Atlantic and Texas coasts, the prevailing longshore current sets to the southwest. This current carries the larval patches down the coast while cross-shelf transport mixes the patches across the shelf. During late summer, on both coasts, the longshore currents reverse, setting to the northeast. This would transport the larvae back up the coast. Onshore winds concentrate postlarvae in the nearshore zone. The net effect is to disperse the larvae and postlarvae along the coast and then render the postlarvae available to potentially be carried into the estuaries.

The postlarval (megalop) influx to the estuary occurs as large, sporadic pulses of high density superposed on a relatively constant, low density. Artificial-substrate megalop collectors deployed on both the Atlantic and Gulf of Mexico coasts indicate that the megalop influx to the Gulf of Mexico estuaries is one-to-two orders of magnitude *greater* than the Atlantic. Yet, the densities of early juveniles in primary habitats on both coasts are about the same. This has led

some researchers to hypothesize that megalopal settlement on the Gulf coast is probably predation-limited, perhaps even self-regulated through cannibalism.

Data on blue-crab abundance collected by Texas Parks and Wildlife (TPWD) was analyzed for San Antonio Bay. This analysis concentrated on collections by otter trawl, since this sampling gear addresses the open waters of the bay, and covered the period 1982-2009. Since 1982, the beginning of the period of analysis for the TPWD blue-crab data, Cedar Bayou has been either closed or only marginally open, and therefore unlikely to have significantly affected the abundance of crabs in the bay. Earlier, during the 1960's and 1970's, substantial influxes of megalops were measured in Cedar Bayou, when it was at its largest recorded dimensions. Post-larval entry during the period of our data analysis would have been principally through Pass Cavallo (and the Matagorda Entrance Channel) to the north and Aransas Pass to the south.

In San Antonio Bay, a consistent annual pulse in abundance and associated size was determined. Four divisions of the year were inferred:

December – March: a marked increase in abundance with stable median size around 50 mm. Crabs hatched in the July-August period would be attaining this size during this period. This would also correspond to the approximate size range in which crabs move out of the marshes and shallows into the bays and bayous.

March – May: crab density more or less stable while mean size increases from about 60 to 90 mm. This could result from grow-out of the existing population so that the sizes shift upward with no change in abundance.

May – September: a monotonic decline in density by nearly a factor of ten, while the median size is relatively constant around 90 mm. One scenario that would entail this result is a loss of crabs of sizes evenly distributed about 90 mm, e.g., to harvesting and predation.

September – December: abundance variable but stable, while mean and median shift downward to smaller sizes. A loss of larger sizes, influx of smaller sizes, or both would achieve this result.

While there are year-to-year variation in the magnitudes of abundance and the calendar period of these stages of the annual cycle, in general these are consistent with the picture of blue crab migration and grow-out that has emerged from the literature survey.

San Antonio Bay was subdivided into six subregions and blue crab data evaluated in each of these. All six regions exhibit the four periods of annual variation identified above. The data do not show a clear sequential progression of blue-crab density variation from one segment to the next, as might have been anticipated from a slow migration into or out of the estuary. Instead, the variation in density in all six segments is generally coherent, suggesting that the crabs enter or leave the estuary population sufficiently quickly that on a monthly time resolution they are synchronous.

Evaluation of abundance versus salinity for individual trawl-event data, and for data averaged monthly and over the entire region of the bay, disclosed no significant variation with temperature or salinity. The above annual pulse of abundance is out of phase with the annual rise and fall of temperature, so the lack of correlation between these variables is not surprising. With respect to salinity, blue crabs are osmoregulators that survive — even thrive — in a wide range of salinity. The only stage of the blue-crab life cycle that requires a narrow range of salinity and temperature is the larval, which needs the warm saline conditions of the ocean. It is seeking these salinity conditions that impels the post-insemination migration of the female to the sea. Otherwise, the blue crab is a remarkably effective osmoregulator, which accounts for its abundance from Sabine Lake to the Laguna Madre. This may also account for the general lack of a simple relationship between salinity and blue-crab density in the TPWD monitoring data for San Antonio Bay. Acclimation is important in the tolerance of the blue crab to a range of salinity. On the lower Texas coast, and in San Antonio Bay in particular, the main threat that salinity presents is its sudden reduction to zero during a major flood hydrograph. The ubiquity of blue crabs in the shallow, marshy regions of San Antonio Bay and other Texas estuaries, which are also typically low-salinity zones, may be for reasons other than lower salinity, as suggested by recent studies on decapod habitat use in estuaries.

Freshwater inflow provides several mechanisms that could plausibly increase the abundance of blue crabs, besides moderating salinity, and therefore it is warranted to seek a direct relation between abundance and inflow. For San Antonio Bay, the correlation proved negligible, though there are some time-lagged responses that suggest an avoidance or mortality response to inflow events, followed by a later increase in abundance perhaps due to beneficial effects of inflow. These analyses are very preliminary and employ only linear statistics. A more sophisticated time-series analysis will be necessary to expose a relation between blue crabs and inflow (as well as salinity).

Since the mid-1980's, a declining trend has been manifested in both the numbers and size, *a fortiori* in total biomass, of blue crabs in the Texas bays. Over the period 1982-2005, there was a 70% reduction in blue crab biomass in the TPWD data. On a bay-to-bay basis, the trend is noisier, as might be expected. For San Antonio Bay, and indeed the Coastal Bend bays, the declining trend is clearly evident. Similar declining trends have been observed elsewhere on the Gulf of Mexico coast and on the Atlantic coast as well. The causes are not understood, and it would be premature to conclude that some large-scale factor is at work everywhere (though that cannot be precluded either). Among the hypothetical causal factors are overfishing, poor water quality, predation, disease and parasitism, habitat loss, and, generally, people.

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1. INTRODUCTION

The purpose of this report is to summarize the ecological attributes of the blue crab (*Callinectes sapidus* Rathbun) as manifested on, or relevant to the Texas coast, and specifically to San Antonio Bay. This summary has three principal objectives:

(1) Present a succinct description of the biology and life cycle of the blue crab, particularly with respect to its migration and utilization of the estuarine environment, and specific, insofar as possible, to the Texas coast;

(2) Illustrate and exemplify the distribution of blue crab in space and time in the San Antonio Bay system;

(3) Provide a physical-chemical-biological framework to inform assessment of the response of the organism to freshwater inflow, i.e., quantify the acceptable ranges of environmental parameters controlled or influenced by inflows to the estuary, required by the organism.

This is a companion study to other investigations conducted within the Coastal Impact Assistance Program that together address the environmental controls on abundance of blue crab in the San Antonio Bay system, *viz*. inflows to the estuary (Ward, 2010a) and status of Cedar Bayou (Ward, 2010b), and is the first phase of a projected two-phase study.

The project formulation grew out of the continued concern in Texas with defining the freshwater inflow requirements of its estuaries, to whose purpose a half century of intensive data collection, analysis and modeling has been devoted on the part of several state agencies, river authorities, academic institutions, and engineering firms. The past decade has seen an intensification of concern among water planners, engineers, scientists and the general public in Texas with "environmental flows" — the flow regime required for maintenance of an aquatic ecosystem — that has culminated in implementation of Senate Bill 3, whose basic objective is the specification

of standards of flow to serve as a means of regulating water demands of human activities that potentially impact the magnitude of flows in the watercourses of the state. Underlying all of this technical activity is the philosophy that there exists a cause-and-effect relation between freshwater inflow and the quality of an aquatic ecosystem, which is capable of unambiguous quantification if the necessary field measurements and sufficiently sophisticated analytical methods can be brought to bear. Despite the acknowledged importance of freshwater inflow to an estuary, and notwithstanding the substantial effort thus far invested in the problem, a satisfactory solution remains elusive. Some of the reasons for this are considered by Montagna et al. (2011).

Clearly, a project with the modest resources of this one cannot aspire to achieve what a half-century of effort has not. The objectives of this project, therefore, are narrowly focused on several fundamental features of the ecology of a single, craftily selected system, whose elucidation may prove helpful to the larger problem (and, perhaps, to the Senate Bill 3 process presently underway). This system, San Antonio Bay, offers some attributes that better delineate the problem of establishing estuary responses to freshwater inflow:

(1) Almost the entirety of the freshwater input to the system enters at the head of the estuary, in contrast to multiple entry points characteristic of most of the Texas bays.
(2) San Antonio Bay has relatively small intensity of development around its periphery, and does not have a deep-draft ship channel transecting its cross section.
(3) The volume of San Antonio Bay is relatively small compared to the flood freshets that enter the bay in the Guadalupe and San Antonio rivers.
(4) San Antonio Bay is located on a climatological gradient between the humid northern coast, and the arid southern coast. On a time scale of multiple years, the bay is exposed alternately to wet and dry hydroclimatology governed by the large-scale movement of atmospheric circulation patterns.
(5) Lacking a direct inlet to the sea, exchange between San Antonio Bay and the Gulf of Mexico takes place through inlets relatively distant from the bay. This

means that the effects of high inflows and low inflows tend to be sustained for much longer periods than is the case for bays with freer exchange.

The combination of these properties suggests that San Antonio Bay should be metastable, shifting from drought conditions to high-inflow conditions, and that each should be sustained long enough to engender a clear response in the ecosystem. It is our premise that the hydrography and organism abundance within San Antonio Bay, both of which are underlying features of its ecosystem, are complex responses to multiple forcing variables, of which one is river inflow, and much of the problem lies in separating the response to inflow from the variance induced by these multiple controlling factors. Corollary to this premise is that explicit consideration of the major controlling factors is required to manage the unexplained variance, accompanied by better mathematical formulations of the relation between inflow and estuarine response.

While features of the structure and function of the blue crab are addressed, this is not intended to be a comprehensive survey, but rather focuses on those aspects that directly affect its ecology and interpretation of its distribution in the bay. Thus, for example, attention is given to osmoregulation and locomotion but not to digestive processes, endocrinology, or neurology. The blue crab fishery is not addressed in this review, and population modeling, in particular, is given a wide berth.

While this report comprises a review and summary of the literature, it must be noted that the blue crab has enjoyed several such surveys in the past, which together represent a comprehensive literature review. These past surveys have been a convenient source for basic information and literature citations on the species, supplemental literature then providing updates and specificity to the Texas coast. In particular, we note the literature surveys of Millikin and Williams (1984), Van den Avyle and Fowler (1984), Hill et al. (1989), Patillo et al. (1997) and, especially, the monumental pandect edited by Kennedy and Cronin (2007b). This notwithstanding, in order to properly relate literature information to the Texas environment, it was necessary that this review be critical, identifying those aspects of the literature results that constrain their applicability,

either geographically, temporally, or technically, for which reference to original papers was necessary.

Generally, the target readership is the interested nonspecialist, so a particular effort has been made to define crucial terminology and to relegate detail to the appendices. However, occasionally a more technical statement necessarily creeps in, which should be construed as addressed to the minority of readers that might find it of value.

A word of explanation is needed about the units. The coastal zone is the intersection of interests of the mariner, the scientist and the engineer, so workers in this area are generally accustomed to converting from one system of units to another. Conversion is always a problem, however, because the precision of the original number cannot be rendered exactly in a different set of units. I have preferred to leave numerical information in the units in which it was reported. When it is necessary to convert to other units, for comparison purposes for example, the Système International, or some metric derivative, has been favored. When a unit is far removed from coastal oceanography, such as the torr or osmole, a converted value in more familiar units has been supplied. Salinity is represented as a mass ratio, in parts per thousand (with the conventional symbol ‰), consistent with use of the data in salt-budget concepts such as transport (and in note of the fact that most of the measurements in the data base used in this work were not measured using the practical-salinity-scale protocol). If a reader prefers the modern practical salinity unit (psu), the conversion is easy.

2. ANATOMY AND PHYSIOLOGY

2.1 Morphology

The blue crab is the most important of nine species of *Callinectes* occurring in waters of the United States (Williams, 1984, 2007), a decapod crustacean in the family of swimming crabs Portunidae. The external morphology of *C. sapidus* is sketched in Figures 1 and 2. The crab exoskeleton is a tough, heavily calcified cuticle, made up of chitin except for its outer layer (the epicuticle), which is a strong but flexible lipo-protein (Warner, 1977). The most prominent anatomical feature of the blue crab is its large carapace with an elongated lateral spine and eight anterolateral teeth on each side (Fig. 1). Specimen size is quantified by its carapace dimensions, either length measured from the center of the anterior carapace (above the rostrum) to the center of the posterior margin, or width measured either between the bases of the lateral spines ("notch-to-notch") or between the tips of these spines ("spike-to-spike"). The dominant practice is to use the last of these, the carapace width between the tips of the lateral spines, as shown in Fig. 1. (Other dimensions have been used as well for studies of form and growth, e.g. Newcombe et al., 1949a, Teissier, 1960. Moreover, the spike-to-spike measurement has been criticized because of its variability and its failure to correlate well with body mass, e.g., Gelpi et al., 2009, who found length to be the best overall measure.)

Body mass (or weight) M is considered to be a monotonic curvilinear function of carapace width W, following the canonical allometric equation:

$$M = A\, W^{b} \qquad (1)$$

The exponent b has an immediate physical meaning, that it is the ratio of the specific growth rate of mass (i.e., the rate of growth per unit mass) to the specific growth rate of carapace width (see Appendix A). It is therefore dimensionless. More importantly, its magnitude indicates the changing proportion of mass to carapace width. For $b = 1$, the two are proportional and said to

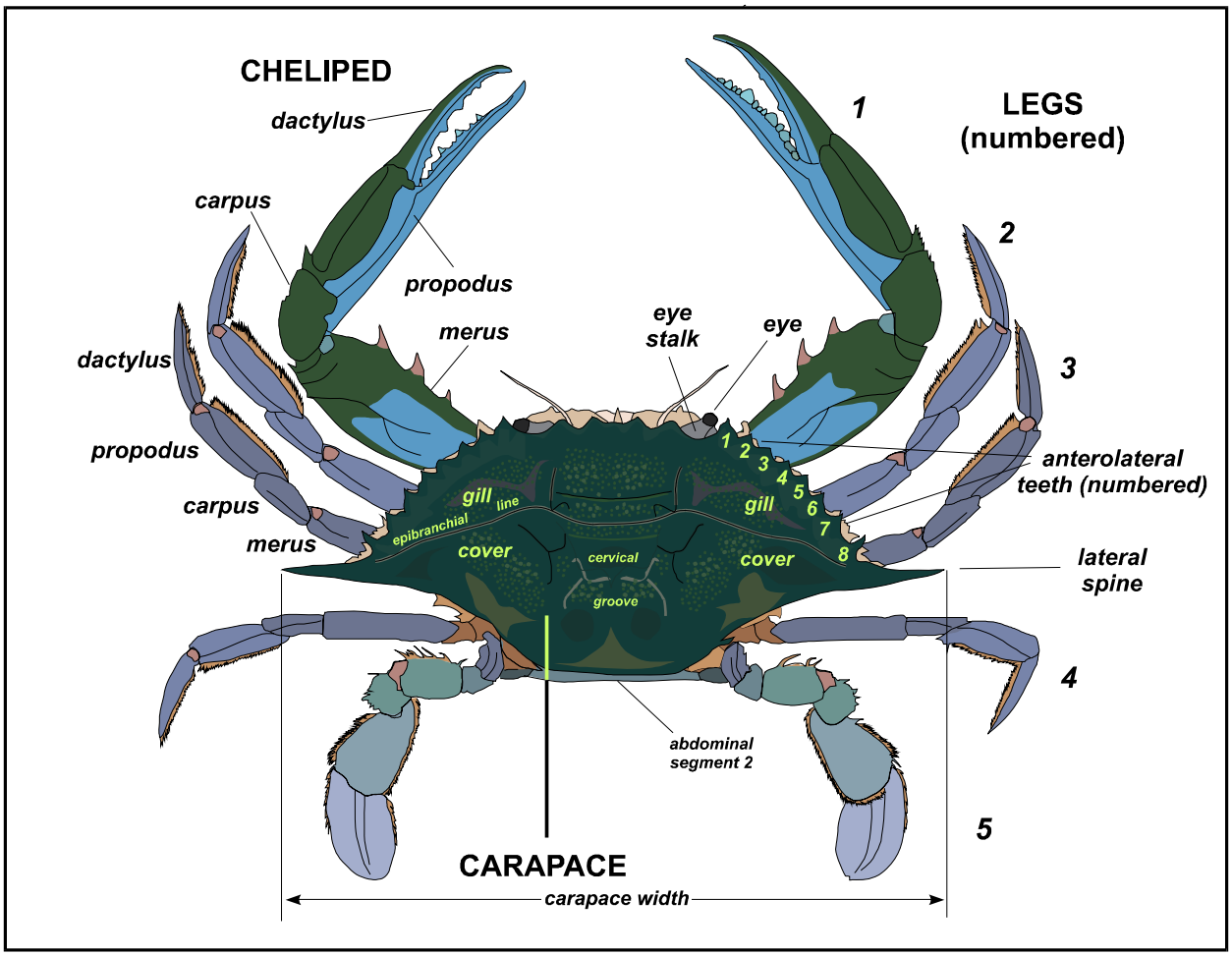


Figure 1 - Anatomy of blue crab, male, dorsal view

be *isometric*; for $b \neq 1$, as the case of *C. sapidus*, mass and width are said to be *allometric*. The coefficient A has been the source of much angst in the literature, in part because many authors believe that it renders equation (1) dimensionally heterogeneous, and in part because of the difficulty of interpretation of (1) where $W = 1$. Gayon (2000) gives a summary of the history of development of the allometric equation (1), and White and Gould (1965) present a discussion of the mathematical issues. The philosophy adopted in this review and the necessary arithmetic are summarized in Appendix A.

Table 1 collects various least-squares fits (see Appendix A) of blue-crab data to equation (1), and the corresponding graphical relations are shown in Figure 3. The bold black line is the relation

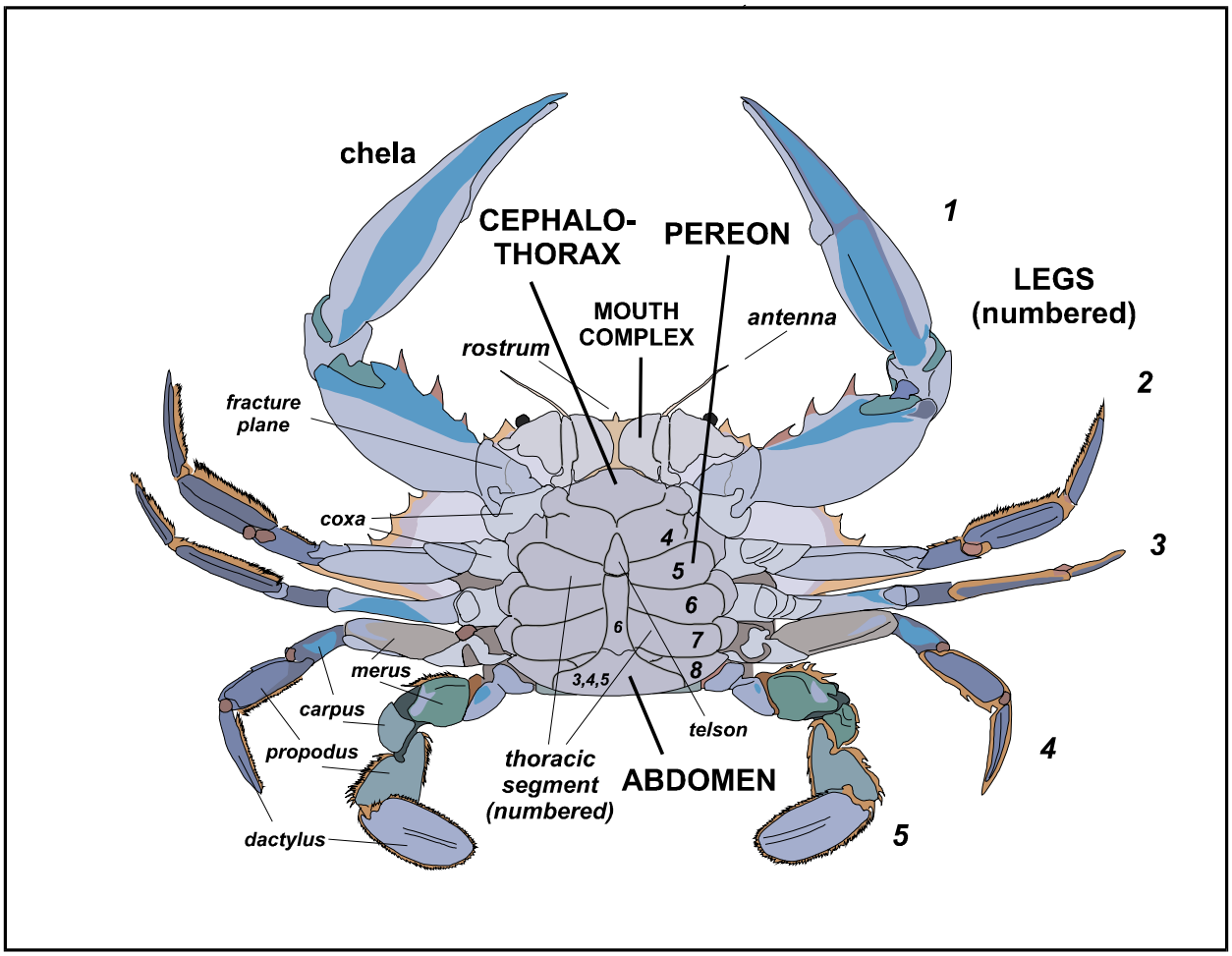


Figure 2 - Anatomy of blue crab, male, ventral view

resulting from the count-weighted averages of the parameters *A* and *k* (see Appendix A). Generally, (1) the blue crab mass is seen to be hyperallometric to carapace dimensions, (2) there is remarkable consistency in the fitted equations over a wide range of geographical areas, (3) males generally have a higher weight for a given carapace dimension (about 10-30%), and (4) the use of the count-weighted-mean relation (without sex discrimination) would enable prediction of crab weight based on carapace dimensions to an accuracy of about ±20%, and about ±12% and ±15%, resp., if the separate regressions for male and female are used. The Pullen-Trent relation, pooled over both sexes, which has been used by Texas Parks & Wildlife Department (TPWD) for many years, underestimates crab weight by about 20% for males and overestimates crab weight by 5-10% for females. (The traditional application that TPWD

Table 1
Literature data on ratio of blue-crab body mass to carapace width fitted by logarithm of equation (1), for mass in grams and carapace width in millimetres

Geographical region	*b*	*A* (g/mm^b)	*number of data*	R^2	*source*
Chesapeake Bay					Newcombe et al. (1949a)
Males	2.669	0.00026	99	n/a	
Females	2.575	0.00034	138	n/a	
Galveston Bay, Texas					Pullen and Trent (1970)
Males	2.775	0.000181	390	n/a	
Females	2.640	0.000287	335	n/a	
Ashley River, South Carolina					Olmi and Bishop (1983)
Males	2.551	0.000624	9221	0.84	
Females	2.108	0.004185	1242	0.92	
Bemelek Lagoon, Turkey					Atar and Seçer (2003)
Males*	2.613	0.000447	317	0.92	
Females*	2.199	0.002475	710	0.91	
Camilk Lagoon, Turkey					Gökçe et al. (2006)
Males	2.861	0.001470	356	0.97	
Females	2.872	0.001360	355	0.98	
Babitonga Bay, Brazil					Peireira et al. (2009)
Males	2.954	0.000089	80	0.92	
Females	2.568	0.004740	117	0.93	
Pooled equations					(see text and Appendix A)
Males	2.576	0.000549	10463		
Females	2.326	0.001442	2897		
Both	2.522	0.000677	13360		
Chesapeake Bay, York estuary					Cadman and Weinstein
Juveniles only*	3.014	0.000065	75	0.98	(1985)

* Authors reported no significant statistical difference between males and females

makes of this relation, for monitoring of year-to-year variation in potential harvest weight, is unaffected by a proportionate error.)

The typical crustacean body segmentation of head, thorax, and abdomen is modified in decapods, in that the head and the first three segments (stomites) of the thorax are fused to form the

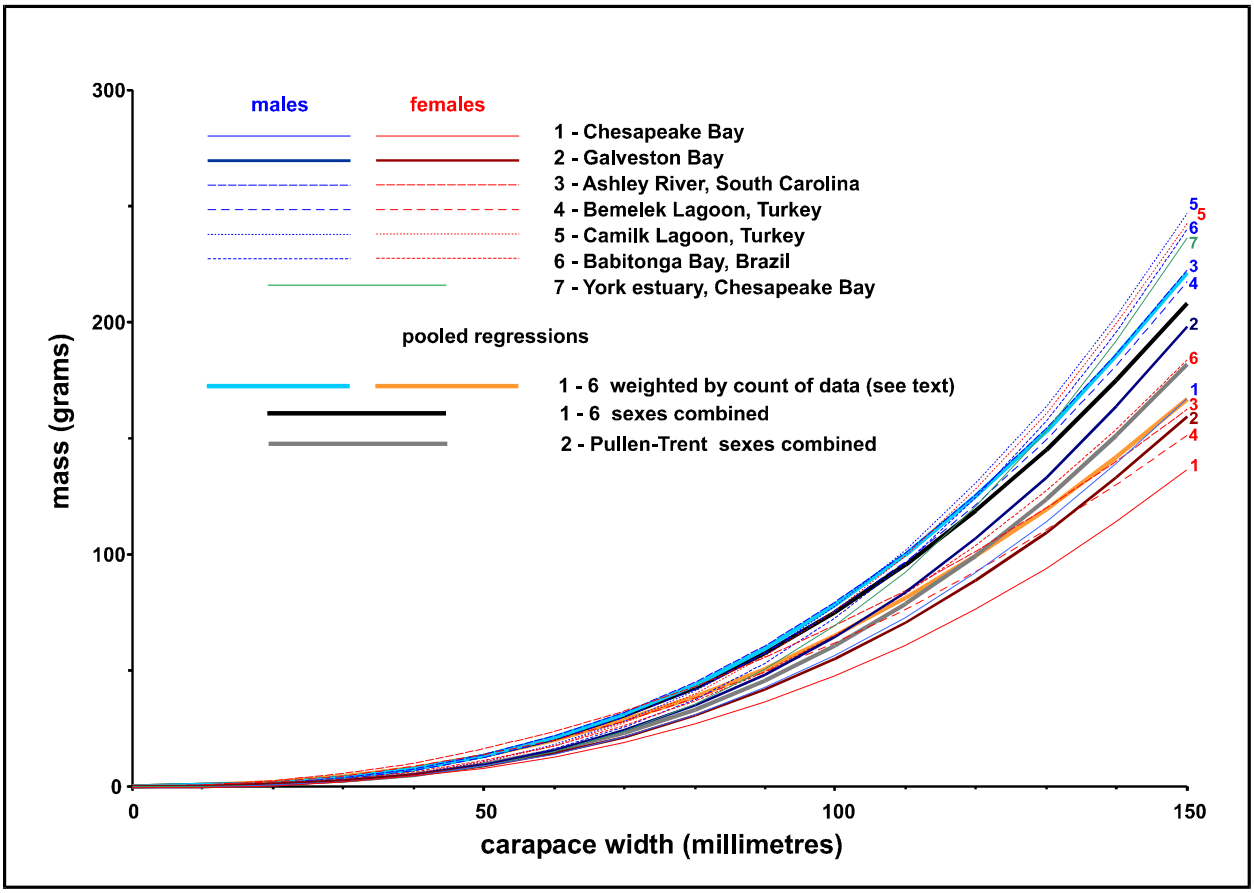
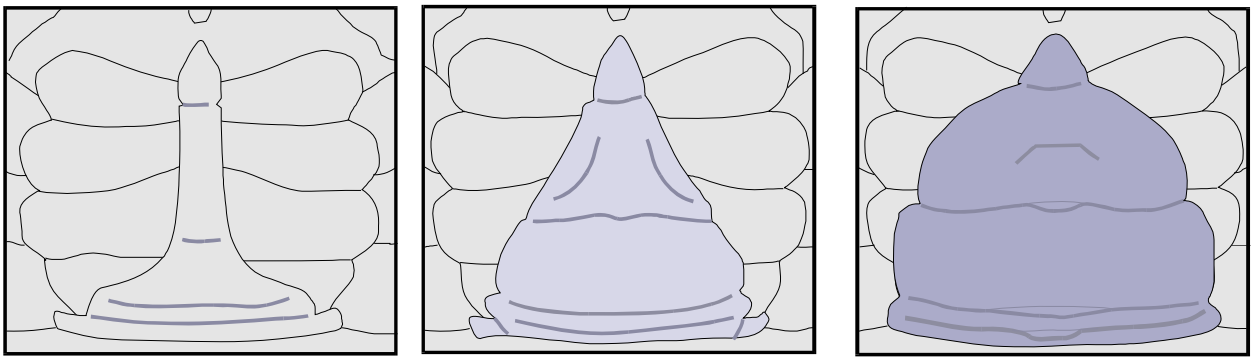


Figure 3 - Literature relations of blue crab mass versus carapace width

cephalothorax, the remaining five thoracic stomites comprising the pereon. The ventral surface (Fig. 2) is made up of cuticle plates (sternites) of the various segments. In the crab, the abdomen (pleon) is considerably reduced, and does not extend behind the body, like, say, a shrimp or lobster, but is folded under and tucked into a depression in the thorax (Fig. 2). In young crabs, the abdomen is tightly held here by a press-button arrangement, a protuberance on thoracic sternite 5 that fits into a socket on abdominal segment 6 (Guinot and Brouchard, 1998). In mature males, the abdomen is loose to facilitate copulation (or it may be an age thing). Sex of subadults and adults can be readily distinguished by the shape of the pleon (or "apron"), see Figure 4, but early juveniles are more difficult to sex.

As a decapod, the blue crab has five pairs of legs (pereiopods), each associated with a thoracic segment, leg *N* corresponding to thoracic stomite *N*+3 in Fig. 2. The segments (podomeres) of



(a) Male **(b) Female, immature** **(c) Female, mature**

Figure 4 - Differentiation of sex from abdomen or "apron" shape

each leg vary in structure depending upon the function of the leg. The outer two segments of the front pair (chelipeds) comprise a claw, or chela, used for manipulation and attack. In these, the penultimate segment, the propodus, is extended below the dactyl, which is moveable and acts as a "finger". The morphologies of the chelae differ. The narrower one with smaller, more pointed teeth is the "cutter", used for shredding and tearing, the other being the "crusher". The cutter chela has less mechanical advantage but greater speed, and *vice versa* for the crusher chela (Warner, 1977, Govind and Blundon, 1985). Like humans, crabs tend to be right-handed, with the larger, stronger crusher chela on the right. The three middle pereiopods (2, 3, 4 in Fig. 1) are walking legs. The last pair (5) is swimming legs, whose propodus and dactyl are enlarged and flattened to function as paddles or fins.

Coloration is highly variable (Hay, 1905, Churchill, 1919, Williams, 1984, 2007, Jivoff et al., 2007). Generally, the carapace is gray-green to dark green, the thorax and abdomen are light gray to gray-blue, the legs are white to blue, and the chelae are blue or white on their inner surface and gray-green, light brown or orange on their outer, though in some males the outer surface of the dactyls may be white. Females may have orange or red ends of the chelae, or this coloration may be limited to the dactyls. White to light-grey (albino) specimens occur occasionally, and individuals have been reported that are entirely blue. Juveniles are reported to change color diurnally, being darker during the day (Fingerman, 1955), see Section 4.1.1. The coloration of Figs. 1 and 2 is schematic only.

2.2 Function

2.2.1 Respiration

The crab breathes through its sides. Water is inhaled through openings around the bases of the legs. (The largest and most important of these are the Milne-Edwards openings, located above the bases of the chelipeds.) It passes through the gills then through the pump where are located the gill bailers (scaphognathites), and is expelled through ports adjacent to the mouth structure. This flow direction is reversed about once a minute for about five seconds (Arudpragasam and Naylor, 1964b, Batterton and Cameron, 1978), whose function is the subject of speculation in the literature, perhaps to flush detritus from the gills (e.g. Warner, 1977) or to aid circulation around the posterior gills (Arudpragasam and Naylor, 1964a). There is little information on the volume of flow circulated. For adult shore crabs (*Carcinus maenas*) of mass about 50 g, the ventilating flow volume has been measured to be on the order of 1 cm^3/sec (Arudpragasam and Naylor, 1964b). Assuming this rate scales with body mass, the circulating flow for an adult blue crab would be about a third of a cubic metre per day. Batterton and Cameron (1978) report the ventilating flow for resting blue crabs to be 111 ± 78 cm^3/min for a 200 g crab, ranging 22-400 cm^3/min, which is about half the rate scaled up from the measurements of Arudpragasam and Naylor (1964b). An active or stressed crab would exhibit higher flows. The flow can be controlled by the crab by altering the bailing rates of the scaphognathites (which the crab can control independently), changing the size of the Milne-Edwards openings, or raising and lowering the carapace to alter all of the inhalant and exhalant openings (Warner, 2007).

The branchial chambers house the gills and are located below the gill covers (branchiostegites) of the carapace (Fig. 1). In each chamber there are eight gill structures (most marine crabs have nine, see Warner, 1977). The gills achieve the transfer of oxygen from, and the rejection of carbon dioxide and ammonia into, the water as it passes through the gill lamellae. In addition to gas exchange, the posterior gills transfer salt ions, mainly sodium and chloride, and therefore play an important rôle in osmoregulation. The oxygen transfer rate from blue crab data compiled by Towle and Burnett (2007) for a resting adult intermolt crab at seawater salinity and temperature 20-25°C averages about 0.11 mg O_2 per gram of body mass (wet weight) per hour.

(Units of dissolved oxygen are summarized in Appendix D.) The measurements of McGaw and Reiber (2000) ranged 50-60 μmol/kg/min. This rate increases with swimming and molting, in both cases more than doubling the resting rate (Towle and Burnett, 2007). The resting rate is also doubled by digestion of food, with peak oxygen demand occurring about 4 hours after ingestion (McGaw and Reiber, 2000). The rate increases with water temperature, roughly doubling per 10°C increase. Oxygen consumption also exhibits an increase with decreasing salinity below seawater, associated with increased synthesis of amino acids as part of the osmoregulatory function. Data compiled by Florkin and Schoffoniels (1969) for *Callinectes* show a 50% ± 10% increase in whole-body oxygen consumption in 50% seawater (about 17‰) due to this mechanism. Towle and Burnett (2007) indicate a more modest increase. In the experiments of Leffler (1975), the oxygen consumption was fairly level at 0.21 – 0.29 mL O_2/g hr over a range of salinity from 50 to 1400 mOsm/L (1.5 to 48‰), with a slight *decrease* as salinity declined below 1000 mOsm/L (34‰), evidencing an ability to acclimate. Leffler (1975) also found a doubling of oxygen consumption if the crabs were suddenly moved from 1200 to 400 (41 to 14‰), or from 450 to 150 mOs/L (15 to 5‰).

The blue crab is an aquatic animal, but is capable of surviving out of water. Air is circulated like water, but the process is much less efficient due to the lower density of the fluid and the tendency of the gills to collapse and/or fail due to lamellae adhering together (Warner, 1977, deFur et al., 1988). While the crab can function in these conditions, it cannot survive indefinitely. The ventilating flow and the rate of oxygen consumption have been found to decline to about one-third to one-half of the immersed value after being in air for as much as nine hours (Batterton and Cameron, 1978, O'Mahoney and Full, 1984). De Fur et al. (1988) found only a 15% mortality after 72 hours in air. This was at 15°C, however, and they note that under refrigeration blue crabs survive in air for several days in the retail trade. The ability of the crab to adjust to hypoxic conditions is related to its ability to survive exposure to air (deFur et al., 1988).

2.2.2 Osmoregulation

One of the more important physiological attributes of the blue crab is its osmoregulatory capability. Basically, the blue crab is a marine organism (e.g., Smyth, 1980, Mantel and Farmer, 1983), and for salinities from 27‰ to 35‰, it is essentially an osmoconformer, that is, its blood salts equilibrate to those of the surrounding water (Tagatz, 1971, Guerin and Stickle, 1997). For salinities below 27‰, the crab maintains blood salt concentrations within a rather narrow range, declining by only 16% as salinities drop to zero (Mangum and Towle, 1977, Mantel and Farmer, 1983). It therefore becomes hypertonic with respect to ambient salinity. When it encounters salinities lower than its blood concentration, diffusion through the permeable surfaces of the crab (the shell, the gut and the gills, in varying proportions) produces an efflux of salts, while osmosis similarly effects an influx of water. Without compensation for these fluxes, the cardiovascular functions would be compromised by the depletion of salts, and the crab would swell due to the accumulation of water, either of which would ultimately be fatal. (Unless it is molting, which is a different matter, see Section 3.1.)

The blue crab has several physiological responses to counter these fluxes, i.e., it osmoregulates. One such response is to decrease the permeability of its surfaces in contact with the external water (e.g., Whitney, 1974, Robinson, 1982). Another is to effect an adjustment at the intracellular level, especially in muscle tissue, involving reductions in the intracellular amino-acid pool to maintain constant osmotic pressure despite the changes in ion concentrations (Florkin and Schoffoniels, 1969, Gerard and Giles, 1972). The major osmoregulatory response, however, is the elimination of water and the intake of salts. Excess water is generally removed in the urine. In fresh water, blue crabs excrete about 20% of their body weight per day as urine (Cameron and Batterton, 1978). Crabs have a peculiar disability in that their urine has the same salt concentration as the blood, so urination entails a loss of salts as well (Warner, 1977, Mantel and Farmer, 1983, Towle and Burnett, 2007), about 30% of the whole-body chloride efflux, and 40% of the sodium efflux (Cameron, 1978, Cameron and Batterton, 1978). It falls mainly to the gills to accomplish the intake of salts to replace the loss of salts through diffusion and urination, a capability that is well-developed in the blue crab.

The gill epithelium has been found to contain two types of cells: thin for gas transport, and thick for ion transport. The thick cells are found in a discrete patch in each lamella of the four pairs of posterior gills. The patch area expands when the crab finds itself in lower salinity waters, the expansion increasing to its new value in about seven to eight days (Towle and Burnett, 2007), somewhat shorter than the 1-3 weeks required for doubling of thick epithelial areas determined by Copeland and Fitzjarrell (1968). This increase in thick-cell area also contributes to reduced permeability of the gills in low salinities (e.g., Robinson, 1982). The transport of ions into the blood by the epithelial cells is counter to the ionic gradient, so energy must be invested. This energy is provided by ATP derived from numerous mitochondria in the thick epithelial cells, particularly in the lower membrane layer.

Transport of ions is a two-step process: from the ambient water to the gills, and from the gills into the blood. Sodium is transported from the gill into the blood in association with the hydrolysis of a protein enzyme (Na^++K^+-ATPase), referred to as the "sodium pump". Activity of this enzyme increases as a blue crab equilibrates to low-salinity water (Towle, 1993, Towle and Weihrauch, 2001). The mechanism of transport of sodium from the external water across the upper gill membrane remains unknown, although there are several candidates (e.g., Péqueux, 1995). Processes for the transport of chloride ions are even more obscure, though it appears that the bicarbonate ion (HCO_3^-) is involved either in exchange for chloride ions or as a catalyst for an ATPase. Towle and Burnett (2007) provide a detailed presentation of the current understanding of all of these processes and extensive citations to the literature.

Some differences in osmoregulatory capability between male and female have been found in experimental studies, but the results are conflicting (perhaps due to temperature variations, see Lynch et al., 1973). Tan and Van Engel (1966) found the male blood salinity to be higher (1.08 osmoles/L) than the female (0.95-1.01 osmoles/L) over a range of 10-20‰ and essentially equal at 30‰ (1.14 vs. 1.18). Ballard and Abbott (1969) addressed the same salinity range, but found the opposite result, lower blood salts in males in lower salinities, with no differences at salinities of 30‰. Lynch et al. (1973) found the same result for salinities below 15‰, and no differences at higher salinities. The present consensus seems to be that differences between male and female osmoregulation are not significant (Tagatz, 1971, Lynch et al., 1973, Guerin and Stickle, 1997).

While the blue crab is an excellent osmoregulator for salinities less than seawater, that is, it can function in low salinities indefinitely, there is less information on its osmoregulatory ability at salinities above seawater. In some studies, it has been found to hypo-osmoregulate at higher salinities (e.g., Tagatz, 1971). Later experiments of Guerin and Stickle (1997), in which juvenile and adult crabs were monitored in constant salinity aquaria up to 60‰, determined that the crab was an osmoconformer from 35 through 60‰.

2.2.3 Other physiological functions

Circulation of blood in the crab is open, that is, blood exits the heart into the body cavity (haemocoel) where it is in direct contact with tissues (Warner, 1977). There are arteries that transport blood to specific organs, such as eyes, hepatopancreas, and the legs, which then returns to the sinuses of the haemocoel. This blood is drawn through the gills from the body cavity, through which gas and ion exchange occurs, and then back into the heart.

The digestive system begins with the mouth complex, which is comprised of several organs that achieve mechanical reduction of the intake material by tearing, shredding and grinding, before moving the material into the esophagus, from which it is passed through two successive chambers. The first of these (the cardium) digests the food by both chemical (digestive enzymes secreted by glands) and physical processes (Kennedy and Cronin, 2007a), and is in effect a gizzard. Physical digestion is accomplished by the gastric mill comprised of an array of ossicles, the "stomach teeth" noted by Aristotle (*On the parts of animals*, Bk IV Ch 5, see, e.g., Ogle, 1882), summarized in detail by Kennedy and Cronin (2007a). The second chamber (the pylorus) is a complex of filters, which passes only colloid-sized particles to the midgut. The remainder of the alimentary canal passes through the center of the thorax thence through the pleon to the anus, which emerges just above the telson and therefore is directed forward (which may account for the temperament of the crab). Food passes through the entire digestive system and out of the crab in about 18 hours (McGaw and Reiber, 2000).

The legs of the crab operate by the principle of the lever, in which the applied force is exerted by a complex of striated muscles usually in opposing pairs, e.g. opener and closer (Warner, 1977, Kennedy and Cronin, 2007a, Govind, 2007). The pair of segments that connects to the body, the coxa and basis, acts as a kind of universal joint, each segment rotating in a plane at right angle to the other thereby combining to be capable of an unrestricted scope of movement. The other leg segments, however, rotate in a common plane. For legs 2, 3, and 4, the plane of movement is in the vertical perpendicular to the longitudinal axis of the body (Kennedy and Cronin, 2007a), so the crab walks on the tips of the dactyls. The plane of motion of the chelipeds is rotated counter-clockwise (viewed from the right) and that of the swimming legs is rotated clockwise (Kennedy and Cronin, 2007a).

2.3 Locomotion and mobility

The newly hatched Zoea I larvae (see Section 3.3) are feeble swimmers, jerking their abdomen (Churchill, 1919) and agitating their thoracic appendages (maxillipeds and setae). As they grow, the abdomen develops, including protolegs (abdominal appendages), which remain shielded in the carapace until stage VII. However, despite these improved organs for swimming, the Zoeae VII still employ only their maxillipeds. Zoeae swim backwards, in the direction of the dorsal spine (Warner, 1977). Their estimated sustained swimming speed is less than 1 cm/s (Forward, 1990, Epifanio, 2007), which is more than an order of magnitude smaller than the coastal and inlet currents typical of the mid-Atlantic coast, and, for that matter, the Texas coast. The zoeae therefore are truly planktonic, distributed by coastal and nearshore currents virtually as passive particles. (In fact, a standard field technique for determining the trajectory of plankton is to release floats of neutral or slightly positive buoyancy marking the location of a plankton patch, whose subsequent movement is then tracked.)

The postlarval megalop stage (see Section 3.3) exhibits much-enhanced swimming appendages and might be expected therefore to be capable of directed movement. Unlike the zoea, the megalop swims forward (Warner, 1977). Luckenbach and Orth (1992) carried out a series of careful observations of blue crab megalops swimming in a continuous-flow flume, and

determined the sustained swimming speed to be about 5 ± 3 cm/s (with no significant tendency to orient in the flow either upstream or downstream), i.e. a speed of about 3 m/min or 0.2 km/hr, which is substantially less than typical coastal currents. Further, megalops are capable of short bursts at even faster speeds, on the order of 20 cm/s (Epifanio, 2007). This data would indicate that megalops remain essentially planktonic, in that their large-scale movement is controlled by currents, but they have some ability for maneuvering, either in the vertical or the horizontal, especially in lower current speeds typical of shallow, peripheral regions of an estuary near the turn of the tidal current.

The subadult and adult blue crabs (Section 3.3) are capable of relatively fast motions, quick bursts of speed and sudden changes in direction (e.g., Hay, 1905). The favored swimming attitude is sideways, for which the streamlined carapace shape and elongated lateral spines are suggested to have been adapted. This was confirmed for the carapace shape by the wind-tunnel experiments of Blake (1985) using a 153-mm carapace, which show a much-reduced turbulent wake for sideways orientation in the flow and much lower drag forces than other orientations. However, Blake determined that the spines have no effect on hydrodynamics of the carapace, so their function must be entirely defensive. Weissburg et al. (2003) performed drag measurements in a flume with flowing water whose results also showed a minimum of drag for the sideways orientation. Minimization of drag may also be an explanation for the granulation on the carapace, to induce turbulence and delay flow separation, analogous to the function of dimples on a golf ball (see Vogel, 1981).

The crab, with a specific gravity of about 1.15, is negatively buoyant (i.e., it sinks) so it must generate lift as it swims. Blake (1985) calculated the minimum swimming speed required to balance its submerged weight to be around 15 cm/s. With a modest angle of attack, the lift-to-drag ratio was found to be maximal for the sideways orientation and range 2 – 4, not as good as a bird but much better than a run-of-the-mill benthic crab. Adjustment of the angle of attack appears to be an important capability that the crab uses for sudden reductions in swimming speed. Weissburg et al. (2003) observed rather abrupt changes in attack angle in response to encountering odoriferous plumes.

Spirito (1972) conducted detailed analyses of the swimming motions of blue crabs (60 - 200 mm) based upon high-speed motion pictures of the crabs in a laboratory flume. The swimming legs (pereiopods 5 in Figs. 1 and 2) describe a forward-up and-rearward-down motion in a plane about 45° off the horizontal, ending with a rotation of the dactyl: a "sculling motion" according to Spirito (1972). (Hay, 1905, and later Truitt, 1939, used the same term.) The leading set of walking legs 2-4 participate with the same motions employed in walking. The leading cheliped is held close to the carapace while the trailing legs 2-4 and the trailing cheliped are extended behind and held rigid (Spirito, 1972), a posture which may reduce hydrodynamic drag by disrupting trailing vortices. In the wind-tunnel measurements of Blake (1985), legs were removed and the sides of the carapace smoothed with plasticene, so these measurements addressed form drag only, and offer no insight into the fluid dynamics of leg positioning. In the flume experiments of Weissburg et al. (2003), the legs were left attached to the body, but their orientation was either fully retracted or fully extended, i.e., no difference between the leading and trailing legs.

In the films, the swimming speed was measured to average about 0.5 m/s and range from 0.2 to 0.8 m/s, much less than speeds above 1 m/s achievable by the crab in the wild, probably because of the constraints of the laboratory flume (Spirito, 1972). With any of Legs 2-3 autotomized, there is no effect on speed, though the phasing of the remaining legs is altered. With one of the swimming legs autotomized, the remaining leg compensates by a faster beat, and there is a minor decrease in swimming speed.

Juveniles and adult crabs engage in movement from a few tens of metres to several kilometers in their normal activities (Hines et al., 2005, Hines, 2007) such as foraging or avoidance. Hines et al. (1995) used ultrasonic tags to track the movements of juvenile and adult crabs in the Rhode River, a sub-estuary of Chesapeake Bay. Their movement was described as "meandering". Based upon distance between successive positions averaged over several days, juveniles were found to average about 12 m/hr, and adults about 24 m/hr, with maximal sustained speeds about twice this. These are considerably smaller than the speeds the crab is capable of, from the flume experiments of Spirito (1972), and are insufficient to generate lift. Clearly, the calculated average speed is substantially reduced by including periods of little or no motion. Seasonally,

crabs undertake larger scale movement, which is more appropriately addressed as migration, see Chapter 5.

While the blue crab is a swimming organism, a significant portion of its life is spent in sediments, which are both refuge and feeding habitat for the crab. When inactive, the blue crab frequently buries itself just below the surface of the bed sediments, especially for long periods of overwintering in the estuaries of temperate latitudes. It pursues infauna prey, and for this reason is a major factor in bioturbation of estuary sediments. Hines et al. (1990) determined that blue crabs foraging for clams were responsible for sediment reworking to depths of some 10 cm. This is substantial enough that blue crabs might have a significant rôle in sediment aeration or benthal nutrient fluxes (e.g., Graf and Rosenberg, 1997, Bertics and Wiebke, 2009).

3. LIFE CYCLE AND LIFE STAGES

Almost by definition, a life cycle cannot be delineated in a linear manner: it is, after all, cyclical. Each section of this chapter requires information in both earlier and later sections, so the starting point is somewhat arbitrary.

3.1 Molting and growth

The basic fact of life of a crustacean in general, and a swimming crab in particular, is that growth is not continuous, but takes place in a series of quantum increases associated with the rupture and shedding of its exoskeleton. This is true of both the larval and juvenile forms of the blue crab, but it is the latter of principal concern here, because these are crabs in both size and morphology, therefore much more accessible for biological study as well as being ecologically and economically significant. (Larvae and their progression of growth stages are addressed in the following section.) Much of the fundamental work on molting in crustaceans was carried out by Drach (e.g., 1939), extended and summarized by Passano (1960), who notes that the principal subject for delineation of stages of the crustacean molting cycle was brachyuran crabs. The molt stage is generally determined by dissection of the integument to determine the structure of the cuticle and hypodermis. Mangum (1985) and Freeman et al. (1987) supplemented these staging techniques with practical criteria, which mainly reflect crabbing practices, for differentiating these stages without injury to the animal. Smith and Chang (2007) review all of these, with appropriate photographs, as well as much additional literature, and summarize the present view of the molting cycle.

The progression of stages between one molt and the next is diagrammed in Figure 5, in which the horizontal bar represents the total time period between molts, and the length of each individual stage (A, B, C_1, etc.) is the proportional duration of that stage. The total time period of Fig. 5 is

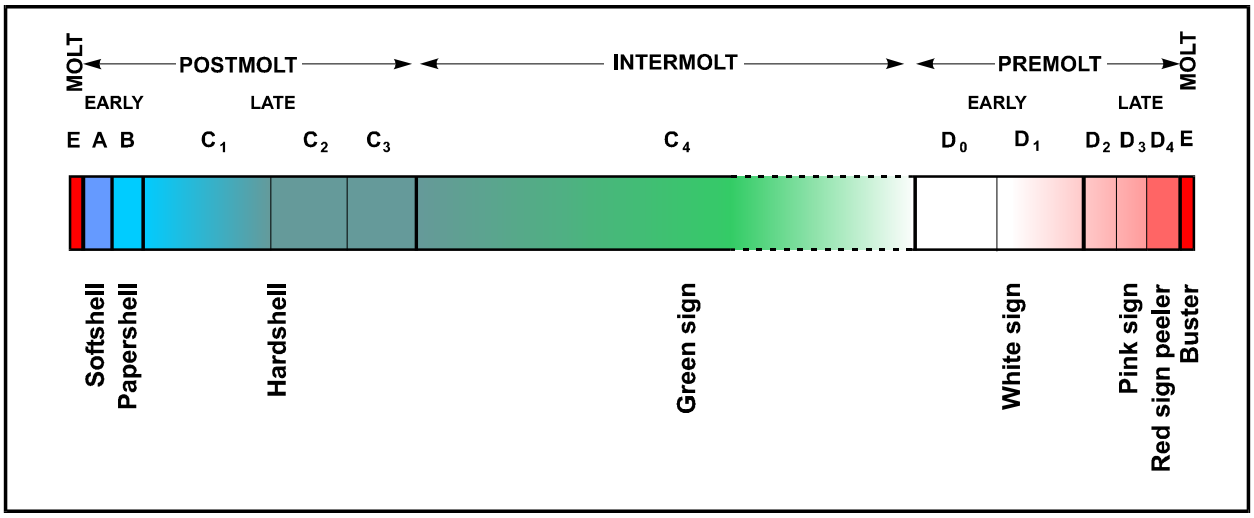


Figure 5 - Intermolt stages showing durations proportional to the total intermolt period (horizontal bar), with common descriptors (below), after Passano (1960), Mangum (1985) and Smith and Chang (2007)

unscaled, so that the progression is applicable to any intermolt period* in the life of the blue crab. In general, the intermolt period and the body weight increase as the crab ages (at least up to a carapace width of around 60 mm, after which the intermolt duration may not depend upon body size, e.g., Freeman et al., 1987). Passano (1960) depicts the life of the crab as a spiral, each loop of which is a molt cycle, and the sequence of Fig. 5 is successively "stretched" from loop to loop, to suggest the growth of the crab. The premolt stages may be diagnosed by color changes or "signs" in the dactyls—paddles—of the fifth legs. These color changes progress from green to white to pink, induced by epidermal retraction, see Oesterling (1995) and Smith and Chang (2007).

Molting (ecdysis) is a dangerous event for the crab. Besides the physiological trauma, it is weakened and immobile. During the premolt period it moves into an isolated sheltered location, typically shallow and vegetated (Wolcott and Hines, 1990). Feeding ceases, and significant changes occur in blood chemistry (detailed by Smith and Chang, 2007). In stage D_4, intake of water by drinking and osmosis begins and the rate increases sharply by the end of the stage

* "Intermolt" is disemous. It can refer to the entire progression from one molt to the next, as in "intermolt stage" or "intermolt period", or can refer specifically to stage C_4 as in Fig. 5 above.

(Neufeld and Cameron, 1994). The increased internal hydrostatic pressure breaks open the old exoskeleton and facilitates its shedding (exuviation). Water intake, by both drinking and osmosis, continues into the early postmolt stage, expanding the body size and stretching out the new cuticle. This is the increment in body size and weight associated with the molt event. At this point, the body mass is more than 85% water and the endoskeleton cannot support the crab's weight. Once this expansion is complete, calcification of the new exoskeleton begins, but the crab is still weakened and immobile, and now has the additional danger of a soft carapace. This is stage A, the true "soft shell" stage that is sought by crabbers—and just about any other predator. In stage B, the cuticle is no longer soft to the touch, but is now brittle, the "paper shell" stage. As the exoskeleton hardens late in stage B, mobility is regained and feeding resumes. Hardening of the exoskeleton continues throughout stage C, though the "hard shell" condition is considered to be attained about halfway through this stage.

The crab is said to be "green" from the late postmolt stage through the early pre-molt. The body size increase achieved in the early postmolt stage (Stage A), around 25% in linear dimension (e.g., carapace width, CW, see Section 3.3), remains constant for the remainder of the cycle until the next molt. Stage C_4 is sometimes described as the "normal" intermolt condition, in that skeletal formation and tissue growth are now complete, and this stage makes up a great proportion of the molt cycle (Fig. 5). However, the crab is already preparing for its next molt, in that synthesized organics in excess of the body requirements are being stored (Passano, 1960). Stage C_4 is of variable duration (Freeman et al., 1987), indicated by the broken lines of Fig. 5.

The act of exuviation is typically completed in less than 30 minutes (Smith and Chang, 2007). The body expansion during and after exuviation requires a period of 1 - 6 hours, with most of the growth concentrated in the first hour of the interval (e.g., Gray and Newcombe, 1938b). Gray and Newcombe (1938b) and Newcombe et al. (1949) present the results of an experiment in which wild-caught crabs were maintained in natural conditions in floating chambers, and their carapace widths measured before and after molting. This work was done in a tributary of Chesapeake Bay. The increment on molting averaged 37% of the pre-molt CW for females and 24% for males. Later, Tagatz (1968b) essentially repeated this experiment in the St. Johns

estuary in Florida (except that Tagatz tracked the crabs' growth beyond one molting), finding average molting increments to be 28% for females and 25% for males in salt water (and about 10% lower values in freshwater). Brylawski and Miller (2006) monitored crabs from Chesapeake Bay in a controlled laboratory setting in two separate experiments of 154 and 182 days. The average growth increment was found to be about 20% of the pre-molt carapace width with no significant difference between male and female.

The intermolt duration depends upon water temperature, which in the work of Tagatz (1968b) translated into seasons, and upon the size of the crab. The molt intervals of winter were three to four times those of molts in the rest of the year. In summer, the molt interval of the smallest width interval, 20-29 mm, averaged 11 days for summer versus 46 days for winter. The molt interval for the largest crabs was 42 days for summer (> 120 mm) versus 124 days for winter (92 mm). No significant dependency on sex or salinity was found. In the laboratory experiments of Brylawski and Miller (2006), intermolt period decreased significantly with water temperature, but only a weak (nonsignificant) increase with crab width was exhibited.

Guerin and Stickle (1997) investigated molting in wild-caught juvenile blue crabs (12-28 mm) from Louisiana waters of 25‰ salinity. The crabs were installed in constant-temperature aquaria of salinities 2.5, 10 and 30‰, the salinity being brought from ambient to the target value in discrete daily steps of 2 - 3‰ over a week, and maintained for 67 days during which the crabs molted 2 to 3 times. No significant effect of salinity on either molt increment or intermolt period was observed. Haefner and Schuster (1954) maintained female crabs undergoing their terminal molt in the salinities at which they were taken, ranging 8-35‰, and measured the molt increments. No significant effect of salinity was found. In laboratory studies of wild-caught juveniles (30-40 mm) from Galveston Bay, Holland et al. (1971) found no effect of salinity in the range 6-21‰ on intermolt period.

A major control on the duration of the intermolt period is therefore water temperature. Intermolt period is a declining curvilinear function of water temperature, i.e., the number of molts per unit time increases with water temperature. Smith and Chang (2007) argue that this effect of

temperature can be more simply quantified if intermolt period is measured by the time integral of temperature, *viz.* cumulative temperature departure above a threshold:

$$\Pi(t) = \int_{t_o}^{t} \max\{0, T(t) - T_{min}\}\, dt \qquad (2)$$

where $T(t)$ is the instantaneous water temperature time function, t measured in days, t_o is the starting time, T_{min} is the threshold temperature below which growth does not occur, and Π is measured in degree-days. If $T(t)$ is replaced with the time series of daily means $\overline{T_i}$, then (2) becomes approximately

$$\Pi(t) = \sum_{i=0}^{N} \max\{0, \overline{T_i} - T_{min}\} \qquad (3)$$

where i denotes the time duration in days after t_o, and $t = N$ days. We note that if $T(t)$ never falls below T_{min}, then (2) and (3) are equivalent, i.e., (3) is exact, not an approximation. Smith and Chang demonstrate that the graphs of intermolt period as a function of carapace width for different water temperatures collapse to a single *linear* function when intermolt period is transformed from days to units of degree-days. The degree-days parameter, a.k.a. *physiological time*, has had some utility in modeling the growth of insects (see Curry and Feldman, 1987), but has had little application to crabs until recently. Brylawski and Miller (2006) employed this in their molt-process growth model, and Darnell et al. (2009) used it as their basic time parameter in studying multiple spawnings in the laboratory.

If water temperature falls below about 10°C, molting is suspended (Hines, 2007), so this is an approximate value for T_{min}. (Churchill,1919, estimated 15°C. Leffler, 1972, found molting to "essentially cease" at 13°C. Brylawski and Miller, 2006, estimated about 11°C—though their graphic suggests a value closer to 12°C.) The nonmolting season (the "winter anecdysis") on the mid-Atlantic coast may be attributed to this temperature-controlled suspension. During this period, the crabs over-winter in the sediments of the bay. A more general form of (2) or (3)

includes a maximum temperature above which growth ceases (see Smith and Chang, 2007). For the blue crab, this appears to be greater than 37°C.

The duration of the intermolt period is decreased (i.e., the number of molts per unit time is increased) if a leg must be regenerated (Skinner, 1985) or if the crab has been wounded (Yudin et al., 1980). The intermolt duration is increased by nutritional deficits, among other factors. For example, progression to the D_0 stage requires addition of dry tissue sufficient to reduce the whole-body water content, apparently to less than 60%. Suspension of molting for these and other reasons has been determined to occur in the C_4 stage (Smith and Chang, 2007 and citations therein), which accounts in part for its variability.

There is good evidence (Smith and Chang, 2007) that molting ends for the female once sexual maturity is attained, though there are rare instances in which a female has a second pubertal molt and additional mates. The males apparently continue to molt after maturity, but with decreasing frequency and size increments. One consequence of the molting process is that determination of the age of a crab in the wild is rendered impossible, other than a rough estimate based on its size.

Very little observational data appear to exist that would reveal the details of molting and growth of the blue crab specific to the Texas coast. Certainly, the higher water temperatures and mild winters in Texas will limit the direct application of results from the mid-Atlantic. Smith and Chang (2007) propose a mathematical model of molting that may offer insight. The two fundamental attributes of blue crab growth are the intermolt period and the size increment at molting. Smith and Chang (2007) assembled data, primarily from the mid-Atlantic and south Atlantic, from which relations were extracted for increment as a function of premolt size, and intermolt period as a function of cumulative warming in degree-days. Development-rate curves were extrapolated to a low-temperature intersection, below which molting is assumed to be suspended. This intersection proved to be about 10°C, which is consistent with several laboratory and field studies noted above.

Smith and Chang (2007) combined these and several other empirical relations into a mathematical model of blue crab growth numerically formulated as a conditional stepwise

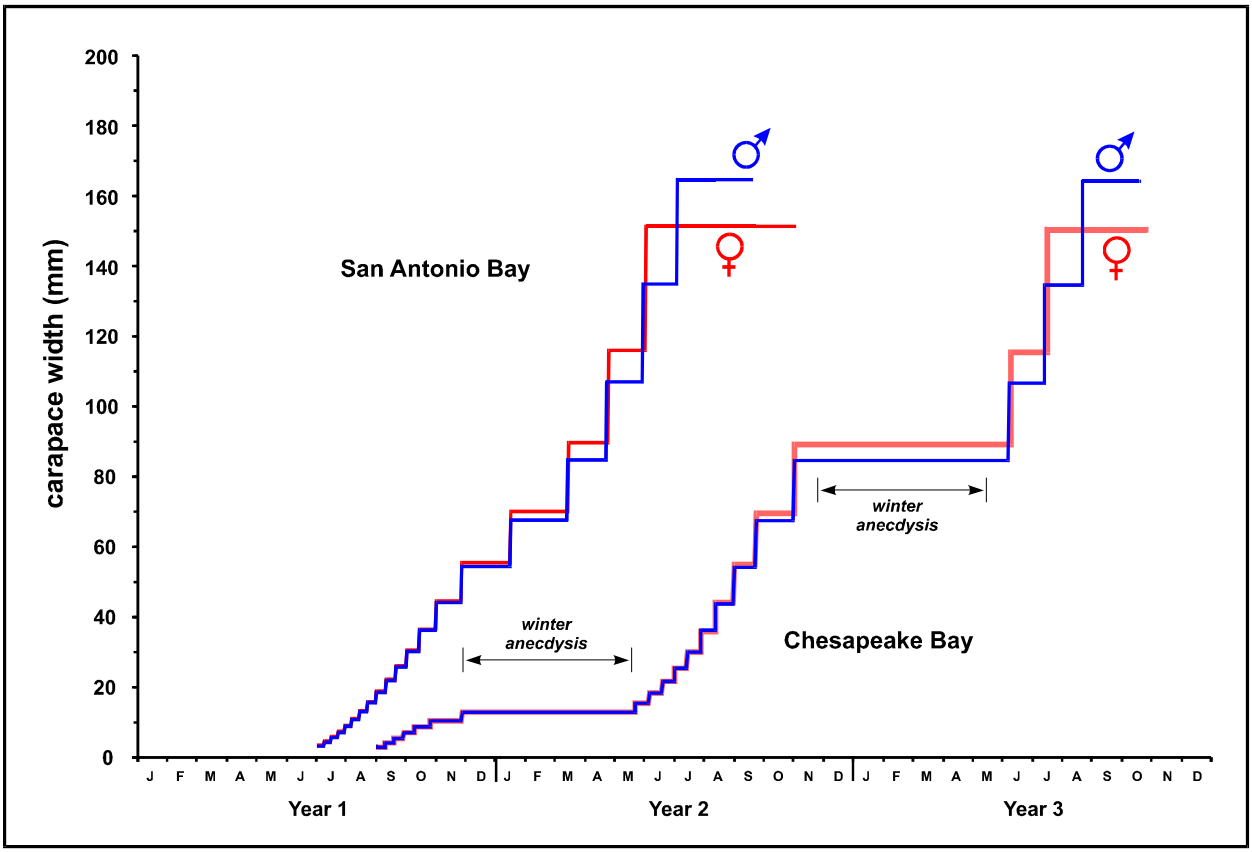


Figure 6 - Simulated growth of blue crabs in Chesapeake and San Antonio Bay, starting at first month of peak settlement, with cycled 2004-08 averaged daily water temperature. Based on model of Smith and Chang (2007).

process, for which a key input is the time series of daily water temperature. The Smith-Chang model was implemented in an EXCEL® workbook and driven with the 2004-08 average daily water temperatures from hydrosondes deployed in Chesapeake Bay (Goodwin Islands, Virginia, NERR) and San Antonio Bay (GBRA-1). The results are shown in Figure 6. The variation of intermolt period in both bays is inversely related to water temperature, which leads to a faster growth rate for the San Antonio Bay crab. The most striking difference between the two, however, is the effect of the winter dormancy period in Chesapeake Bay in extending the grow-out period compared to San Antonio Bay. Given the parameters of the model, the San Antonio Bay crab grows to adulthood in about a year, compared to over two years for the Chesapeake Bay crab. (There are additional molts for the latter that occur in Year 4, not plotted in Fig. 6.)

3.2 Mating, spawning and reproduction

Mating is triggered by the ripeness of the female, which is signaled by her terminal (or pubertal) molt. The pre-pubertal female is identified by the broadened abdomen, Fig. 4(b), which becomes dark blue or purple prior to the terminal molt. After the terminal molt, the abdomen is dome-shaped and dark, Fig. 4(c). Maturity of the male is more difficult to establish. Three physiological criteria are necessary for complete reproductive functioning of the male, in the order in which they develop: (1) prominence of the anterior vasa deferentia, indicating presence of spermatophores, (2) abdomen free (or easily retracted) from the sternum, (3) penes and pleopods functionally coupled (the penis and the intromittent spine of the second pleopod are inserted in the base of the first pleopod, on each side), see Van Engel (1990) and Jivoff et al. (2007). These are capable of inspection in the field, but not conveniently, and thereafter the crab may not be of further use. The minimum size for male maturity is estimated to range 82-89 mm (Gray and Newcombe, 1938a, Van Engel, 1990, Jivoff et al., 2007).

With the advantage of pheromone detection, the mature male crab is even better at identifying an impending pubertal molt than human crabbers. The detection works in the opposite direction as well, as evidenced by the practice of "jimmie potting" in softshell crabbing, in which a trap will be "baited" by a large, aromatic male to attract female "peelers" approaching their puberty molt (e.g., Otwell and Cato, 1982, Oesterling, 1995). There is an elaborate pre-pubertal courtship leading to the pairing of crabs, detailed for the prurient reader in Jivoff et al. (2007 and citations therein), including photographs. The male guards the pre-pubertal female while she matures, carrying her underneath him for several days. Literally within minutes of completing her pubertal molt, the female is turned over on her back and copulation begins, which proceeds for several hours to a couple of days (Churchill, 1919). Afterward, she is turned right-side up, and the male resumes guarding for several more days during which her cuticle hardens.

Reproductive organs are paired in both sexes and arranged with bilateral symmetry about the thoracic centerline. (Yes, there have been bisexual individuals reported with a full complement of male organs on one side and female on the other, see Jivoff et al., 2007.) In copulation, the

male lowers his abdomen away from the sternum for coupling. Each penis (there are two, which may account for the temperament of the crab) is placed in a pleopod (gonopod) exposed by the retracted abdomen, which is then inserted into the matching oviduct in the 6th sternite of the female. The sperm is transferred via each oviduct into the corresponding spermatheca of the female, a sac-like organ that stores the sperm, this transfer assisted by the second gonopod of the male. From this single mating, the female acquires a potential lifetime supply of sperm, which is then used multiple times to fertilize eggs. Recent studies indicate that over 10% of females mate a second time (with a different male) during this intermolt (Jivoff et al., 2007). Males mate multiple times. However, new research (Wolcott et al., 2005) indicates that as the number of his conquests increases, the male is more likely to simply eat the female.

Because mating is governed by molting, the effect of temperature on molting has an indirect effect on the mating season. On the Florida coast, a minimum temperature of 22°C is required (Steele, 1982). In the St. Johns estuary of Florida, Tagatz (1968a) observes that mating occurs year-round, but is concentrated in two main periods March – July and October – December. The summer hiatus suggests that high water temperatures (or perhaps thunderstorms) may limit this activity. Archambault et al. (1990) noted a similar summer hiatus in mating in Charleston Harbor (South Carolina), based upon a reduced abundance of pubertal females. Effects of salinity, if extant, are more subtle. Whether the preferential occurrence of mating in the upper reaches of mid-Atlantic estuaries is due to lower salinity remains controversial in the literature.

Spawning is controlled by water temperature, requiring at least about 15°C (e.g., Archambault et al., 1990). In spawning, eggs are forced through the spermathecae to be fertilized. This must wait for about two months after insemination in order for the viscous seminal fluid to dissipate, and an additional 1.5-2 months for the spermatophores to vanish and the spermathecae to thin (Wolcott et al. 2005). In the mid-Atlantic, the principal mating season is summer, so this additional time extends into the fall period of rapidly declining water temperature. (The earlier literature underestimated the time between insemination and brood production.) Consequently, most females overwinter before spawning. Retention of sperm this long can affect its viability, which introduces variability in the breeding success of the crab (Wolcott et al., 2005, Jivoff et

al., 2007). On the Florida Atlantic coast, those crabs that mate in fall or winter delay spawning until the following spring (Tagatz, 1968a).

After fertilization, the eggs are extruded onto the pleopods (swimmerets) of the female's abdomen. The first brood consists of some 1-6 million eggs (Truitt, 1939, Jivoff et al., 2007), which are carried in a mass, or "sponge", held between the abdomen and thorax, the female being described as "ovigerous". The eggs are carried for about 15 days around 28°C until they are ready for hatching, the time increasing as water temperature decreases. Results of Tilburg et al. (2008) indicate a somewhat shorter brooding period, 17 days at 20°C decreasing to 10 days at 25°C. As the eggs develop, the egg mass changes color from its initial yellow or orange, to become successively darker, brown then black when ready to hatch (e.g., Tilburg et al., 2008). The larvae are released into the water, facilitated by action of the crab with its walking legs, described variously as raking its legs through the sponge, and picking apart the sponge while beating the abdomen (e.g., Hench et al., 2004). The success of hatching seems to require salinities exceeding 18‰ (Davis, 1965).

In the spawning season of the mid-Atlantic (May to September), a female may produce one to several broods. In lower latitudes, spawning ceases only during the winter, depending on weather conditions, or may continue throughout the year, and a female may produce as many as eight broods per year (Jivoff et al., 2007). On the Florida Atlantic coast, spawning occurs March through September, and may occur in February and October if water temperatures are suitable. Tagatz (1968a) reports that a female may spawn a second time either within the same spawning period or extending into the next. This is based upon examination of the carapace for evidence that the female has been in the ocean (dull appearance and fouling, especially barnacles), and the abdomen for stressed appendages and eggshell fragments. However, this evidence for a second spawning would neither preclude nor differentiate additional spawnings.

Dickinson et al. (2006) captured 124 mature females and maintained them in minnow traps in shallows near Beaufort Inlet during the summer spawning season. They determined that the longer the crabs were held, the more broods they produced. Two-thirds had multiple broods in the 18-week observation period, with 6% having six or more sponges. Dickinson et al.

extrapolated these rates to the May – October spawning season and inferred that on average eight broods would be produced. Finding that larger crabs produce larger broods but less frequently, Dickinson et al. determined that the total larval production output is equivalent across crab sizes. Darnell et al. (2009) used a similar procedure, but were careful that the captured crabs were mating or had just mated, and maintained the crabs throughout their life in order to better assess their total reproductive capacity. They found that crabs produce 3 to 7 broods over their lifetime (encompassing 1-2 spawning seasons), increasing with carapace width and survival. Clutch volume, quality and larval fitness were all determined to decrease with additional broods after the first.

3.3 Life stages and growth

Various terminologies are employed to describe the life stages of the blue crab. The zoea and megalops are well-defined forms, the former characterized by prominent dorsal and lateral spines and a free abdomen, the latter by an enlarged carapace and chelipeds. Usage in the literature of more general terms, such as "larva", "postlarva" and "juvenile", has been imprecise or inconsistent, and has varied geographically and over time. Examples are collected in Appendix C. In this report, larva means zoea (and prezoea), postlarva and megalop are equivalent, and juvenile means an immature crab. Other qualified descriptors, such as "small juvenile", generally follow the convention of the author(s) cited when literature is reported. For summary or generalized statements when only approximate size is indicated, we refer to "small juveniles", "large juveniles", and "adults", in the sense of the first definitions, respectively, in Appendix C. To indicate sexual function, "juvenile" or "immature", and "mature" are employed. For reasons that will emerge, crab size is favored over instar number when specific size ranges are known.

Delineation of the larval stages of blue crab in the field was problematic through the first half of the twentieth century. Inference from plankton samples provides little information on age, and the larvae may be confused with those of other crabs. In the laboratory, on the other hand, it proved difficult to culture the larvae (Robertson, 1938, Truitt, 1939, Epifanio, 1995). The classic laboratory study of growth is that of Costlow and Bookhout (1959, and subsequent papers, see

also Kennedy, 2007), whose description of the larval stages remains authoritative after more than 50 years (Epifanio, 1995, Epifanio, 2007, Kennedy, 2007). Costlow and Bookhout followed the growth of newly hatched eggs, usually from the same female in an experimental series, under different combinations of temperature and salinity, describing in detail the morphological differences of the larvae between molts (instars). Figures 7 and 8 reproduce their drawings of the general appearance of the larvae, except the side and ventral views are paired, all have been reduced or enlarged to a uniform scale (shown at the top of each figure), and have been adjusted to exhibit similar positions for ease of comparison. Clearly, these are different individuals, and in some cases even the side and ventral pairs are not the same individual. Costlow and Bookhout (1959) remark that the sizes of the larvae at the same stage were highly variable, so the relative change in size from one stage to another depicted in Fig. 7 is, at best, approximate. The stages of development are determined by the details of morphology (e.g., the number and positions of spines and setae), elaborated by Costlow and Bookhout (1959) and by Kennedy (2007), not the size or general appearance of the instars.

Eggs grow about 10% in size (20% in volume) while carried by the female, from an average dimension of 0.27 mm to about 0.30 mm before hatching (Davis, 1965, Kennedy, 2007). The first unequivocal stage after hatching of blue crab larvae is Zoea I (using the designations of Kennedy, 2007), with erect rostral and carapace spines (prominent dorsal and two lateral, the latter visible in the ventral views). There may be an occasional intermediate hatchling stage or prezoea that molts within minutes into a zoea, but this is controversial in the literature (Robertson, 1938, Davis, 1965, Kennedy, 2007, see also comments of E. Norse following Harris, 1982). The larvae progress through six moltings, from Zoea I through Zoea VII. The seventh molt usually is the metamorphosis to the megalop stage. Infrequently, the eighth zoea stage occurs, especially in laboratory cultures, but these usually do not successfully develop into megalops. Data on larval grow-out in the laboratory provided by Costlow (1965) display increased variability in the larval stage morphology after Zoeae IV, with several individuals developing into megalops after eight zoeal stages. A stage sequence analogous to the juvenile, Fig. 5, applies to the megalop as well, based upon retraction from the cuticle exhibited in the maxillipeds and uropods (Metcalf and Lipcius, 1992).

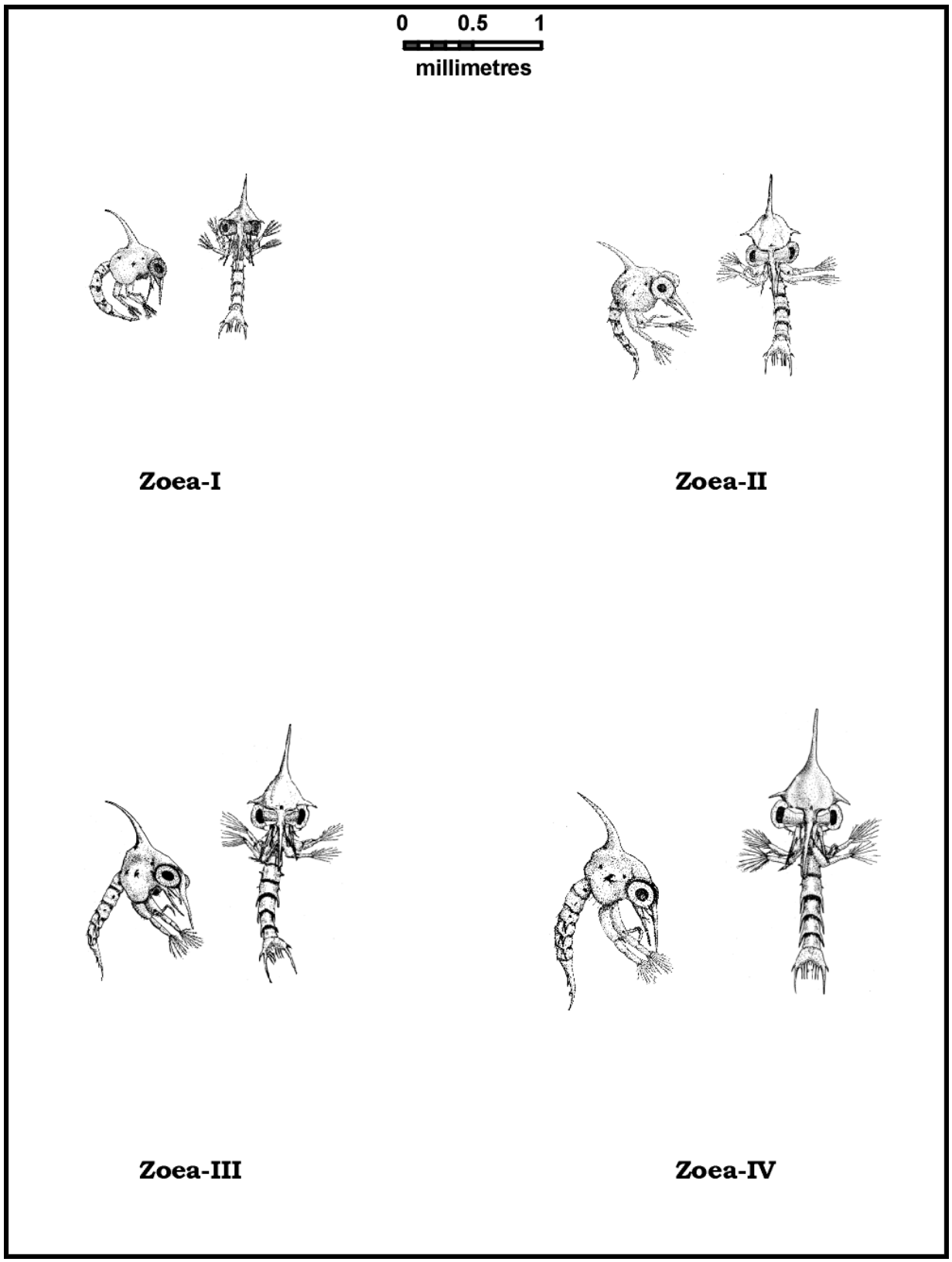


Figure 7 - Sketches of side (left) and ventral (right) views of blue crab zoeae, adapted from Costlow and Bookhout (1959)

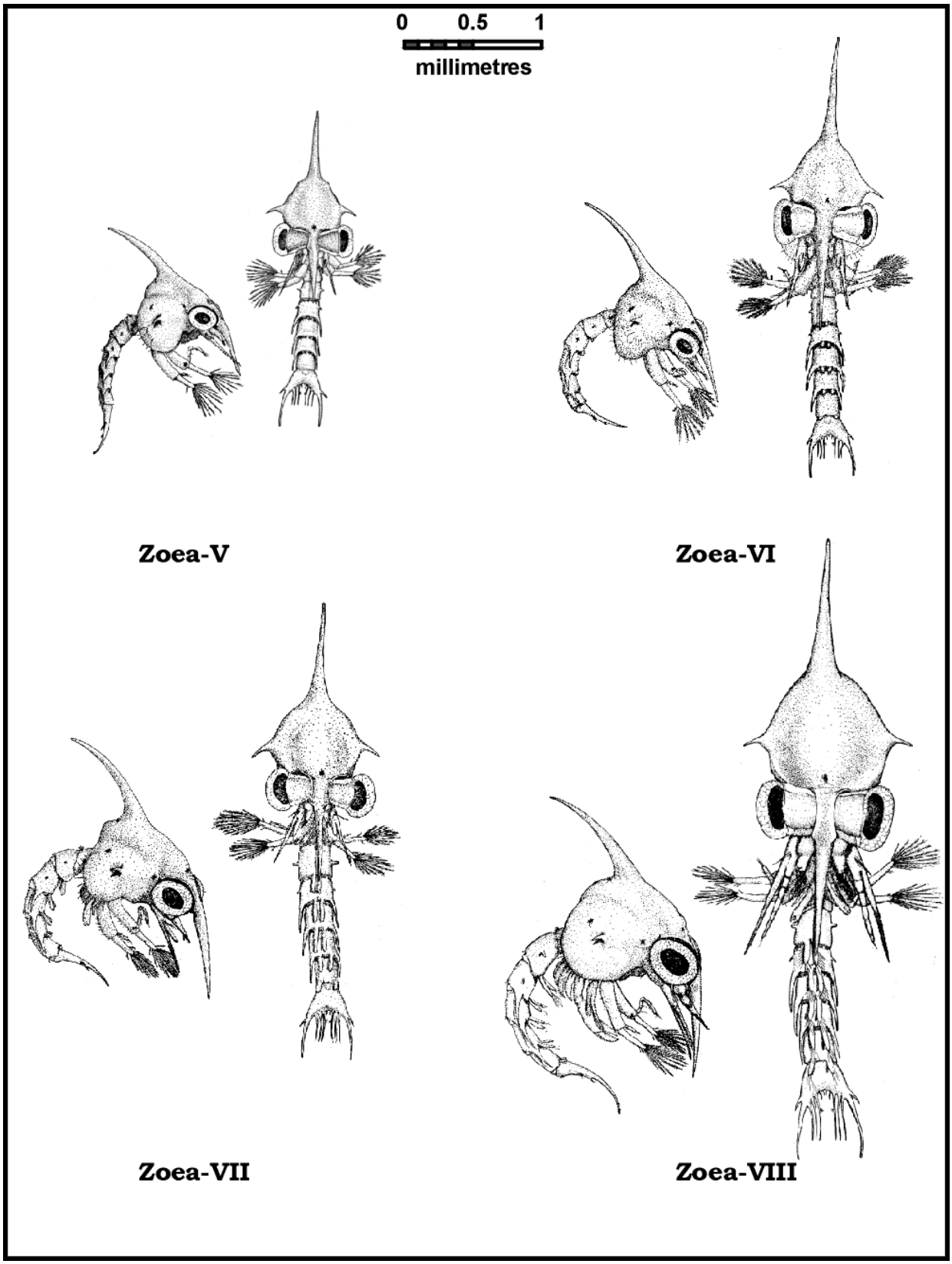


Figure 7 - continued

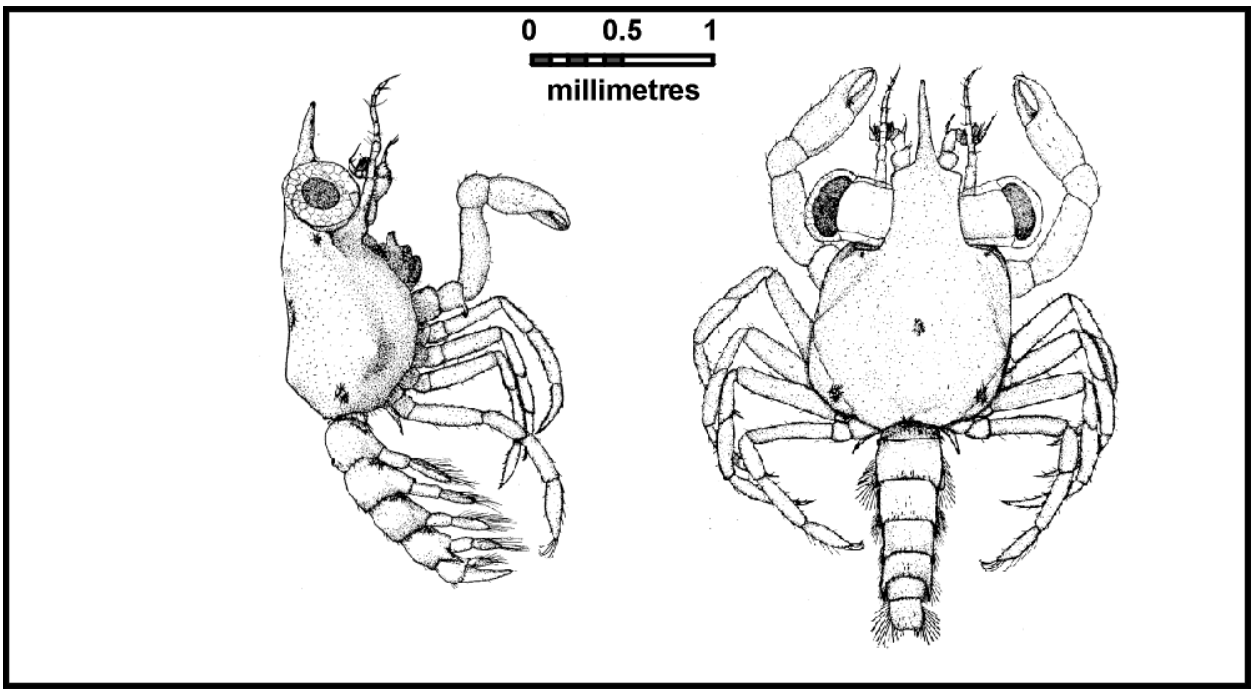


Figure 8 - Sketches of side (left) and ventral (right) views of blue crab megalop, adapted from Costlow and Bookhout (1959)

Costlow and Bookhout (1959) recorded the ranges of time duration after hatching for each molt and the number of individuals surviving to each larval stage. These data have been extracted from their paper and presented graphically in Figure 9. (In one experimental series for 26.7‰ salinity at 25°C, the eggs were taken from three females and their development tracked separately. For the purposes of Fig. 9, these data have been combined.) Survival of the larvae into the advanced zoeal stages was a continuing problem, as is evident from this figure. Generally, there were relatively few representatives for all stages more advanced than Zoea III, which means that measurements and intermolt (instar) durations are especially uncertain. (Those for Zoea VI and VII and megalop for 20.1‰ salinity at 25°C in Fig. 9 are based upon one individual.) Clearly, there is a wide range of variation in the time of progression through the larval stages. In the laboratory growth data of Fig. 9, 30-50 days after hatching the larvae reach the megalop stage. Some indication of the dispersion among individuals is provided by the much larger data set of Sulkin and Van Heukelem (1986), of time to successfully molt to megalop of 1,157 sibling larvae maintained at 23°C and 30‰, conditions representative of the mid-Atlantic

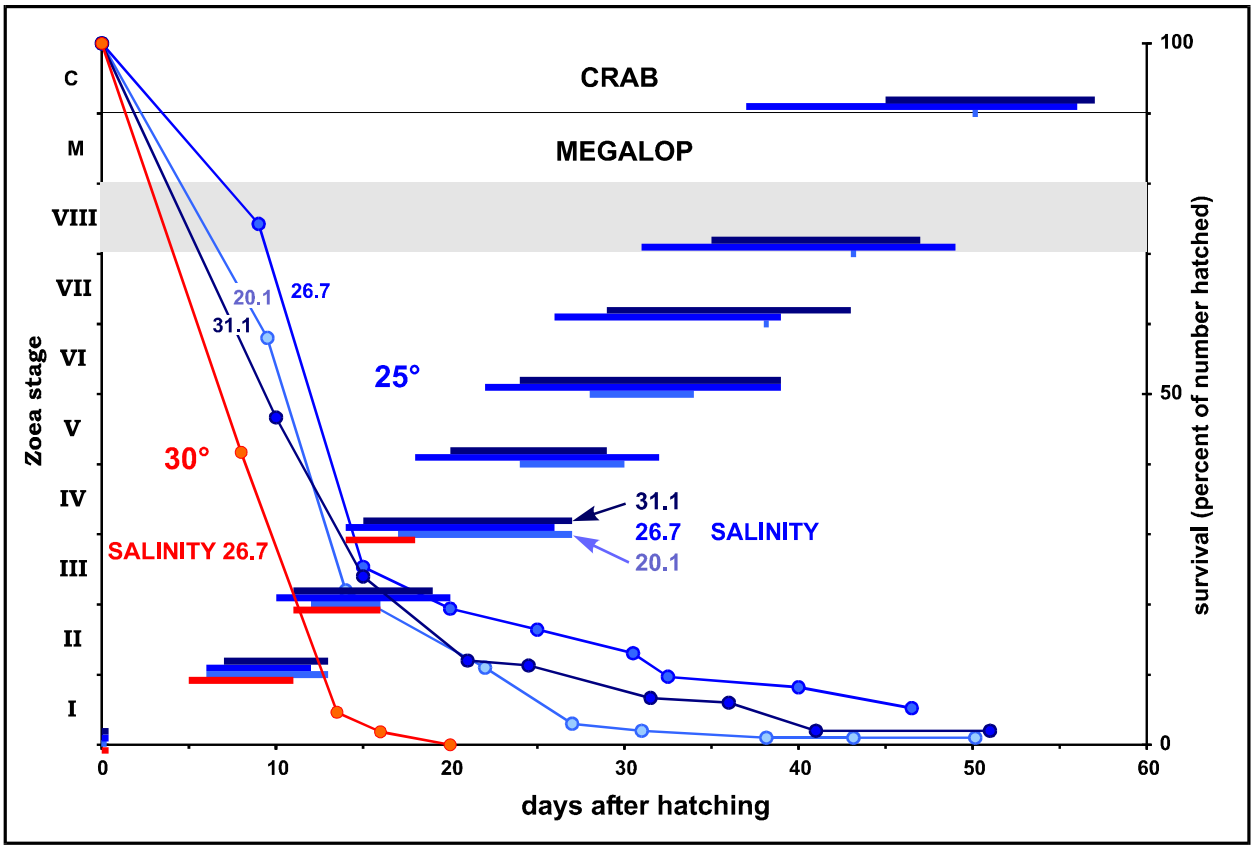


Figure 9 - Range of time after hatching for molt of blue crab larvae (horizontal bars), and survival (connected data points) from data of Costlow and Bookhout (1959)

shelf waters in summer. This data, with a mean of 40.1 days and standard deviation of 4.7 days, is essentially consistent with that of Costlow and Bookhout, and has been extracted and replotted as frequency distribution and ogive in Figure 10. Somewhat shorter times are suggested for larvae in the field, on the order of 3 – 6 weeks in the mid-Atlantic coastal zone (Natunewicz and Epifanio, 2001).

The blue crab has exactly one postlarval stage, *viz.* the megalop, which represents both a change in appearance (Fig. 8) and a change in life style, transitional between the passive planktonic existence of the larvae and the more active benthic life of the juvenile crab. The duration of the megalop stage is highly variable. Costlow and Bookhout (1959) found this stage to range from six to twenty days, depending on salinity, *viz.* 6-9 days at salinities 20.1 and 26.7‰, and 10-20

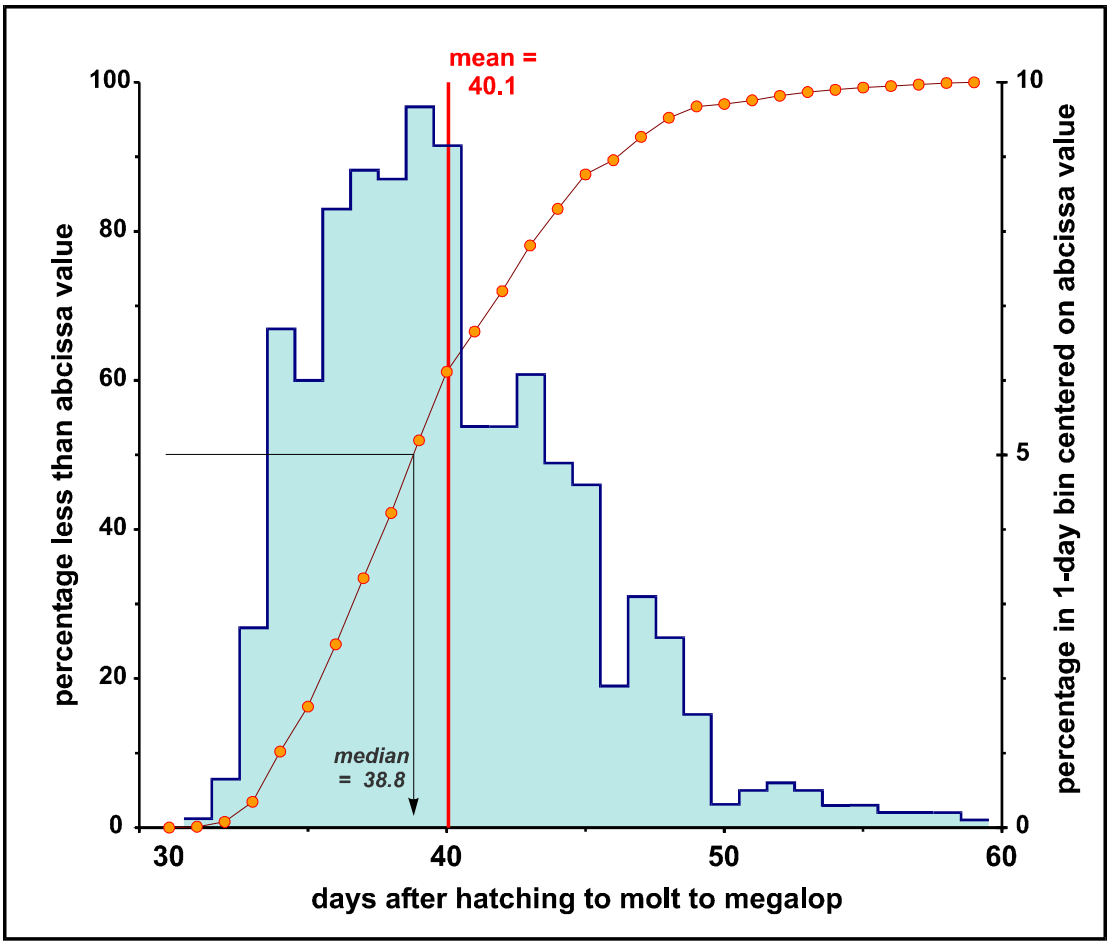


Figure 10 - Range of time (days) after hatching for molt to megalop, of 1,157 sibling larvae at 23°C and 30‰, from data of Sulkin and Van Heukelem (1986). Mean = 40.1 days, standard deviation 4.7 days. Cumulative frequency ogive (connected data points) left axis, frequency diagram right axis.

days at 31.1‰ (all at 25°C), but the small number of individuals (Fig. 9) raises the question of whether the observed variability with salinity is an artifact. Costlow (1967) presented more substantive laboratory data on duration of the megalop stage as a function of salinity and temperature (as well as survival of megalops to the first crab stage, discussed in Section 4.2.1). These data have been extracted from Costlow's paper and presented graphically in Figure 11 (cf. Fig. 14). This shows the principal control on megalop duration to be temperature: the nearly horizontal isopleths indicate little influence of salinity. Indeed, more recent studies (reviewed in Smith and Chang, 2007) indicate no variation of megalop and juvenile intermolt periods with salinity.

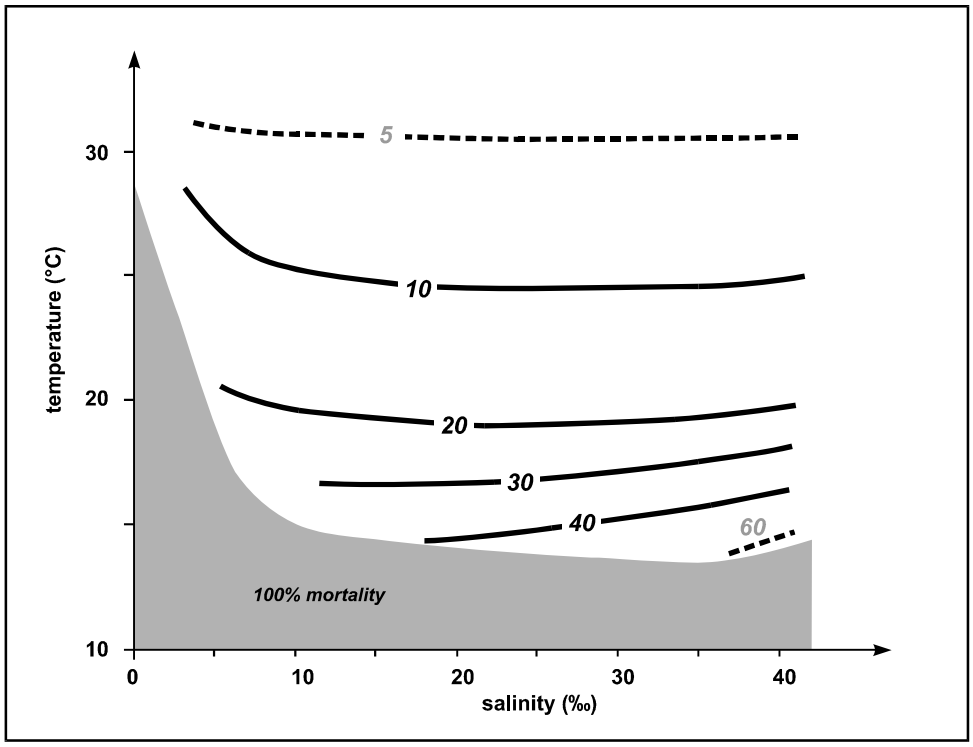


Figure 11 - Duration (days) of megalop stage from data of Costlow (1967). Broken contours extrapolated from range of data.

Sulkin and van Heukelem (1986) presented statistics of the duration of the megalop stage from their culture of sibling larvae. Based upon the central plurality of Fig. 10, i.e., the individuals attaining the megalop stage on days 33-39 after hatching, which represents 43% of the individuals of Fig. 10, the pooled average duration of the megalop stage is 37 ± 20 days, with a range of 15 – 95 days. These are pooled over cultures in four baths of (15°C & 21°C) x (30‰ & 35‰), representing conditions typical of the mid-Atlantic shelf. The total grow-out period from hatching to metamorphosis to the first juvenile instar of 95% of the specimens, combining these results with those of the larval grow-out above, would therefore range around 45-125 days. This is for sibling larvae, chosen from the central range of larval duration, cultured in constant, similar temperature and salinity. In the wild, individuals and conditions would be much more variable. If this isn't enough sources of variation to please the reader, the duration of the megalop stage in the wild is also related to migration and settlement, as will be seen (Section 5.4).

The next molt is a second metamorphosis, this time from the megalop to the juvenile crab. Although the relative body proportions of the crab vary as it ages (Gray and Newcombe, 1938a, Newcombe et al., 1949), it now exhibits the general appearance of an adult crab. The first intermolt stage (instar) after the megalop has a typical carapace width of 2-3 mm. Thereafter, these early juveniles molt at intervals of 6-7 days (Tagatz, 1968b).

The classic study of the development of early young juveniles is that of Newcombe et al. (1949), who tracked the growth in the laboratory of individuals from wild-caught megalops. (The data of Newcombe et al., 1949, is examined in Appendix B.) The practice of characterizing young juveniles (carapace width less than 15 mm) by their instar numbers appears to be based primarily on this work. Figure 12 summarizes the results of Newcombe and associates overlaying a representative (Pile et al., 1996) of the modern convention. Several inferences can be drawn from this figure:

(1) There is considerable variation in the carapace widths for a given instar that leads to overlap in the size ranges (gray boxes in Fig. 12).
(2) The size categories of Pile et al. (1996), which are mainly based on Newcombe et al. (1949) but adjusted to eliminate overlap, *must* misidentify instars due to the range of variation of size of an instar.
(3) The modern convention of identifying instars is in fact a code for size range (e.g., Forward et al., 2004b).

Using the means and standard deviations of the carapace widths of the early instars reported by Newcombe et al. (1949), the probability of each instar falling in the Pile et al. categories can be computed, from which the summary of Table 2 may be extracted. (Details are given in Appendix B.)

As the crabs grow, the intermolt period increases. Because of the effect of temperature on molting, low temperatures lengthening the intermolt period (Cadman and Weinstein, 1988), the

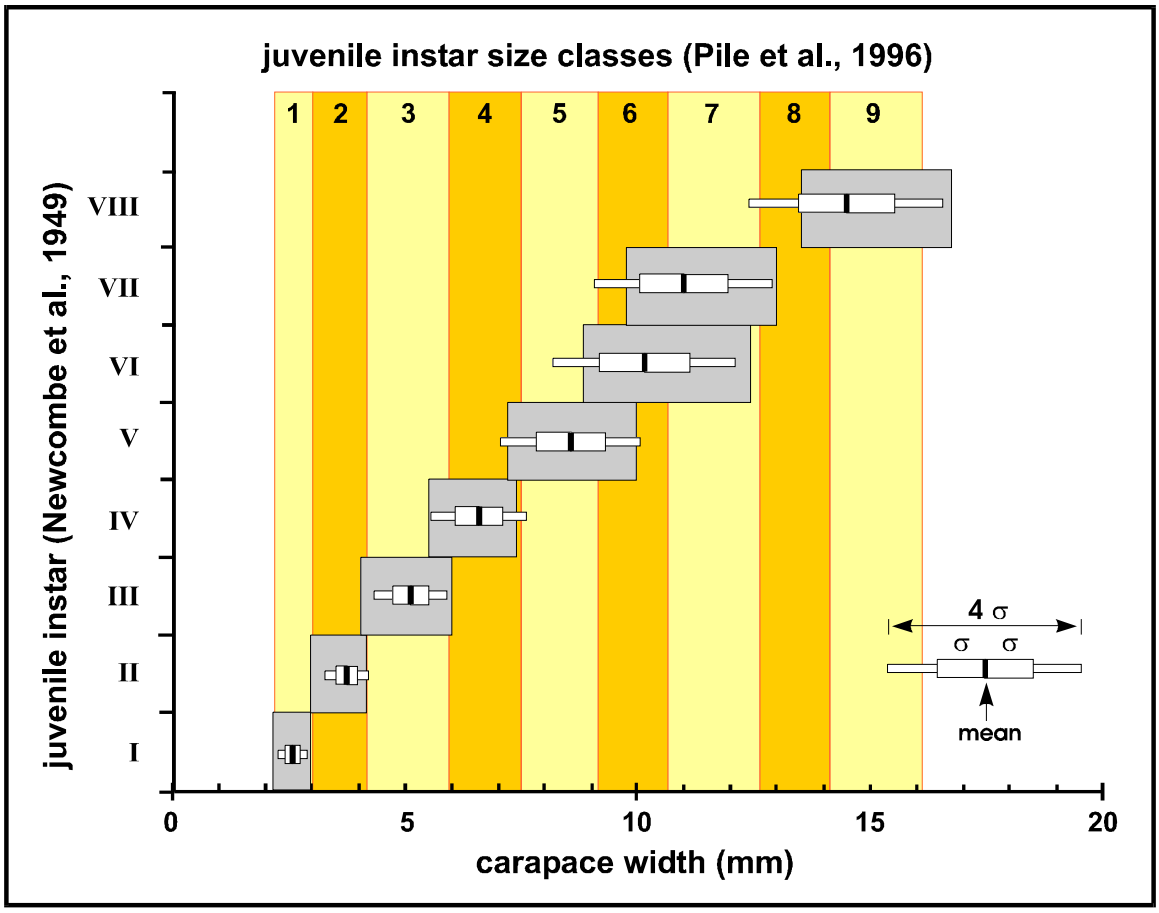


Figure 12 - Instar size ranges from Newcombe et al. compared to current convention of size classes. Grey boxes indicate size ranges for instars I – VIII from Newcombe et al. (1949), with mean, 2 x and 4 x standard deviations (68 and 95% of population, resp.), see Appendix B. Vertical bands indicate size classes used by Pile et al. (1996).

time required for a juvenile crab to mature varies with location. In the Chesapeake Bay area, 6 - 20 months are required (Van Engel, 1958, Hines, 2007), and in the St Johns River, Florida, 10-12 months (Tagatz, 1968a, Millikin and Williams, 1984).

The largest recorded blue crab in the scientific literature seems to be a 254-mm female from Charleston Harbor, South Carolina (Archambault et al., 1990). However, "Juice" McKinney, a Chesapeake Bay crabber, contributed a male behemoth to the Virginia Institute of Marine Science (VIMS) that measured 272 mm (0.893 feet) spike to spike, which had just molted when

Table 2
Probabilities of given instar falling in size categories of Pile et al. (1996)

	Pile et al. instar categories:							
	1	***2***	***3***	***4***	***5***	***6***	***7***	***8***
Fraction (%) of occurrences of instar falling in Pile et al. category for that instar:	97.3	98.3	95.7	89.4	75.7	59.5	64.6	31.3
Fraction (%) of all instars falling in Pile et al. category that are correct:	99.4	97.9	92.5	93.4	82.5	53.2	66.2	93.2
Fraction (%) of all instars incorrectly falling in Pile et al. category:	0.6	2.1	7.5	6.6	17.5	46.8	33.8	6.8

caught in 1998 (Malmquist, 2004). Mature females typically are 90-100 mm carapace width (Jivoff et al., 2007), ranging up to 180 mm (Hines, 2007). The variation for males is greater. For Chesapeake Bay, the reported range is 52 to over 200 mm (Williams, 1984, Jivoff et al., 2007, Hines, 2007). In the data reported by Van Engel (1990) from the York River, 50% of the males in the range 105 – 110 mm were mature. On the Maryland side, Uphoff (1998) reports 50% of 132 mm females as mature. In the St. Johns estuary, on the Atlantic coast of Florida, Tagatz (1968a) reported mature females ranging 99 to more than 177 mm (i.e., an immature female of 177 mm CW was found). The mature males were smaller than reported in the Chesapeake: of males in the range 145-155 mm, 50% were mature (but Tagatz based this on the appearance of the vasa deferentia, which may be one or two moltings before complete sexual maturity is attained, see Section 3.2).

On the Texas coast, Fisher (1999) pooled females-only data from trawl and seine collections of Texas Parks and Wildlife (TPWD), from which he developed the distributions of number of individuals versus carapace width, shown in Figure 13. It is apparent that both immaturity and maturity extend over a wide and overlapping range of carapace size.

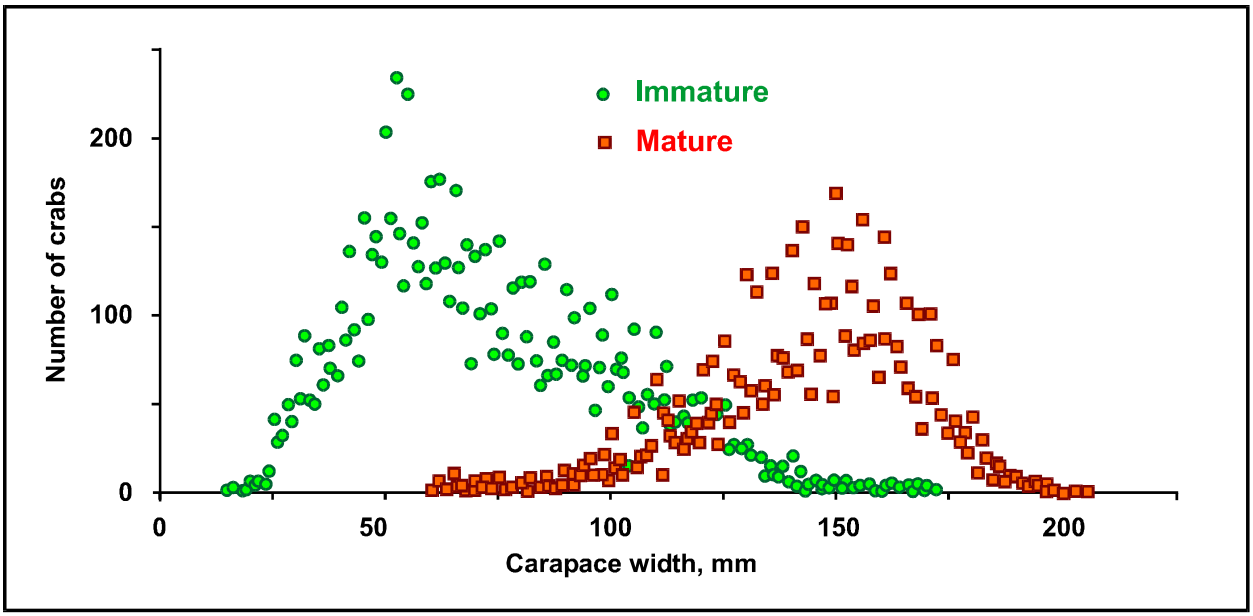


Figure 13 - Distribution of female blue crabs taken in TPWD trawls and seines for Texas coast 1984-87 versus carapace width. Data of Fisher (1999), replotted.

Both males and females are considered to molt 18-20 times before reaching maturity. As relatively few crabs have been observed over their lifetime, this is largely an estimate from growth rate (Truitt, 1939) derived from size increments on molting, beginning in the literature with the "theoretical number of instars" calculated by Newcombe et al. (1949). (An earlier calculation of this sort was given by Churchill, 1919. As his limited data indicated a larger increment per molt, his theoretical number of instars was smaller, *viz.* 15.) For a constant growth increment, the width after *n* molts is

$$w_{n+1} = w_1 (1 + R)^n \qquad (4)$$

where R is the molt increment as a fraction (not a percent) of the pre-molt width. Assuming a carapace width w_1 upon metamorphosis from the megalop (molt 0) to be 2.5 mm, and mean increment of 0.25 of the pre-molt width (see Section 3.1), the resulting widths after molting are given in Table 3. Tagatz (1968b) reports two crabs he tracked after metamorphosis to the first

Table 3
Theoretical carapace widths for each instar, from equation (4)

instar	*CW (mm)*	*instar*	*CW (mm)*
1	3	11	23
2	3	12	29
3	4	13	36
4	5	14	45
5	6	15	57
6	8	16	71
7	10	17	89
8	12	18	111
9	15	19	139
10	19	20	173

instar, finding that one required 10 molts to reach 20 mm, the other nine molts, which closely agrees with Table 3. (Time required was 68 and 69 days, resp.)

If R varies by instar, as is the case for the data of Newcombe et al. (1949) and Tagatz (1968b), see Appendix B, then the appropriate calculation is

$$w_{n+1} = w_1 \prod_{i=1}^{n} (1 + R_i) \qquad (5)$$

where $R_i \equiv (w_{i+1} - w_i) / w_i$. According to the data in the above-cited sources, the female exhibits a somewhat higher growth increment than the male (Appendix B).

4. ECOLOGICAL INTERACTIONS

4.1 Chronobiology

Chronobiology in general is the study of rhythmic, or periodic, variations in the behavior of organisms (Naylor, 2001). Typical periodicities are annual, seasonal, and daily (circadian), all related directly or indirectly to the apparent position of the sun in the sky, and monthly, related directly or indirectly to the apparent position or phase of the moon (circalunar). In the case of marine animals, in addition to circadian and circalunar variation, there is also circatidal, which includes fortnightly (14-day), and lunar-day-diurnal or circalunidian (i.e., 24.8-hour) variations. A central consideration in the literature is whether a manifested rhythm is exogenous, i.e., induced by external forces following that periodicity (such as temperature or light), or endogenous, i.e. controlled by an internal "clock", so that the rhythm continues to occur when the organism is isolated from external stimuli.

In the present context, our concern is to summarize periodicities of potential ecological importance in the behavior of blue crabs (which may appear as variation in integrated measures such as abundance or recruitment) and their likely stimulus or external forcing. Although the *approximate* periodicity of some feature of organism behavior can be provisionally identified from observations, the *precise* periodicity may remain elusive because of random variability, or "noise", in the basic data, hence the prefix "circa-" in "circadian" and "circatidal". More comments on the isolation of periodic behavior are offered in Section 4.1.4, below.

4.1.1 Circadian and circatidal rhythms

A circadian rhythm correlated with the diel variation in daylight is exhibited by most of the life stages of the blue crab (Sulkin et al., 1979, Forward et al., 1997, 2003b). Detailed and rigorous studies of both solar and tidal periodicities in the blue crab have been carried out in the laboratory and in the field by a number of workers, summarized by Tankersley and Forward

(2007). Circadian behavior in the early zoeal stages is disputed. Sulkin et al. (1979) determined that circadian swimming activity is induced in early-stage zoeae by 24-hr light-dark cycling, but the rhythm is apparently exogenous, because it subsided under constant-light conditions. They hypothesized that this swimming response in conjunction with an upward orientation (geotaxis) could be a mechanism for depth maintenance. On the other hand, data of Forward (apparently unpublished) indicates no such circadian swimming behavior but rather that the zoeae simply swim to the surface (reported in Forward et al., 2004b).

A pronounced circadian rhythm is evidenced in the megalop stage. Tankersley and Forward (1994) videotaped the activity of wild-caught megalops in a laboratory chamber. They found that megalops in darkness swim high in the water column during the times of daylight and lower during the times of night, with a distinct diurnal periodicity (the tide is semidiurnal in the field area) so this is a true endogenous circadian rhythm. This circadian behavior was not altered by tidal phase shifts relative to daylight, changes in salinity or the presence of substrate or eelgrass (*Zostera marina*) (Forward et al., 1994, 1997). Similar results were found in later experiments by Forward et al. (2003b). Over the continental shelf, which is the oceanic zone in which megalops spend most of their existence, this circadian movement would place the megalops near the surface during day and at depth at night, which is confirmed by sampling on the inner shelf (see Forward and Rittschof, 1994, Forward et al., 2003b). In the coastal zone, however, this diel migration would expose the postlarvae to daylight predators, so its ecological value is not immediately clear, and moreover is counter to that exhibited during estuarine reinvasion.. (This becomes apparent in the larger context of migration, see Section 5.4, below.) In the estuary, this vertical migration is suppressed, apparently by chemical cues, so that the megalops are found at the surface only at night (see Section 4.1.2 below).

Careful laboratory experiments determined that vertical movement of blue crab megalops was distributed uniformly with respect to tidal variation, i.e., there was no circatidal rhythm, and additional experiments have failed to induce a circatidal response in movement or depth regulation of megalops (Forward et al., 1997, 2003b).

A circadian vertical migration is observed in early juveniles, but in the opposite sense of that of megalops, i.e., the juveniles enter the water column in darkness, but are rarely found there in daylight. Forward et al. (2005b) used wild-caught first and second instars or newly metamorphosed first instars from Albemarle-Pamlico Sound in controlled laboratory experiments and found an endogenous circadian vertical movement (not continuous swimming but ascents and descents) at night time only, which confirms the field observation that these early instars are found in the water column only at night. A separate study (Forward et al., 2004b) addressed larger juveniles 6-9 mm (probably 4th and 5th instars according to Fig. 12), also from Pamlico Sound, both in field collections and in the laboratory. In the field, these crabs were mainly caught at night. In the lab, the crabs exhibited a diurnal variation in swimming. The data are noisy, with periods ranging from 23 to 25.5 hours, but showed no coherence with tides, so this was interpreted as circadian.

Color change in juveniles less than 40 mm was studied by Fingerman (1955) using specimens from Lake Pontchartrain. These juveniles were kept in darkness and monitored at hourly or six-hourly intervals for the black-pigment stage (dispersion) of leg melanophores. Over an observation period of 26 days, he was able to separate both a circadian (24-hour) and a circalunidian (24.8-hour) component (which he calls "circatidal"), whose relative phase coincided every 14.5 days, which confirms the periods. (Fingerman's interpretation is that the endogenous tidal rhythm has a 12.4-hour periodicity, rather than 24.8, though this reviewer must confess that his reasoning seems obscure, especially given the noise in the data and the coarse sampling interval.)

Motivated by the observation that ovigerous females in the lower Newport River apparently use selective tidal-stream transport in their spawning migration down the estuary (see Section 4.1.2, below), Forward et al. (2003a) evaluated ovigerous females in laboratory chambers under constant reduced light conditions. They found that periods of vertical movement corresponded to the ebb portion of the tide cycle, i.e., 2-5 hours before high water according to the measured tide at a NOAA station in the lower Newport estuary, but not to the expected light-dark cycle. The authors interpret this behavior as consistent with an endogenous circatidal behavior, whose period ranged 12.2-13.7 hours (the tides in the Newport are semidiurnal). This circatidal

behavior was most manifest in crabs with late-stage eggs, and least in crabs with early stage eggs. A subsequent study (Forward and Cohen, 2004) clarified that the circatidal rhythm occurred in all female crabs with mid-stage embryos (3-4 days from hatching). Darnell et al. (2010) employed the same basic protocol, and performed separate experiments with pre-pubertal, mature but unspawned, and ovigerous females, finding that only the last exhibited an endogenous tidal rhythm. They tested ovigerous females from three different sites, with semi-diurnal, diurnal and minimal tides, and identified circadian, circatidal, and circalunidian frequencies with rigorous spectral analysis of the time series of crab activity. However, the tidal variation in activity expressed by the crabs varied among individuals from the same source waters. Darnell et al. (2010) offer the important hypothesis that the internal clock in blue crabs is mutable, i.e. phenotypically plastic, and can be "tuned" or entrained to any of the three basic rhythms (circadian, circatidal, circalunidian), depending upon the tidal environment.

A detailed field study with tethered crabs was performed nearby in Bogue Sound by Hench et al. (2004), see 4.1.2, below. These basically confirmed a tidal (12.4-hr) variation in vertical motion, though with more of the crabs active during the night. These researchers conclude that the crabs with late-stage egg masses are responding to an endogenous circatidal rhythm, while crabs with early-stage egg masses and those that have released their larvae are responding mainly to environmental cues, perhaps reinforcing a weak endogenous cycle. Similar equipment and strategy were used by Darnell et al. (2012) to compare the swimming activity between crabs from sites around Beaufort inlet with semidiurnal tides and a site in Albemarle-Pamlico with negligible tide. Swimming activity was highly variable, from none at all in the Albemarle-Pamlico site to significantly tidal in the site located in a migratory corridor. Activity was correlated with ebb, independent of light conditions. These researchers suggest that the swimming response is strongly affected by a suite of environmental cues that is highly variable in space.

4.1.2 Selective tidal-stream transport

The single most important rhythmic variation of the blue crab, at least on the mid-Atlantic coast, is a vertical migration to take advantage of the direction of tidal currents, called selective tidal-stream transport (STST). The organism remains on or near the bottom when the tidal current is in an adverse direction, then enters the water column to be carried by the current when the direction is favorable. STST is not unique to the blue crab but is now known to be employed by a number of organisms in their migration upstream or downstream in an estuary, including other brachyuran crabs such as the fiddler (Tankersley and Forward, 1994, Tankersley et al., 1995), penaeid shrimp (Dall et al., 1990), oyster larvae (Wood and Hargis, 1971), and juveniles of several catadromous fish including the American eel (Wippelhauser and McCleave, 1988), and is suspected in the migration of other catadromous crustaceans. As a hypothesis, STST has appeared in the scientific literature for at least a century, and may have originated with work of Johannes Schmidt (1906) on eels in Europe (who notes that the behavior is well known to fishermen) and Julius Newton (1917) on oysters of New Jersey, see also Carriker (1951). Reviews of this behavior are presented by Naylor (1985, 1988) and, specifically for the blue crab, Forward et al. (2003b).

Blue crab megalops are considered to employ this strategy to move into the estuary from near its mouth, then up the estuary, riding the flooding current. In the mid-Atlantic, where the dominant tidal cycle is semidiurnal (i.e., 12.4 hours), the megalops do not ride every flood current, but mainly those that occur at night (Olmi, 1994). Thus they are found near the estuary mouth at night at high tide. (The behavior of the tide as a standing wave, in which slack water coincides with high or low stage, is acquired as the tide propagates up the estuary, but it enters the estuary as a progressive wave in which the current extrema coincide with stage extrema, see Ward and Montague, 1996.) More generally, in these estuaries they are not found in the water column during the day, independent of tidal condition, and are found in the water column at night only during the flood current (DeVries et al., 1994). This is a reversal of the endogenous circadian photoperiod response exhibited by megalops offshore (Section 4.1.1).

Since there is no endogenous circatidal rhythm of the megalops, it follows that any tide-related behavior must be a response to external conditions. Forward and Rittschof (1994), see also Forward et al. (1995), exposed megalops to the same light field in columns of two different waters, offshore and estuarine, at the same salinity and temperature. In the offshore water the megalops exhibited its endogenous circadian behavior, but in the estuarine water, this photoresponse was absent (but when placed back in offshore water, the megalops reverted to the offshore daylight response of swimming higher in the water column). Apparently, the circadian photoresponse is inhibited by a chemical signature of estuarine water. This, of course, is not a complete explanation for the estuarine behavior of megalops, because it does not account for their presence in the water column at night, only their absence in daylight. Moreover, only a minority of the experimental crabs exhibited the above responses in both offshore and estuarine water.

Experiments (Tankersley et al., 1995, Welch et al., 1999, Welch and Forward, 2001, Forward et al., 2003b) have determined that two separate and sequential factors induce vertical movement in megalops: (1) an increase in salinity, (2) increased kinetic energy of turbulence. The initial upward movement is stimulated by the salinity increase. Tankersley et al. (1995) found that blue crab megalops exhibit a swimming response to a rate of increase in salinity as small as 5×10^{-4} ‰ s^{-1}, with a constant, even declining, response for rates of increase greater than 1×10^{-3} ‰ s^{-1}. Welch et al. (1999) determined that in a tidal current, the response of a megalop to increasing salinity would diminish even faster (because the megalop is now carried with the flow) unless accompanied or followed by an increase in turbulent kinetic energy. However, an increase in kinetic energy does not stimulate vertical movement if not preceded by an increase in salinity. There appears to be a kinetic-energy threshold above which the maximal swimming response is stimulated, around 1 cm^2s^{-2} corresponding to a current speed of 10 cm s^{-1} (in the flume of Welch et al., 1999). The results of Welch et al. (1999) are compelling, but the quantitative relation of response to kinetic energy is unclear (and not exhibited by at least 40% of the megalops).

Additional laboratory studies of Welch and Forward (2001) provided some support for the hypothesis that during ebb, though the kinetic energy is sufficient to stimulate a swimming response, the decrease in salinity does not evoke the same initial upward movement as the

increase in salinity in the flooding current. In these experiments, the megalops were not entirely cooperative, showing some movement into the current and maintenance in the water column despite decreasing salinity, though in smaller numbers than the experiments with increasing salinity. Welch and Forward (2001) speculate that the smooth surfaces of the laboratory flume do not provide the same purchase as the estuary bed, so that these megalops are unwillingly entrained into the current. When current speed, and therefore kinetic energy, is minimal, i.e. at slack water, megalops in the water column settle to the bottom. This has been observed in the lab (Welch et al., 1999) and in the field (Tankersley et al., 2002).

In summary, the present conceptual view of estuarine STST in blue-crab megalops (Forward et al., 2003b, Tankersley and Forward, 2007) is:

(1) under daylight conditions, megalops remain at or near the bed (due to chemical cues in estuary water which reverse the endogenous circadian pattern of their offshore development) independent of tidal conditions,
(2) under nighttime conditions, rising salinity associated with flooding current induces the megalops to become active, entering the water column,
(3) kinetic energy associated with the tidal current induces the megalops to swim, maintaining their position in the water column, and thus being carried by the flooding current,
(4) as the tidal current slackens, the kinetic energy diminishes, the megalops cease swimming and settle back to the bed,
(5) because the ebbing current is associated with a salinity decrease, the megalops do not re-enter the water column but remain on the bed.

We note that in this conceptual model two hydrographic properties are necessary for STST to operate in an estuary: a horizontal gradient in salinity that can be advected by tidal currents, and the occurrence of flood current during a sufficient proportion of the night.

The STST strategy is used by the blue crab in a mature stage, namely by inseminated females in their spawning migration. The details of this migration in the mid-Atlantic have been evolving

over the past decade. Tankersley et al. (1998) observed the migration of crabs past an observation platform just inside the mouth of the Newport River estuary (Beaufort, North Carolina), and determined that few crabs were seen during the daylight, at night most crabs were not actively swimming but riding the tidal current, almost all ovigerous crabs were observed in ebb currents, and almost all (98%) crabs riding the flood current lacked egg sponges (and all of these captured for examination showed evidence of having recently spawned). These researchers conclude that the ovigerous females were employing STST seaward, i.e., selective ebb transport (SET) and after hatching were using STST landward, i.e., selective flood transport (SFT), to return to the estuary.* This would of course entail vertical migration to enter a favorable tidal current.

Forward et al. (2003a) evaluated ovigerous females, caught at the same site, in laboratory chambers and found apparent endogenous circatidal behavior corresponding to tides in the lower Newport (see 4.1.1, above). This circatidal behavior was most manifest in crabs with late-stage eggs. Larvae were released in the laboratory chambers during the expected ebb period and shortly after the expected sunrise. The circatidal behavior ceased after the eggs were released. These researchers note that the above SFT observed by Tankersley et al. (1998) was not replicated in the laboratory, and may be subject to a different control. In a subsequent study, Forward and Cohen (2004) determined that the circatidal behavior occurred in all female crabs with mid-stage embryos, independent of whether they were engaged in SET when captured, and occurred independent of the light/dark cycle, i.e., was unaffected by a light/dark cycle corresponding to that in the field (but much lower intensity than natural sunlight). These results open the possibility that ovigerous crabs may employ SET during the day, but remain too deep for observation. Alternatively, there may be a separate, exogenous control related to light intensity.

A detailed field study in Bogue Sound, North Carolina, was carried out by Hench et al. (2004) consisting of census of swimming crabs and electronic monitoring of tethered individuals. The

* The conventional designations in the literature are ebb-tide transport (ETT) and flood-tide transport (FTT). This writer, admittedly anal-retentive, prefers the above terminology in this report, because the transport is effected by the tidal current, not the water-level variation that is the tide. The former ebbs and floods, the latter rises and falls. Sigman and Maxwell notwithstanding, there is no ebb tide.

censuses were performed in summers of 2001 and 2002, a total of 19 nocturnal ebbs being sampled. All crabs observed in the census were mature females (except for one young male) and all were swimming with the current (i.e., seaward). In both years, a substantial number of these (21% and 46%) were nonovigerous. Females with late-stage egg sponges were most common.

In the tether experiments, recording pressure sensors were attached to ovigerous female crabs (130-166 mm), which were tethered in depths of 2.2 m near a bottom-mounted acoustic- doppler current velocity profiler (ADCP) and attached recording CTD. Sampling rate was 0.5 Hz, accumulated in a 6-min window and averaged. The 5-m tethers allowed the crabs the full scope of water depth. A total of eight so-equipped crabs were monitored during the field observation period of 38 days in late summer 2002, two of which extruded a second egg sponge, and three of which were lost to predation during the course of the experiment. Tides during the tethering experiment were semidiurnal (12.4-hr period) and about 95% astronomical, with stage leading velocity by 1.7 hours (i.e., after high water, with stage dropping, the flood current continued for 1.7 hours; similarly after low water, the ebb current continued), indicating that the tide was predominantly progressive, as one would anticipate this close to the inlet.

The tethered crabs exhibited vertical motion primarily on ebb currents, particularly that portion of the ebb in which water levels were falling. While this activity took place in both night and day, the majority of crabs were more active during the night. There was substantial variability from crab to crab, a few ascending *only* during the nocturnal ebb. After egg release, vertical ascensions declined on average, but there was considerable variation among the crabs, crab 7 being particularly erratic (see Hench et al., 2004). Two crabs that continued the ebb ascensions extruded a second egg sponge. Five of the egg releases occurred at the turn of the current before ebb, two during the ebb race, and one (crab 7, again) during flood about 2.5 hours before slack. About half the crabs released larvae within three hours of sunrise, but one released at sunset (not crab 7 this time). Very few of the crabs exhibited vertical ascents during flood after larval release, in contrast to the SFT observed by Tankersley et al. (1998). Hench et al. (2004) surmised that a return to the estuary might occur on longer time scales than the duration of their study, or may require some sort of oceanic environment cue, which these crabs, being tethered, did not experience.

A follow-up series of laboratory experiments were reported by Tankersley et al. (2005) seeking to resolve the conflicts between the field work of Hench et al. (2004) and the laboratory work of Tankersley et al. (2003a). These experiments basically confirmed the field studies. Females with immature embryos exhibit swimming activity at times of ebb currents in the field (a minority on alternate ebb cycles), and the activity becomes more pronounced as the embryos mature. This activity ceases upon larval release, but is re-acquired several days later, implying continued selective ebb transport. This is speculated to be a re-entrainment of the tidal cycle driven by pressure changes. There is no apparent reason for the discrepancies between the two laboratory studies. It is, however, noteworthy that the lab results of Tankersley et al. (2003a, 2005) were based on 26 and 25 crabs, resp., and the tether experiments of Hench et al. (2004) on 8 crabs. Moreover, neither the field tethering study nor the laboratory experiments explain the switch from SET to SFT observed in the field by Tankersley et al. (1998).

4.1.3 Other rhythms

There is a tradition that blue crab molting is associated with the phase of the moon, presumably due to light (van Montfrans et al., 1990), but perhaps through the operation of the tide. Nearly a century ago, Churchill (1919) investigated growth of crabs in field enclosures and determined that the frequency of molting was independent of the phase of the moon. Smith and Chang (2007) carefully analyzed the intermolt-period versus length data from blue crabs in the wild, and found no hint of periodicity in the variance, which should have been present if in fact there were some form of lunar control on molting. These authors argue that the "synchronous molt" responsible for a spring pulse in soft-shell crabs is in fact a response to the springtime rise in temperatures. The folklore continues, however (see, e.g., Otwell and Cato, 1982, Oesterling, 1995). In contemplating their (unexplained) observations of high-density pulses of megalops correlated with the full moon, van Montfrans et al. (1990) speculate that association of a full moon with ecdysis may begin with the first molt to juvenile crab. Bishop et al. (1984) in their experiments with peeler-pot design in South Carolina noted that catches peaked "dramatically" in the week before full moon.

The settlement pulses of blue crab megalops on the Atlantic coast are sometimes asserted to be associated with lunar periodicity. This topic more properly falls under migration, because these pulses are considered to quantify megalop recruitment in the estuarine crab population, and to drive settlement in nursery habitats, see Section 5.4. In the present context, it is appropriate to examine the extent to which this rhythmic behavior is supported by the available data. A representative sampling of the recent literature is given in Table 4. Inspection of this table yields a first impression of general inconsistency, from year to year at a site, between sites, and between estuaries. While there is occasional "lunar periodicity" exhibited in Chesapeake Bay, this may be associated with a single lunar phase (29-d period) or with opposite phases (14.5-d period). One disquieting observation is that the periodicities found greatly depend on the details of the analysis methods. The work of Forward et al. (2004a) in the Newport estuary is revealing. A clear association of settlement pulses with neap tides was found. These neap tides happen to fall within the night period. Forward et al. suggests that these are in fact the result of nocturnal SFT, in which the megalops are settling at the turn of the tide. In the Gulf of Mexico, there was some accord that settlement pulses favored small-range tides (though wind was the dominant control). In the Gulf, of course, these small-range tides are associated with zero lunar declination (i.e., equatorial tides), whereas on the mid-Atlantic with quarter lunar phase (i.e., neap tides).

Blue crabs sometimes feed more under twilight (crepuscular) conditions. Tankersley and Forward (2007) note that the maximum visual sensitivity of blue crabs at 500 nm is mismatched to the typical light environment of estuaries in the range 570 – 700 nm, due to the re-radiation from yellow humics in the water. However, in twilight conditions, the ambient downwelling light shifts to 490-520 nm, so that the crabs would be better able to exploit visual cues.

4.1.4 Comments on the detection of periodic behavior

This review has only sampled the confusing and often conflicting farrago of reports of periodic behaviors of the blue crab (and there is more to come). One general attribute of all of these results should be noted: the data on crab behavior from which they are inferred are generally

Table 4
Lunar periodicity of megalop settlement pulses reported in recent literature

Estuary	*Measurement*	*Data period*	*Lunar association*	*Citation*
Delaware (Broadkill)	substrate	1989-92	no correlation with lunar phase	Jones and Epifanio (1995) van Montfrans et al. (1995)
Chesapeake (York)	substrate	1985-88	lunar phase: maximal at full moon	van Montfrans et al. (1990)
Chesapeake (York)		1989-92	lunar phase: maxima after full & new	van Montfrans et al. (1995)
Chesapeake (York)	substrate	1989-92	semilunar: full & new, 4-d lag much interannual inconsistency	Metcalf et al. (1995)
Chesapeake (York)	fixed plank-ton net	1987-89	14 d fortnightly in 1988, weak semilunar: 5-d lag after new & full	Olmi (1995)
Banks Channel, NC	substrate	1990-92	no significant autocorrelation	van Montfrans et al. (1995)
Banks Channel, NC	substrate	1990-92	lunar phase: new moon	Mense et al. (1995)
Albemarle-Pamlico	substrate	1996-2005	no significant variation with lunar phase	Eggleston et al. (2010)
Newport River, NC	pumped plank-ton nets	1992	no correlation with lunar phase, but abundance highest on nocturnal rises	DeVries et al. (1994)
Newport River, NC	substrate	1993-2002	lunar phase: settlement max on nocturnal neap tides; 2/7 years fortnightly (semilunar) period	Forward et al. (2004a)
Charleston Harbor, SC	substrate	1987-88	semilunar: 1st & 3rd quarters, minimal at full moon	Boylan and Wenner (1993) & van Montfrans et al. (1995)
Coastal marshes, GA	substrate	2005	no correlation with tide height, no tidal period peaks in power spectrum	Bishop et al. (2010)
Mobile Bay and Mississippi Sound (east)	substrate	1990	settlement favored under equatorial tides, but mainly controlled by wind	Morgan et al. (1996)
Mississippi Sound	substrate		higher settlement during 2nd quarter but no year-to-year consistency	Rabalais et al. (1995)
Terrebonne Bay	substrate	1990-91	higher settlement during 1st lunar quarter but no year-to-year consistency,	Rabalais et al. (1995)
			higher settlement during small-declination, i.e., minimum tidal range	Hasek & Rabalais (2001a)
Galveston Bay	substrate	1990-91	higher settlement during 1st lunar quarter but no year-to-year consistency	Rabalais et al. (1995)

noisy. Moreover, the noise arises not only from imprecision of observation, but variation in the behavior of individual organisms or discrete populations. In general, the statistical diagnosis of the action of many specimens is confounded by high dispersion of the data. The only means for surmounting the noise problem is to observe a greater number of data points. For cyclic phenomena, this translates to increasing the number of measurements and, in addition, extending the observing period over many wavelengths of the suspected cycle.

The most common biological periodicity, and the easiest to establish, is the annual cycle. Even at this period, it is rare to find precise synchronicity in populations. For example, while a small number of species of fish may spawn during a set few days every year, such as those analyzed by Cushing (1969), spawning is typically spread over a period of weeks, or in the case of the blue crab months, whose position in the calendar varies from year to year. Where behavior of individual crabs can be followed, such as in laboratory settings or tethered or tracking experiments in the field, there is considerable variation among individuals, with a large proportion often failing to exhibit the hypothesized rhythm. This intrinsic variability creates problems in precisely quantifying a periodicity in behavior, or separating the influences of several nearly equal periodicities.

Qualitative association with a postulated cyclic behavior is therefore difficult to establish, unless many cycles are represented in the data. This has historically presented a challenge in field biology. Since data collection is labor-intensive and prosecuted under potentially inclement conditions, the data have tended to be irregularly sampled at long intervals over relatively limited durations. Frequently a cyclic pattern seemed to be manifested at one site, or in one sampling period, only to be absent in the next. This type of aberrancy is compounded when the postulated cyclic behavior is episodic rather than quasi-continuous, such as the megalop pulses of Table 4. For example, Mense and Wenner (1989) suggest an association between phase of the moon and the abundance of megalops. However, their data collections were performed at biweekly intervals and plotted against either new or full moon (presumably the predominant phase for the respective half of the month). In their 16 month study, six pulses of megalops occurred, the three largest of which coincided with full moons. With uncertainty in the timing of a pulse resulting from the biweekly sampling interval and the representation of full moon as a large interval of

days, any correspondence with the apparent full moon of half of the maxima is probably coincidental. (It should be noted from their data that in the five months of 1987, there is an exact correlation of the five maxima of salinity with a full moon!)

Modern technology is beginning to provide extended and detailed biological time series. A prime example in the study of blue-crab life cycles is the use of moored artificial-substrate megalop collectors (the majority of the data from Table 4), which is reviewed in Section 5.4.4 below. The increasing acquisition of quantitative biological time series has motivated the availability of software to facilitate analysis in the frequency domain (see, e.g., Dowse and Ringo, 1989, Ives et al., 2010). But even at this, the spectral content typically departs significantly from the postulated periodicity. This is exactly analogous to the departure of a sample mean from a theoretical population mean. Both are manifestations of the statistical dispersion of the raw data. An excellent example is the work of Forward et al. (1997), who used ingenious laboratory instrumentation to monitor the numbers of megalops swimming as a function of time ("actograms") in their study of circadian rhythms. Usually less than half of the megalops were in motion, and the spectral peaks for eight different experiments, all of which were considered to manifest circadian rhythm (i.e., 24-hr period), ranged 19.2 – 29.6 about a mean of 25.7 hrs. Clearly, this level of uncertainty would undermine the assertion of a diel periodicity, and confound the differentiation of solar-diurnal and lunar-diurnal periods (which differ by only 0.8 hours).

4.2 Water quality requirements

Water quality is quantified by the concentrations of constituents carried in solution or suspension in the water. There are many (see Ward and Armstrong, 1997, who analyze some 192 water or sediment constituents in the Coastal Bend bays), some of which are beneficial, some of which are toxic, and some—in fact, most— have more complex interactions with aquatic organisms. In the present context, however, the focus is on the basic environmental parameters of temperature, salinity and oxygen. The distributional patterns of each of these parameters in an estuary is different, because each responds to different geographical distributions of controls, and each is

dictated by different suites of physicochemical processes ("kinetics"), which in turn influence their response to hydrodynamics.

The determination of acceptable ranges of these environmental parameters required for biological functioning of the blue crab in the literature is based upon two classes of information:

(1) the physiological success of the crab in controlled experiments, usually in a laboratory setting.
(2) those ranges in which the crab is found in the wild,

Both of these have limitations. The former has the deficiency that the animal is in an artificial setting, usually stressed by its capture and handling, with the potential for biasing its responses. Also, there are several metrics for "success", which may not measure the entire complement of organism requirements. The latter has no means of detecting whether the crab is in a particular environmental range, say, of salinity, for physiological reasons, or for other reasons, e.g. feeding or mating, for which the ambient salinity is coincidental. While there have been relatively few studies addressing the distribution of blue crabs with respect to the full suite of environmental attributes, other decapods, notably penaeid shrimp, have been studied fairly extensively. Recently, the Guadalupe-San Antonio Basin and Bay Expert Science Team (GSA-BBEST) reviewed current literature on the salinity preference of white shrimp, generally regarded as a species that favors lower salinities (roughly, mesohaline), and concluded, "In essence, it appears that although juvenile white shrimp may often be more abundant in the lower salinity parts of the estuary, physiological constraints are not driving their distribution, but rather some other biotic or abiotic aspect of the upper reaches of estuaries provides high quality habitat that attracts juvenile white shrimp to those areas" (GSA-BBEST, 2011, p. 4-41). (One candidate aspect is the extent and complexity of marshes in the upper estuaries, King et al., 2005.) As will be seen, a similar reservation may be expressed for blue crab.

4.2.1 Temperature

Temperature has little variation in the horizontal across an estuary, with a few exceptions addressed below. Because of this lack of gradient, horizontal current advection has little direct effect on temperature. Temperature is determined principally by thermodynamic heat exchange at the water surface, which generally varies on larger space scales than the dimensions of an estuary, so is approximately equal everywhere in the system. Energy enters the water column at the surface as direct sunlight, longwave radiation (from the atmosphere) and conduction (from the atmosphere). There are substantial variations in water temperature in the estuary with season, driven directly or indirectly by the changing altitude of the sun in the sky. Energy leaves the water surface by the processes of conduction, longwave radiation, and evaporation. Because of the high heat capacity of water, its temperature responds slowly to changes in the surface heat budget, acting as a time-integrator of the net heat flux. The deeper the water, the more effective the water column is in dampening the variability in heat budget. Temperature may vary in the vertical, depending upon the intensity of mixing processes and the depth of water. In the Texas bays, and in San Antonio Bay in particular, temperature is usually homogeneous and well-mixed (see Ward and Armstrong, 1997, for detailed evalutions in the Coastal Bend bays).

One exception to these statements is extremely shallow areas, especially those near shore and those in the upper reaches of the system. These tend to track atmospheric temperature more closely, because there is less water mass to absorb heat exchange. These are therefore warmer in summer and cooler in winter than the open, deeper waters of the estuary. Another exception is in the vicinity of a point source of water substantially different from ambient, notably power-plant cooling-water returns. A third exception, which has limited relevance to Texas, is the case of large estuaries whose circulation interacts with significant hydrographic structure of the adjacent ocean. Fjords are a prominent example.

The larval forms of blue crab are generally regarded to be stenohaline and stenothermal, requiring salinities greater than 20‰ and temperatures above 25°C for complete development. The published basis for this seems to be the relatively few reports on laboratory culturing of the larvae, e.g. Sandoz and Rogers (1944), Costlow and Bookhout (1959), and Costlow and

Bookhout (1962). In the modern view, laboratory results are supplemented by the evolutionary development of the blue crab. "These larvae are incapable of development outside the tropic-like conditions that occur seasonally in surface waters of the inner continental shelf throughout the range of the species," concludes Epifanio (2007). A review of environmental requirements of the blue crab, including temperature and salinity, is presented by Tankersley and Forward (2007).

The laboratory should be an ideal environment for testing temperature (and salinity) requirements of blue crab at various life stages, because all other potentially confounding factors can be eliminated or controlled. This is especially true of the larvae, since their development can be closely followed with the microscope. Culturing can be a challenge, however, as reviewed in Section 3.3, and may account for the relative scarcity of results in the literature. The early experiments of Sandoz and Rogers (1944) examined hatching and growth of larvae through the first two or three instars over a range of temperature from 14 to 31°C and salinity from 0 to 33‰. They found hatching success to be abruptly bounded between 19 and 29°C. The hatched zoeae successfully molted through the first three stages for temperatures between 20 and 29°C.

In the larval growth experiments of Costlow and Bookhout (1959), eggs were set up in baths of salinities 10.5, 15.0, 20.1, 26.7, and 31.1 ‰, each at temperatures of 15°, 20°, 25° and 30°C. No hatchings occurred at 15°, and none developed beyond Zoea I at 20°C. The only combinations for which zoeae developed beyond two moltings are those shown in Fig. 9, from which it is difficult to discern any clear dependence of growth upon salinity or temperature. One additional series was set up of salinity 32‰ at 30°C, of which less than 1% developed to the crab stage — which is not substantially worse than the survivors of the other combinations, see Fig. 9 — but the data on intermediate stages were not reported. On the basis of success of hatching and longevity of the zoeae, these controlled experiments suggest a requirement for temperature in the range 25-30°C for zoeae to survive beyond the third molt.

Laboratory data from Costlow (1967) on survival of megalops to the first crab stage are presented graphically in Figure 14 (*cf*. Fig. 11). The nearly horizontal isopleths in the range of salinity 10-35‰ show the principal control on both mortality and megalop duration to be

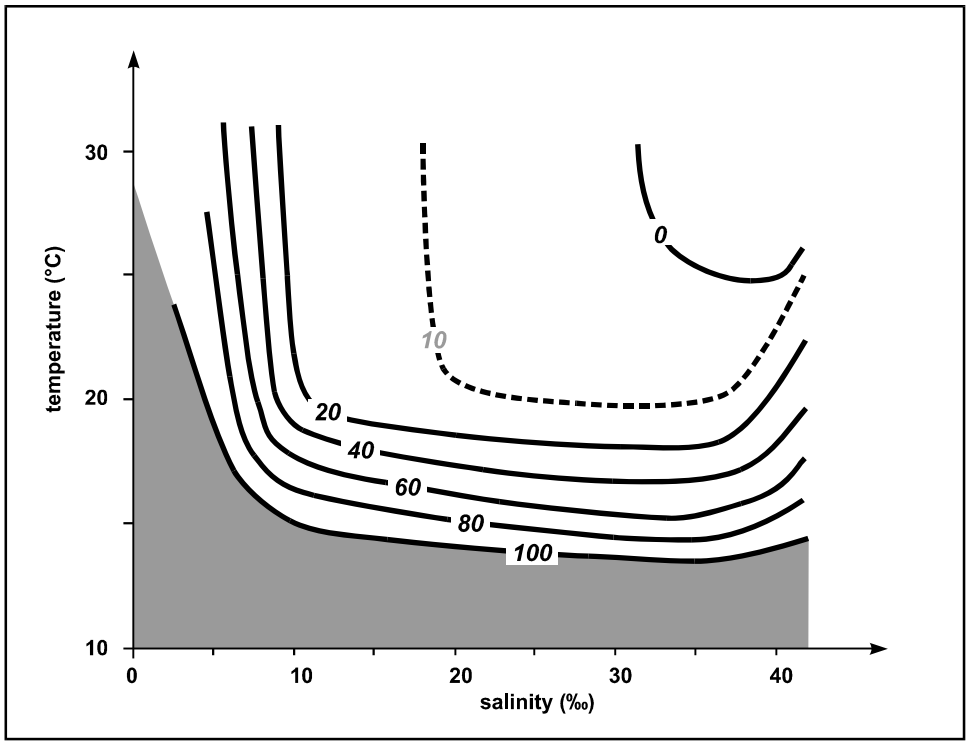


Figure 14 - Megalop mortality (percent of megalops failing metamorphosis to first crab stage), from data of Costlow (1967)

temperature, over this salinity range. For salinities below 10‰, there is a pronounced increase of mortality with decreasing salinity.

Temperature is an important control on molting in juveniles, as noted in Section 3.1 above, both in affecting the duration of the intermolt periods and in shutting down the molting process if temperatures fall too low (or become too high). Generally, the rate of molting increases with higher temperatures, i.e., the duration of the intermolt period decreases. Careful laboratory work of Leffler (1972) established that growth rate and mortality increase as temperature rises. Several lines of research, summarized in Section 3.1, indicate that below 10°C blue crabs cease molting, and become torpid. In the wild, at these temperatures they burrow into sediments and await spring. More (1969) noted a difference in behavior between males and females in Texas, the females being active down to 10°C while the males remain buried below 15°C.

Table 5
Upper and lower* lethal limits of temperature for blue crab
determined experimentally by Tagatz (1960), average 48-hr LC50 in °C

	juvenile		*mature female*	
20% seawater	2.3	35.2	2.3	35.0
100% seawater	1.9	36.6	1.8	35.9

*Lower 48-hr LC50's are overestimated, because the lowest temperature employed by Tagatz was 0°C, and many of the crabs survived dormancy at this temperature.

Based on growth and food conversion, the optimal temperature range for juvenile blue crab (30-40 mm) was determined to be 29-30°C by Holland et al. (1971), but mortality increased quickly at temperatures above this. Temperatures in excess of 40°C proved lethal after a few hours (and a few minutes at 42°C). Tagatz (1969) carefully determined the 48-hour LC50 (the temperatures at which 50% of the crabs survived after 48 hours) for juveniles (40-60 mm) and mature females. His results are summarized in Table 5.

Holland et al. (1971) speculate that wild crabs may be able to survive natural summer temperatures in the range 31-35°C because of relief due to diurnal variation in temperature. (The plausibility of this hypothesis was established experimentally by Rosenberg and Costlow, 1976, for zoeae of the mud crab, *Rhithropanopeus harrisii*, by comparing survival in constant temperature baths to that in baths with cycling temperatures.) Leffler (1972) found that blue crabs tolerate temperatures as high as 34°C if exposure is limited to less than 48 hours, but mortality increases sharply for exposures longer than this.

Rome et al. (2005) carried out experiments to examine the effect of cold temperatures on blue crab. The acclimation issue (see below) was avoided by collecting crabs from the upper reaches of Chesapeake Bay during late winter. Crabs were placed in baths at constant temperatures of 1, 3 and 5°C at salinities of 8, 12 and 16‰ for 60 days, and mortality assessed every 5 days. (The 1°C bath was raised to 3°C after 30 days.) Their data indicate a modest increase in survival at

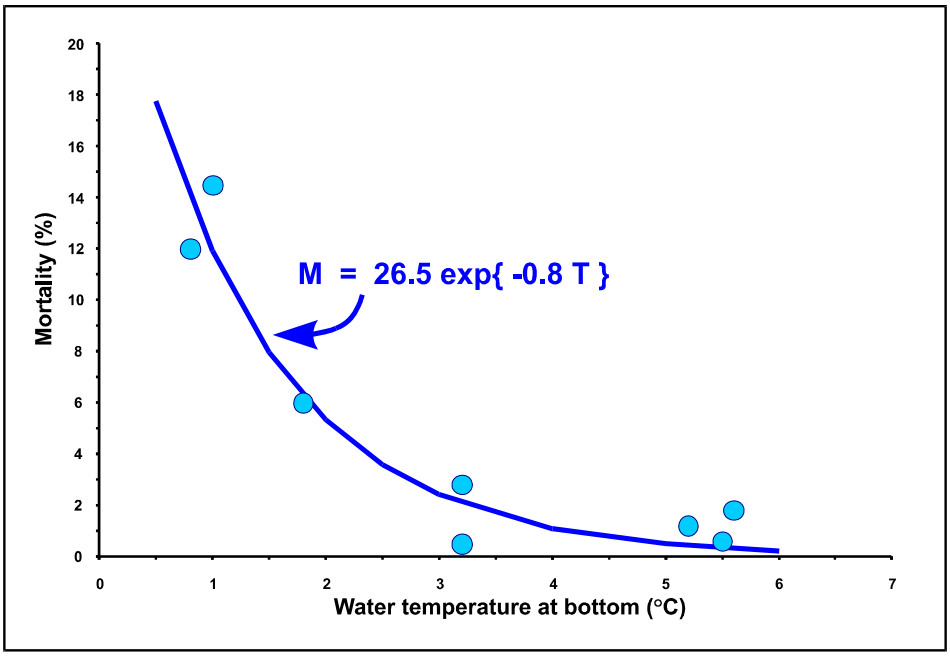


Figure 15 - Mortality of overwintering crabs in Chesapeake Bay versus February mean water temperature, data from Rome et al. (2005), replotted. Best-fit exponential, explained variance = 93.1%.

higher salinities, and an LT50 (duration in days at which 50% of the crabs survive) of about 5 days at 1°C and 3°C for mature females. These findings are generally consistent with those of Tagatz in Table 5. However, Rome et al. found the juveniles to be markedly more tolerant to cold temperatures than the mature females (LT50 of about 25 days, versus 5 for the females), which is inconsistent with Table 5. The field data of Rome et al. (2005) from dredge surveys of overwintering crabs, shown in Figure 15, are not directly comparable, because time of immersion at low temperatures is unknown, the water temperatures are variable, and the data are pooled over all crabs in the dredge. Qualitatively, as noted by Rome et al., the mortality in the field is evidently less than that in the laboratory experiments, though there is clearly a substantial increase in mortality for temperatures below 3°C.

Abrupt changes in temperature frequently prove compromising or fatal to crabs in laboratory studies, so there is an increasing practice to acclimate crabs before beginning tolerance experiments. Typically the practice is an acclimation period over several days over which the laboratory bath is altered stepwise to the test temperature, e.g. Holland et al. (1971) acclimated

crabs for six days. Tagatz (1969) determined that a longer period, on the order of three weeks, was necessary and that the acclimation conditions needed to better approximate those of the waters from which the crabs were collected. Even at this, he found a positive relation between the LC50 and the acclimation temperature prior to immersion at the test temperature. (The results of Table 5 are averaged over all acclimation temperatures.)

4.2.2 Salinity

Unlike temperature (or dissolved oxygen, see Section 4.2.3), most of the action for salinity in an estuary is in the horizontal. Sources and sinks in the estuary are virtually negligible. The exception is the net flux of water across the surface in response to evaporation and precipitation, which alters salinity in the estuary on time scales of weeks to months. A gradient across the estuary is established by the difference in salinity between freshwater inflows (near-zero salinity) and the ocean (saltwater, about 35‰ in the open ocean, somewhat variable in the western Gulf of Mexico, typically ranging 32 – 36‰ in the nearshore). The horizontal distribution is the result of internal circulations in the estuary transporting and mixing salinities of different magnitudes. For this reason, salinity is the quintessential estuarine parameter, acting as a hydrodynamic water tracer as well as a key biological control (Ward and Montague, 1996). Salinity also subtly influences water circulations, because ocean water (high salinity) is denser than fresh water (low salinity). Much of what is known about circulation in San Antonio Bay has been inferred from patterns of salinity (see, especially, Childress et al., 1975).

As noted above, the larval forms of blue crab are generally regarded to be stenohaline and stenothermal, requiring salinities greater than 20‰ and temperatures above 25°C for complete development (Tankersley and Forward, 2007), based largely on relatively early reports on laboratory culturing of the larvae, e.g. Sandoz and Rogers (1944), Costlow and Bookhout (1959), Costlow and Bookhout (1962), and Kalber (1970). Sandoz and Rogers (1944) examined hatching and growth of larvae over a range of temperature from 14 to 31°C and salinity from 0 to 33‰. They found hatching success over a fairly wide range of salinity, being maximal in the 27-30‰, tailing off slowly for salinities less than 27 down to 10‰, below which hatching failed.

For salinities above 30‰, hatching success dropped quickly to zero above 32‰. This is in contrast to the abrupt hatching failure outside of temperature range 19 to 29°C.

In the larval growth experiments of Costlow and Bookhout (1959), described in Section 4.2.1 above, no hatchings occurred at salinity 15‰. While some hatched at 10.1‰, none developed beyond the first stage. The only combinations for which zoeae developed beyond two moltings are those shown in Fig. 9, from which it is difficult to discern any clear dependence of growth upon salinity. On the basis of success of hatching and longevity of the zoeae, these controlled experiments suggest a requirement for salinity in the range 25-31‰ for zoeae to survive beyond the third molt. Kalber (1970) determined that the first stages of zoeae exhibit some osmo-regulatory capacity, but this is lost in the later stages (which is consistent with the results of Costlow and Bookhout), then regained as megalops.

As seen in Section 4.2.1 above, for values in the range 10-35‰, salinity has little effect on mortality of megalops (i.e., on their failure to attain the first crab stage), as shown by the horizontal isopleths in this range of Fig. 14. For salinities below 10‰, these data show a sharp rise in mortality to 100%. For salinities above 35-40‰, there is a modest increase in mortality. These results are consistent with those reported by Rosenberg and Costlow (1976) for blue-crab megalops through the third-instar juvenile, of survival (at crab 3) of 80% (mortality 20%) at salinity 10 and 40‰, and survival of 100% at 20‰ and 30‰.

While temperature has been found to be an important control on molting in juveniles, the rôle of salinity is murky. Early work (e.g., Van Engel, 1958) indicated greater growth increments in fresh water, but the float experiments of Tagatz (1968b) found the opposite effect. Somewhat larger growth rates were also found by Cadman and Weinstein (1988) in the molting of small juveniles, however in their data temperature was the dominant parameter, the intermolt period strongly diminishing with increased temperature. Millikin and Williams (1984) state, "Salinity values ranging from 6 to 30 ‰ do not differentially affect growth of juvenile and adult blue crabs." Guerin and Stickle (1997) found no effect on growth rates, intermolt period, or molt increment of juvenile crabs after being maintained in salinities of 2.5, 10 and 30‰, with all other environmental variables constant. Their earlier work (Guerin and Stickle, 1992) found an

increase in intermolt period with salinities only above 35‰, except for a modest increase (from 8 days at 3‰ to 10 days at 35‰) for crabs from the hypersaline Laguna Madre. Cházaro-Olvera, and Peterson (2004), in contrast, found growth rates to nearly double and intermolt period to be reduced by 40% in salinities from 5 to 25‰. (These crabs were collected in Camaronera Lagoon, Mexico, from salinities 22 - 35‰.)

Juvenile and adult blue crabs occur in salinities ranging from fresh to hypersaline on the Atlantic and Gulf coasts, being reported in salinities as high as 119‰ (Williams, 1984). In Chesapeake Bay, juvenile and adult abundance in shoreline habitat was found to increase (*NB*) with salinity, but also with the amount of shoreline marsh, and watersheds with higher detrital loads (King et al., 2005, Hines, 2007). Blue crabs occur along the entirety of the Texas coast (Hammerschmidt, 1982). Breuer (1962) reported juvenile blue crabs throughout the Lower Laguna Madre when he surveyed the area in 1954-56. Juveniles were common in the spring months, adult females in the summer, and adult males "in large numbers" year-round. The period of his observations, it should be noted, was during the Drought of the 1950's, and the median salinity was 39.1‰ (with outer hexiles 32.0 and 44.5‰), ranging up to 55‰.

Cházaro-Olvera and Peterson (2004) grew out blue crabs to the 16th instar from megalops in controlled conditions, and found no difference in mortality over the salinity range 5 - 25‰. In the experiments of Guerin and Stickles (1997) in which juvenile and adult blue crabs from Louisiana waters of 27‰ and 23‰, resp., were maintained for over two months in tanks of 2.5, 10, 25, 35, 50 and 60‰ salinities, adults proved to be slightly better osmoregulators than juveniles at salinities below 35‰, and both become osmoconformers (more precisely, slight hypo-osmoregulators) at 35‰ and higher. Gifford (1962) found similar results for large crabs maintained in 61‰ salinity, which had been caught in the Guadalupe River (13‰) and Laguna Madre (51‰) and acclimated at 38‰ before being transferred to 61‰.

The ability of blue crabs to thrive over such a range of salinity seems to be in part a matter of acclimation. In laboratory experiments involving changing salinities, it is common practice to alter salinities gradually so that the crabs may equilibrate, e.g. Guerin and Stickles (1997) brought crabs to each respective target salinity from ambient over a one-week period in daily

steps of 2-3‰. Crabs acclimated in one range of salinity introduced rather suddenly into another exhibit signs of stress and frequently die. Gifford (1962) found that crabs from the Laguna Madre were able to survive sudden immersion in higher salinities (survival 4-5 days or longer after transfer from 38‰ to 58‰) much better than crabs from Port Aransas channel (survival less than 1 day after transfer from 32-40‰ into 48‰), and their lethal limit for an abrupt change was around 70‰. Even after 10 days of acclimation in 38‰ water, a sudden transfer to 60‰ was lethal within 24 hours for Guadalupe River crabs, but not for Laguna Madre crabs. (Acclimation in 38‰ water proved fatal after 36 hours for nearly 60% of the river crabs.) Sudden transfer into low salinities was similarly stressful, in this case Guadalupe River crabs having the advantage. Both sets of crabs survived sudden transfer to 16‰, but a sudden transfer to 2‰ was fatal within 24 hours for the Laguna Madre crabs. Breuer (1962) noted that a sudden drop in salinity associated with local river flooding in the Lower Laguna Madre frequently killed blue crabs.

A gradual change in salinity in a laboratory setting, whether carried out over hours (e.g., Cházaro-Olvera and Peterson, 2004) or days (e.g., Guerin and Stickles, 1997), may be less important than the salinity of the native waters *per se* of the crab. Experiments were carried out by Guerin and Stickles (1992) in which crabs from a Grand Isle (Louisiana) salt marsh and from the upper Laguna Madre (Texas) were maintained in salinities ranging 0 - 70‰, in which the crabs were acclimated by a sequence of salinity changes of 3‰ per day from the native salinity to the treatment salinity. The Grand Isle salinities were polyhaline, ranging 20-30‰, while the Laguna Madre salinities were hypersaline, ranging 30-45‰. The high-salinity 21-day LC50's were determined to be 56.0 and 66.5‰ for the Grand Isle and Laguna crabs, respectively, a difference of about 10‰. The Grand Isle crabs survived indefinitely salinities down to and including 0‰, while the Laguna crabs exhibited a low-salinity 21-day LC50 of 0.5‰.

Though it is an effective hyperosmoregulator in very low salinities (e.g., Ballard and Abbott, 1969, Guerin and Stickles, 1997), the ability of the blue crab to live in freshwater appears paradoxical, because it needs to make up the loss of blood salts in urine by concentrating salts from ambient water, see Section 2.2. It appears that this ability to survive in freshwater is determined either by the "freshwater" being in fact oligohaline (chlorides 0.1 – 1 ‰), or the crab

having access to higher-chlorides water within 30-40 km, according to studies by H.T. Odum (1953) of blue crab invasion in Florida waters, see also Tagatz (1968b). Apparently blue crabs thrive in the freshwater zone of the St. Johns estuary because it is really oligohaline, and in addition has high concentrations of calcium chloride and localized zones of high sodium chlorides. Mangum and Amende (1972) investigated the population of blue crabs reported in the freshwater environment of Mill Creek on the upper James River, and determined that the crabs appeared only late in the summer, and that the Creek was in reality oligohaline with chlorinities ranging 1-3‰ (salinities 2-5‰). The blue crabs captured on intake screens in the freshwater reach of the Delaware, reported by Ettinger and Blye (1981), were taken in salinities in the lower oligohaline range. These authors suggest their presence this far up in the Delaware may have resulted from population pressure in Delaware Bay.

It is noteworthy that salinities on the order of 1‰ have been found to be lethal in controlled experiments of Holland et al. (1971), and the mortality sharply decreased at slightly higher salinities, around 5‰. All of the deaths occurred during or just after molting. In the field, of course, only survivors at these low salinities are evident, since dead crabs sink to the bottom and are quickly consumed. These researchers speculate that the lethality of low salinity may be an interaction effect with warmer temperatures, but this conflicts with more recent work that warmer temperatures facilitate osmoregulation in low salinities. In their report on blue crabs in Mill Creek, Mangum and Amende (1972) note that the high temperatures of late summer enabled the crabs to more easily osmoregulate than other times of the year.

In San Antonio Bay, blue crabs are found in environments generally considered fresh, *viz*. above the salt barrier in the San Antonio and Guadalupe Rivers, and in Green Lake, among others. According to Cameron (1978), these crabs do not reproduce, and their populations are replenished during high water events. The blood salts were found to be high, comparable to crabs in the estuarine range of salinity (5-35‰), and there was no alteration in the efflux of urinary salts, leading Cameron (1978) to conclude that these crabs maintain their salt balance by increasing the uptake of salts across the gills, which entails very high metabolic energy costs. This is not an effective adaptation to fresh water existence, and Cameron observes that these

crabs would be at a disadvantage "…in all but the most restricted freshwater habitats". These crabs are ecologically isolated, and play no part in the larger bay ecosystem.

On the basis of osmoregulatory capability, the "optimal" salinity range for the blue crab was estimated to be 25-30‰ by Romano and Zeng (2012). A low- salinity environment relative to the iso-osmotic concentration brings an energy demand that can translate to poor feed conversion and reduced growth rates. While "optimal" *sensu* Romano and Zeng (2012) is from the standpoint of aquaculture production, it has relevance to crabs in the wild. The most energetically costly mode of ion transport for the organism is the sodium pump, which is increased in a low (or sub-optimal) salinity environment, see Section 2.2.2. A related measure of "optimal" was addressed by Guerin and Stickle (1992): the energy stored by the crab that is available for growth, i.e., the net energy of food intake remaining after debits for excretion and respiration (which implicitly include osmoregulation). With this measure, the range of salinity with greatest available energy for growth was found to differ depending upon the native waters of the crabs, *viz*. 10-25‰ for crabs from the brackish Grand Isle marsh and 35-50‰ for crabs from the hypersaline Laguna Madre.

4.2.3 Dissolved oxygen

Like temperature, most of the action in an estuary is in the vertical for dissolved oxygen, the primary drivers being the transfer of oxygen across the water surface (reaeration), and the production and consumption of oxygen in the water column and at the seabed. There is a muted variation in the horizontal arising from the effect of salinity on solubility. Like temperature, there are local areas, primarily peripheral shallows—in which the smaller depth of water alters the relative importance of terms in the DO budget—or the vicinity of discharges of low oxygen content or high oxygen demand, in which there can be more variation in the horizontal than in open, unaffected regions of the estuary. Unlike temperature, the kinetics of oxygen are much more variable in space, due to gross primary production from algae and uptakes of oxygen by respiration, which can vary substantially with position in the estuary. In regions with substantial horizontal gradients in DO, horizontal advection is rendered a potentially more important

component of the oxygen budget than would be the case in the generally open, homogeneous regions of the estuary. It is not unusual for an estuary to exhibit a range of oxygen conditions, from hypoxic to supersaturated, depending upon the relative imbalance of the oxygen budget.

As an aerobic organism, the blue crab indubitably requires dissolved oxygen in the ambient water. However, the literature is conflicting on its specific DO requirements. In the experiments of Das and Stickle (2004), blue crabs statistically relocated to waters with pO_2 ranging 98 – 125 Torr (about 4.5 – 5.8 mg/L, see Appendix D), which they interpret as optimum. There is some evidence that sustained exposure of adults to dissolved oxygen below 50 Torr (about 2.5 mg/L) can be lethal (Carpenter and Cargo, 1957, deFur et al., 1990). Exposures of adult male crabs for 7-25 days in water at 50 Torr resulted in 20% mortality in the experiments of deFur et al. (1990). Das and Stickle (1993) exposed juvenile blue crabs in chambers with a range of depressed oxygen and found that the LC50 at 28 days was 106 Torr (about 5.5 mg/L, toward the high end of "optimum" from their later experiments, see above), with total mortality after 6 days for $pO_2 \leq$ 25 Torr (DO $\leq$ 1.3 mg/L).

In the field, the basic response to blue crabs encountering hypoxia ($pO_2 < 50$ Torr) is avoidance. A prominent example of the avoidance response is the thronging of blue crabs (along with numerous other macrofauna) into the shallow waters of Mobile Bay during "jubilee" events (Loesch, 1960, May, 1973). Zones of low dissolved oxygen have been reported to be barriers to migration of blue crabs in the Chesapeake and its secondary estuaries (e.g., Van Engel, 1982). Eby and Crowder (2002) used data from the Neuse River (NC) to determine an avoidance threshold of 2.5 mg/L for blue crab, i.e., crabs were systematically absent from regions of the estuary with DO's less than this threshold. However, in the laboratory experiments of Das and Stickle (1994) in which blue crabs were placed in an "avoidance" tank where a horizontal gradient in DO was maintained, the crabs showed no statistically significant avoidance response to hypoxia over a range of 0 – 4.2 mg/L. (This is in contradistinction to the congener *C. similis*, which exhibited a significant avoidance response.) They speculate that when the blue crab is routinely exposed to diurnally varying DO, it may have reduced need, hence ability, to sense and avoid low oxygen concentrations. This is somewhat supported by the results reported by Eggleston et al. (2005), that in the Neuse under prolonged hypoxic conditions, adults migrate to

the shallower waters (increasing predation of juveniles exponentially), whereas under shorter-term hypoxic upwelling, there is no invasion of the shallow areas by adults (and no change in predation rate of juveniles).

A mechanism for enduring exposure to hypoxia is hyperventilation, i.e., increasing the throughput of water as well as the cardiac rate. This is accompanied by a decrease in oxygen consumption roughly correlated with the depression of pO_2 (e.g., Batterton and Cameron, 1978). In adult crabs, this persists for 5-25 days, after which the crab adjusts to the reduced oxygen conditions by a sequence of adaptive changes in blood chemistry (de Fur and Pease, 1988, Towle and Burnett, 2007). Batterton and Cameron (1978) report a marked increase in the rate of reversal of ventilating flow (see Section 2.2.1) in hypoxic conditions, as well as in low salinities, and surmise that this may be a generalized response to irritation.

More (1969) reported crab kills (mainly in crab pots) in upper Galveston Bay in the mid-1960's apparently due to oxygen crashes. Aeration was impaired by low tides, high temperatures and slack winds, compromising the supply of oxygen to the water column. The main crab mortalities occurred just before sunrise, which suggests phytoplankton respiration as a contributing factor. Blue crabs are also susceptible to gas embolism due to oxygen supersaturation (Shields and Overstreet, 2007, and citations therein), which could become problematic in regions with algae blooms.

4.3 Disease and parasites

The blue crab is subject to a range of viral and bacterial infections, some specific to the organism, and some exchanged among crustaceans. In addition there are parasites and other symbionts such as fungi, protozoa, flatworms, and leeches, as well as fouling crustaceans that infect or infest the crab. A useful overview of blue crab diseases is provided by Messick and Sindermann (1992), and a detailed listing of diseases and parasites specific to the Gulf of Mexico is given by Guillory et al. (2001). Shields and Overstreet (2007) present a comprehensive account of present knowledge about infectious and parasitic organisms, their propagation, and

impacts. The present section has a much more modest goal: to enumerate those that may figure prominently in the crab population, particularly in Texas, and what governing factors in the environment may influence the infection or infestation.

White spot virus is a well-known penaeid shrimp infection, particularly notorious among shrimp farmers, that is capable of transmittal to the blue crab. Occurrences have been reported in the Gulf of Mexico, but there is not evidence at present of large-scale mortality in the blue crab populations (see Shields and Overstreet, 2007).

With respect to bacteria, several species of *Vibrio* are commonly found in blue crabs, mainly in the blood but also in small concentrations on the carapace (Davis and Sizemore, 1982, Shields and Overstreet, 2007). The greatest danger to the crab is a rapidly developing infection that seems to be brought on by some sort of stress, such as capture and handling, or change in temperature or salinity (Shields and Overstreet, 2007). The frequent mortality of captured individuals by crabbers may be attributed to stimulating *Vibrio* infections. Data from Galveston Bay (Davis and Sizemore, 1982) show substantial presence of *Vibrio* spp. in crab blood throughout the year, but peaks in concentration of *Vibrio* in the summer. (A much greater dependency upon water temperatures is exhibited in the mid-Atlantic estuaries, Shields and Overstreet, 2007.) The pathogens *V. parahaemolyticus* and *V. vulnificus*, which are favored by warm-weather conditions, were isolated in more than half of the crabs sampled by Davis and Sizemore, while *V. cholerae* was isolated from 3.5% of the crabs and only during the cool months of winter and spring. Some twenty years after the work of Davis and Sizemore (1982), the largest outbreak of *V. parahaemolyticus* in the United States (to that time) occurred May-June 1998 in Galveston Bay, not from blue crabs but from oysters consumed raw (DePaola et al., 2000).

One of the more important blue crab infections is the pathogenic amoeba *Paramoeba perniciosa*. This is the agent responsible for "grey crab disease", which has caused major mortalites in the mid-Atlantic (see comments following Couch and Martin, 1982). Fortunately, the disease does not (yet) occur in the Gulf of Mexico (Shields and Overstreet, 2007).

A parasitic dinoflagellate *Hematodinium perezi* is found in the Atlantic and Gulf of Mexico nearshore environments, in waters of elevated salinity (greater than about 11‰), and frequently infects crustaceans, including the blue crab. The infection is usual fatal to the animal. In some harvested crabs, it is responsible for the "bitter crab disease" but this apparently does not occur in blue crabs (Shields and Overstreet, 2007). The heavily infected crab is lethargic and ceases eating, and eventually exhibits a yellow coloration in the blood. *H. perezi* is highly contagious and may be responsible for the local elimination of some blue crab populations (see citations in Shields and Overstreet, 2007). In the Atlantic, the disease peaks in late fall to early winter then vanishes over winter. Since juveniles are particularly prone to infection, the parasite could have impacts on the survivorship of the summer spawn just recruiting into the pelagic population. The disease has been reported in the Gulf of Mexico, notably the panhandle of Florida (Couch and Martin, 1982), Mississippi (Shields and Overstreet, 2007) and Texas (Messick and Shields, 2000).

Among the protozoans that infect blue crabs are several ciliates, notably *Lagenophrys callinectes*, which attaches itself to the flat surfaces of the gills. This is a surface infestor of decapod crustaceans, including shrimp (in which it is responsible for black-gill disease). Technically not a parasite, since its holdfast is cemented to the gill surface and does not penetrate the gill, a heavy infestation of *L. callinectes* can compromise the exchange capacity of the gills (Guillory et al., 2001, Shields and Overstreet, 2007). Frequently interspersed with *L. callinectes* is another ciliate, *Acineta* sp. Maximum prevalence occurs in the warm-water months of late summer and early fall. Molting rids the crab of the ciliates, since the gills are left behind with the old exoskeleton, but re-infestation is probable. These protozoans occur in Atlantic and Gulf waters (Murchelano and Rosenfield, 1980, Fontaine, 1985, Guillory et al., 2001b).

The fluke (digenean or flatworm) *Microphallus basodactulophallus* is ubiquitous throughout the North American range of the blue crab, and is its most prevalent digenean. The crab is one (secondary) host in a complex lifecycle. The adult fluke lives in the intestine of shore mammals (the definitive host), mainly raccoons and rats (Shields and Overstreet, 2007). The mammal deposits its feces, which contain large concentrations of eggs of the fluke, on or near the shore, especially in marshes. The feces are ingested by mud snails (Hydrobiidae) and each egg

ultimately produces thousands of larvae (cerceriae) in the host snail, which are released into the water. (There has to be a match between the fluke and the species of mud snail, but there seem to be ample hydrobiid snails available.) The water is drawn into the crab's branchial chamber in respiration, where these larvae form cysts on the gills from which they penetrate the gills and enter the bloodstream. They subsequently invade the tissues of the crab, most conspicuously the musculature, where they form cysts. Consumption of crab meat by the afore-mentioned host mammals completes the cycle. This fluke itself has a parasite, the protozoan *Urosporidium crescens*, which renders the metacerceriae of the fluke swollen and darkened, making them visible in muscle tissue (Messick and Sindermann, 1992). The resulting appearance of the crab meat is known as "buckshot" or "pepper spot". At present, it is unknown whether *M. basodactulophallus* or its parasite *U. crescens* is harmful to the blue crab, nor is there information available on effects of environmental variables such as temperature and salinity (see Shields and Overstreet, 2007). Infected crabs are found year-round in Mississippi Sound (Perry and Stuck, 1982). Buckshot has been reported on the Texas coast (More, 1969).

Ribbon worms, or nemerteans, *Carcinonemertes carcinophila*, inhabit the gills of blue crabs and feed primarily on yolk of the crab's eggs. Other species of *Carcinonemertes* infest various crab species including Dungeness crab and the red king crab, where they are thought to be responsible for declining stocks (Shields and Overstreet, 2007). In the blue crab, *C. carcinophila* lives in mucous sheaths between the gill lamellae of female crabs. Molting eliminates the infestation, because the gills remain attached to the old exoskeleton, but it is likely that the worm quickly relocates to the soft-shell crab. When the host extrudes the egg mass, the worm leaves the gill lamellae and moves into the sponge, building a new mucus tube for habitat, and remains there to feed on the embryos and mate. This is also where it lays eggs, thought to hatch at the same time as those of the host, by analogy to the life cycle of other species of *Carcinonemertes*. After laying its eggs, the adult ribbon worm returns to the gill lamellae. The infestation of the egg mass can be high, hundreds to over a thousand, and seems to be keyed to the reproductive state of the host, i.e., proximity to its pubertal molt (Shields and Overstreet, 2007). In the Gulf of Mexico, the prevalence of ribbon worms appears to be associated with warmer water temperatures (May through August). Generally, the opinion in the literature is that ribbon worm infestations are a phenomenon of higher salinity waters, based mainly on analogy to infestations

of other species of *Carcinonemertes* in other crabs. However, controlled studies of dependencies on salinity and temperature have not been performed for *C. carcinophila*, and it is possible that its perceived salinity and temperature preferences are dictated by the spawning and migration of the female crab. Its impact on the blue crab in the Gulf is unknown, but the ubiquity of the infestation raises the potential of a rôle in reproductive fecundity. More (1969) reports 78% of crabs in Gulf surf at Galveston to be infected. Infections were also found in crabs in lower Galveston Bay, but no data were provided.

As a hard surface in a marine environment, the cuticle of the blue crab is a target for fouling organisms. There are many of these (Guillory et al., 2001), including bryozoans, corals, mussels and oysters, but mainly cirripeds. These are not true parasites, and affect the crab only in adding weight or limiting mobility. These include several species of acorn barnacles, whose preferred site of attachment is the carapace. The gooseneck barnacle, *Octolasmis mülleri*, enters the inhalant port to the branchial chamber and attaches to the gills, and if the infestation is sufficiently high, can inhibit gill function and even compete for oxygen. In the Galveston surf in 1967-68, 57% of the mature females were infected, according to More (1969). Several crabs had at least 500 barnacles attached to the gills. Males were also infected, but at a considerably smaller rate. All of these barnacles are marine organisms that are most prolific in warm, high-salinity waters. Shields and Overstreet (2007) suggest that study of barnacle deposition on the blue crab carapace may offer a means of aging instars (if the age classes of the barnacles were defined) or determining the salinity history of a mature female.

There is one barnacle, however, that is a true parasite, the rhizocephalid *Loxothylacus texanus*. The barnacle, which doesn't look like a barnacle, infects young juvenile crabs less than 20 mm, penetrating the joint membranes and eventually migrating to the midgut. Its external expression is a brood pouch (externa) under the crab's abdomen. Growth of infected crabs is stunted because they cease molting, and male juveniles are effectively castrated, taking on the appearance of a female. The life cycle and details of the biology of the barnacle are given by Shields and Overstreet (2007), see also Tindle et al. (2004). It is mainly a threat in the Gulf of Mexico, and appears to require higher salinities, generally above 25 ‰, for survival (Shields and Overstreet, 2007). Apparently, the larval forms, especially the nauplii, are impaired at salinities

below 20‰, but the literature is conflicting on this (Tindle et al., 2004, Shields and Overstreet, 2007). Since juvenile crabs are infected and removed from the population, it is difficult to estimate the impact of this parasite, but it clearly has the potential to significantly reduce the blue crab population. Guillory et al. (2001) estimate that this infestation has eliminated as much as half of commercial blue crab stocks in some regions of the Gulf of Mexico.

Infestations of *L. texanus* have long been a concern in Texas. In his collections in 1941-42, Gunter (1950) found a prevalence of about 1.5% in crabs from Aransas and Copano Bays, 96% of which were taken in Aransas Bay. A special study was carried out by the Texas Game & Fish Commission (TGFC) in 1947-50 (Daugherty, 1952), in which an expert on the barnacle from Washington, D.C., participated in summer of 1950. This study concentrated on Aransas Bay and adjoining systems including Cedar Bayou. On average, about 8% of the crabs were found to be infected. The focus of the infection was determined to be Mud Island in lower Aransas Bay, where over 25% of the crabs displayed externa. More (1969) reports surveys of *L. texanus* infestation in blue crabs from the mid-1960's in which every bay except Sabine Lake exhibited this infection. The prevalence generally increased with salinity, with all of the bays being less than 1%, except the Laguna Madre (Upper Laguna 6%, Lower Laguna 8%). In contrast, in the sampling of stations throughout Terrebonne and Timbalier Bays in Louisiana reported by Adkins (1972b), there was no clear relation of infestation to salinity, which ranged 0.9 – 29.7‰. The greatest infestation he found was 11% at Moss Bay, where salinities ranged 5 - 21‰. Temperature, not salinity, was the predominant environmental control, with which the infestation was directly correlated.

Infections of the barnacle in lower Mobile Bay over the period 1989-91 are reported by Hsueh et al. (1993) to range up to 95%, being especially prevalent in open-bay stations compared to marsh and shoreline. The infestation varied seasonally, but no dependency on temperature or salinity was noted. The study was focused on the relative abundance of the closely related species *C. sapidus* and *C. similis*, the latter being found to be predominant except in marsh regions. No *L. texanus* infection was found in *C. similis* anywhere in the bay. Wardle and Tirpak (1991) report surveys of crab infestations in Galveston Bay during a *Loxothylacus* outbreak in 1989. The overall incidence of externa was about 11%, but there was no clear association of the extent of

infection with salinity. In fact, the highest rate of infection (39%) occurred at one of the lowest-salinity stations (Hanna's Reef, 10-19‰), and the next highest (38%) at a midrange-salinity station (south of Texas City Dike, 20-25‰). Incidence of externa was 0 in seven of eight high-salinity stations, the exception (West Bay, 25-32‰) exhibiting 20% infection.

Moreover, higher rates of infection in higher salinity regions do not necessarily imply that the crabs are more exposed to infection in those regions. This may instead reflect a behavioral response of the crab to *L. texanus* infestations contracted elsewhere. Researchers in Mexico studying the Mexican blue crab, *Callinectes rathbunae*, have discovered that *L. texanus* depresses the blood salts of the crab (Alvarez et al., 2002), requiring a greater influx of salts from ambient water to compensate (Section 2.2.2), and also elevates the oxygen consumption by 60-140% (Robles et al., 2002) thereby further increasing the energy investment needed by the crab for respiration in low-salinity environments (Section 2.2.1). As both of these effects can be mitigated by increasing ambient salinity, these researchers suggest that infected crabs can be expected to move from low- to high-salinity regions of the estuary.

Finally, a symbiosis (more precisely, phoresis) has been described by Cake (1983) between the southern oyster drill (*Thais haemostoma floridana*) and the blue crab. The crab provides transport for the drill into the estuary. The drill, typically a juvenile, attaches to the crab, typically an adult, apparently while the crab is inactive on the bed or moving about in detrital habitat near the seaward end of the estuary, and feeds on fouling organisms on the carapace, notably barnacles and oysters. When the crab approaches an oyster reef, the drill dismounts. Almost all of the crabs carrying drills collected by Cake were females, and some drills were observed feeding on the eggs of ovigerous crabs. Drill occurrence on the crabs ceased in late summer when female migration toward the sea began. Cake exhibits a photograph of a blue crab with seventeen drills attached, sixteen on the carapace and one on a chela.

4.4 Prey and predation

The blue crab is an omnivore and a scavenger, an opportunistic predator whose diet includes epibenthic and infauna invertebrates, particularly bivalves, motile crustaceans and fish, plant detritus, carrion, excrement, and other blue crabs. A detailed summary of blue crab prey is presented by Hines (2007), which shows a spread of over ten phyla and nearly 100 species. The diet shifts from benthic arthropods and annelids as the young juvenile matures and develops the speed and hardware to prey upon fish and molluscs (Laughlin, 1982). The chelae are generally capable of cracking the shells of bivalves, which make up the majority of the diet of adult crabs, at least in the mid-Atlantic (Hines, 2007). For those bivalves with heavier shells, like *Rangia* or large oysters (greater than 35 mm standard height), the crab chips the edges to gain access to the adductor muscles, which once-severed allows prying open the shell (Eggleston, 1990). Blue crabs track their prey by both visual cues, responding to movement of the prey, and odor. There is considerable variation in the diet of the crab, seasonally and spatially, both within an estuary and between estuaries. This variation is dictated largely by what is available where the crab is (Laughlin, 1982, Hines, 2007). Even temporal variation, such as correlation with high-tide, may be dictated more by prey availability than deliberate activity of the crab. When a variety of prey is available, the blue crab is sensitive to relative profitability of a food choice, *viz*. energy derived from the food compared to energy expended in capture and handling (Hines, 2007 and citations therein).

Less is known about the prey of larvae and postlarvae. In laboratory cultures in mid-twentieth century, blue crab zoeae were reported to survive only on a yellow dinoflagellate (*Gymnodinium* or *Amphidinium*, perhaps, Marshall and Orr, 1960), and sea urchin (*Arbacia*) or *Artemia* nauplii (Costlow and Bookhouse, 1959). Later work, particularly motivated by the prospects of aquaculture, found that zoeae could be successfully fed on rotifers and polychaete larvae (Epifanio, 2007). Even at this, there remains a high mortality of cultured larvae. The prey of zoeae in the wild is presumed to be similar nauplii-sized zooplankters which the zoeae randomly contact, but remains unknown (Epifanio, 2007). Apparently, availability of food in the wild is an important factor. McConaugha (1988) reports that as much as 50% of late-stage zoeae (VI and VII) from the inner shelf were found to have been subjected to starvation.

Megalops prove easier to please than zoeae in the laboratory, and survive satisfactorily on *Artemia* nauplii. Possessing chelae and greater swimming ability than the larvae, the megalop is considered to more aggressively pursue its prey. The prey of megalops in the wild, however, like that of zoeae, is unknown. Like zoeae, the main predator of megalops is thought to be planktiverous fish (Morgan and Christy, 1996), see Section 5.2. Megalops may more successfully evade predators because of their better swimming capability, including bursts of 20 cm/s (see Section 2.3).

The list of predators for the blue crab is even more extensive than the list of prey, see Guillory and Elliot (2001) and Hines (2007). Hines (2007) offers the judgment that reptiles (notably alligators and sea turtles) and birds probably have a minor overall impact on the population of blue crabs. In terms of size of the populations, geographical distributions and food requirements, the fish as a category probably represents the greatest aggregate predatory impact on the blue crab population, with two possible exceptions, *C. sapidus* itself (i.e., cannibalism, discussed below) and *Homo sapiens*. While there is some data on the proportion of diet comprised by blue crabs for individual species (see Scharf and Schlight, 2000, Guillory and Elliot, 2001, Hines, 2007), there is generally a lack of quantitative data on the scale of fish predation. On the mid-Atlantic coast, the striped bass (*Morone saxitilis*) is considered the most important predator on small juveniles because of its prevalence in primary and secondary habitats of the crab (Lipcius et al., 2007). Two quantitative studies of fish predation in seagrass beds of lower Chesapeake Bay are available in the grey literature, *viz*. Orth et al. (1999) and van Montfrans (2005), reviewed by Hines (2007). The first found that fish-predation mortality was on average less than 1% of total abundance per 12 hours, and this was dominated by striped bass. The second found even lower rates, on the order of 3% of total crabs available per spring or fall season, again primarily striped bass, with Atlantic croaker (*Micropogonias undulatus*) a distant second.

For the Gulf of Mexico, Guillory and Elliot (2001), see also Guillory et al. (2001b), presented a resourceful and valiant quantification of blue crab predation in Gulf estuaries. From literature data, they compiled lists of species known to include blue crab in their diet based on stomach content analysis, plus species that generally consume crabs. All told, they found 93 species known to consume some life stage of blue crab. (Whooping cranes are not included, possibly

Table 6
Predation indices for principal estuarine fish preying on blue crabs,
computed by Guillory and Elliot (2001), see text,
in descending order for highest eight species

Red drum (*Sciaenops ocellatus*)	545	Spotted seatrout (*Cynoscion nebulosus*)	24
Sea catfish (*Arius felis*)	110	Gafftopsail catfish (*Bagre marinus*)	3
Black drum (*Pogonias cromis*)	33	Atlantic croaker (*Micropogonias undulatus*)	2
Sheepshead (*Archosargus probatocephalus*)	26	Southern flounder (*Paralichthys lethostigma*)	1

because their numbers are so few as to have little impact on crab population.) A predation index was formulated as the product of the fraction of diet composed of blue crab (from the literature compilation), the abundance of the species, and the average weight. The calculation was limited to fish, and the last two parameters were based upon gill and trammel net data of the Lousiana Department of Wildlife and Fisheries. Their results for the top eight predators are given in Table 6. (See Guillory and Elliot, 2001, for details.) This index is proportional to the physical consumption of blue crab by the population of the predator species, and therefore quantifies the relative importance of these species as predators. There are qualifications, of course, most important being the implicit assumption that the predator species has the same access to crabs as the specimen(s) whose stomach contents were reported in the literature. (Moreover, the constant of proportionality is unknown, because Guillory and Elliot do not report the units of the net data or the species weight.) Since Table 6 is based upon Louisiana net data, the applicability to Texas, specifically to San Antonio Bay, is unknown, but presumably is much more appropriate than data from the mid-Atlantic coast. No grouping of fish by predation habitat was done, so these results may not strictly apply to specific habitats, such as salt marshes. For example, on the Gulf of Mexico coast, pinfish (*Lagodon rhomboides*) and several similar species are thought to be important predators on the post-settlement juveniles in seagrass beds because of their ability to move among the stalks, yet pinfish is ranked much lower by predation index of Guillory and Elliot. Finally, without an estimate of the stock of blue crabs on the coast, in the same units as the predation index, the absolute impact on blue crab mortality cannot be quantified.

One organism that is both prey and predator for the blue crab is the organism itself. There is increasing evidence that cannibalism is a major source of blue crab mortality (Lipcius et al., 2007). Small juveniles eat megalops or first-instar crabs. Larger juveniles eat smaller juveniles. Adult and subadult blue crabs eat juveniles. Hard-shell crabs eat soft-shell (i.e., freshly molted) crabs. Hines and Ruiz (1995) estimated mortality of juveniles from cannibalism to range 75-97% in some habitats in Chesapeake Bay. Hines (2007) cites a tethering study sustained for 16 years in central Chesapeake Bay in which there were no instances of fish predation but more than 92% mortality was due to cannibalism. The mortality of juveniles due to cannibalism is especially high in nonvegetated habitats. One particular type of cannibalism may be most important in terms of limiting the juvenile population, namely early life-stage, intra-year, inter-cohort cannibalism, in which first-arriving instars, as young juveniles, feed on settling megalops or newly molted juveniles. This results in several patterns of density-dependent mortality, explored in careful mesocosm experiments by Moksnes et al. (2003), which they suggest may make the juvenile population self-regulating.

In the Gulf of Mexico, the settlement studies of Rabalais et al. (1995) and Spitzer et al. (2003), reviewed in Section 5.4 below, show the abundance of early-instar juveniles after high-density megalop settling events (pulses) declining within a few days to background levels, as would be manifested in density-dependent mortality, elaborated by Moksnes et al. (2003). While this does not diminish the potential of intense fish predation, it raises the possibility that cannibalism is at least a contributing, and perhaps dominating component of young juvenile mortality.

5. MIGRATION

Migration is keyed to the various life stages of the blue crab and is driven by the habitat requirements of these respective stages. The bulk of knowledge on the movement of populations of blue crab in the wild is founded on studies on the mid-Atlantic coast, especially in Chesapeake Bay. The other populations of blue crabs on the Atlantic and Gulf coasts have received only a fraction of the attention and effort that have been applied to the mid-Atlantic. Therefore, the conventional starting point, and that observed here, is to delineate these migrations, comparing and contrasting work in other systems. Inferences of the movements of crabs and the underlying controls are based upon three strategies of data collection:

(1) entrapment in the field (e.g., trawl, seine, dredge) together with data on depth, time, location, occasionally water chemistry, and, rarely, current velocity;
(2) crab-tracking experiments in the wild, including mark-and-recapture, caging, tethering, and acoustic tagging;
(3) experiments under controlled conditions, including aquaria and mesocosms, which we refer to generically as "laboratory" experiments, not so much in the sense of venue, but in the sense of careful control of external variables.

Each of these has advantages and deficiencies, and none provides entirely suitable data on crab movement. Of course, the scope and technology involved are highly variable and underlie the generality and confidence of the results.

The physiological process of mating is summarized above in Section 3.2. In the present context, our concern is in geography and seasonality. In the mid-Atlantic, mating occurs mainly in the upper reaches of the estuaries (Churchill, 1919, Van Engel, 1958). Hines et al. (1987) report that the low-salinity upper reach of the Rhode River (Chesapeake Bay) is favored by molting juvenile males, whereas the brackish middle reach is used for mating hence favored by pre-pubertal females. In Charleston Harbor (South Carolina), however, mature crabs of both sexes are found preferentially in higher salinities and the juveniles of both sexes in lower salinities. Mating

occurs throughout the length of the estuary, inferred from the presence of mature male and female crabs in Charleston Harbor in all salinities over the range 10-35 ‰ (Archambault et al., 1990). Mating appears to favor the shallow tidal creeks, from which the inseminated females move into the open bay waters (Whitaker et al., 1998). Farther down the southeast Atlantic coast, in the St. Johns estuary of Florida, mating is observed to occur from the mouth inland over 200 km (Tagatz, 1968a), which is well beyond the limit of salt intrusion.

In the temperate climate of the mid-Atlantic, the mating season is summer to early fall, principally the late summer. In Chesapeake Bay, in the warmer deeper waters near the mouth of the estuary, females begin their terminal molt earlier in the year, so, depending upon meteorological and hydrographic conditions, there may be an earlier season of mating activity in the spring (Jivoff et al, 2007). As noted in Section 3.2, in the St. Johns, mating occurs throughout the year, but the peak seasons are spring to early summer (March – July) and fall (October – November) with low activity in the coldest months December – February, and the warmest months August – September.

The early view of migration based upon Chesapeake Bay was that the lower bay functions as a nursery where zoeae develop into young juvenile crabs, after which they would migrate to the upper bay, maturing on the way, and perhaps overwintering in transit (e.g., Churchill, 1919, Truitt, 1939). The modern view is much more complex. Zoeae develop offshore on the inner shelf, then reinvade the estuary at the megalop stage, populating various nursery areas. As juveniles grow, they shift to shallow soft-bottom nursery, before finally recruiting into the pelagic population. The migration of the crab is described in this section, starting with the post-insemination movement of the female and progressing through the successive stages of migration, the associated life stages, and potential controlling factors. When information is available beyond the mid-Atlantic, the order is to proceed south to Florida, then to the Gulf of Mexico from Florida to Texas.

5.1 Migration to the mouth

The seaward migration of the inseminated female crabs in the mid-Atlantic estuaries is conventionally subdivided into two "phases" (Jivoff et al., 2007). Phase I is the migration from the mating area to the lower estuary, where the crabs spawn. Phase II is the migration from the lower estuary to the mouth, where the eggs are hatched and the larvae released. Both phases are governed by climatology, specifically water temperature. After mating, the females remain in the upper estuary where they feed, building reserves until fall (Turner et al., 2003). The Phase I migration then occurs from September through November, presumably triggered by lowering temperatures (Aguilar et al., 2005, Hines et al., 2008). The females concentrate in the deeper, warmer water of the estuary axis. Several studies in the mid-Atlantic estuaries (e.g., Hench et al., 2004, Aguilar et al., 2005) have demonstrated that the female crabs use selective ebb transport (SET) to achieve net seaward movement on the order of several kilometers per day. This behavior is reviewed in more detail in Section 4.1.2, relating to the manifestation of circadian and circatidal rhythms. Other studies report that the females also move along the bottom (Aguilar et al., 2005, Jivoff et al, 2007, Hines et al., 2008), so that they continue the migration even if currents are adverse.

Reaching the lower estuary, females bury themselves in the sediments and overwinter. Brood production occurs in the next year when water temperatures warm sufficiently, in late spring to early summer (Davis, 1965, Aguilar et al. 2005, Jivoff et al., 2007). It has been suggested that burial has another advantage, as the sediments facilitate adherence of the egg mass to the pleopods by a mechanism still unknown (Jivoff et al., 2007). The female crabs, now with sponge, undertake the Phase II migration to the estuary mouth in early summer. Tilburg et al. (2008) conducted studies of Phase II migration in the Delaware, from the brooding grounds in the lower estuary, through the mouth into the hatching grounds of the coastal ocean. A time series of larval hatching (estimated from the egg stage of ovigerous females) was constructed showing basically episodal hatching events from June through October with greatest peaks in July and August.

Female migration in Chincoteague Bay revealed by tag-recapture experiments is described by Cargo (1958). This lagoonal estuary is small, approximately 10 x 30 km (roughly the size of San Antonio Bay measured from the Guadalupe delta to Matagorda Island), with its long axis paralleling the Atlantic coast. It has a small watershed and minimal inflow, and inlets at both the north and south ends, the latter being the natural, and, once, only inlet. From four separate blue-crab tag-and-release experiments, the majority (61% of all crabs recaptured) move south down the bay. Discounting the 36% that were recaptured at or near the point of release (most after a few days, a few after several months), 93% of those recaptured elsewhere exhibited southward movement. This bay shares the climatology of Chesapeake and Delaware Bays, but the reason for migration in this southward direction is unclear. Because of the low freshwater inflow, the bay generally displays salinities greater than 25‰, typically slightly hypersaline in summer. There is usually a slight southward increase in salinity (see, e.g., Allen et al., 2007), but during his tagging experiments, Cargo (1958) notes that the salinity gradient was the reverse of this, increasing slightly to the north. Tidal influences are reported to be approximately equal at the two inlets, and tidal currents within the bay are negligible (Allen et al., 2007).

Medici et al. (2006) report tag-recapture studies of post-insemination females in 2001-02 in the Albemarle-Pamlico Sound, in which crabs were released in the mating areas, i.e. inland reaches of the Sound (in the Neuse, Pamlico and Albemarle), and in the estuary region inside two of the major inlets (Ocracoke and Hatteras). The crabs moved in a general seaward direction, toward the nearest inlet, at a speed of several km/day. Crabs that were recaptured more than once seemed to be using the Intracoastal Waterway as a corridor. Detailed tracking of crabs equipped with pingers could be carried out for a shorter period —several days — than the tagging experiment. These crabs generally moved seaward, mainly at night, remaining less active during the day. Also, these crabs favored the periphery of sloughs and channels to either the deep or shallow areas of the estuary, and favored no particular habitat.

Carr et al. (2004) equipped ovigerous female crabs with ultrasonic emitters and released them 4-10 km in the estuary behind Beaufort Inlet (NC), then tracked them on a boat equipped with hydrosondes and GPS. All crabs moved seaward, moving “episodically”, i.e. in random bursts of speed, or “swimming bouts”, separated by longer durations of little or no motion. Under ebb

at night, the crabs were observed to be moving with the current, while other times, i.e., under flood or under daylight ebb, the crabs moved much more slowly downestuary (against the current when it was flooding), averaging 6.5 km/day. Carr et al. interpreted this as SET.

The use of STST by migrating crabs presumes there is a tidal current to exploit. In many estuaries, tides are secondary to other currents, such as wind-driven circulations, for example estuaries in a microtidal region such as the Gulf of Mexico. Also, lagoonal estuaries with narrow tidal inlets will have tidal effects localized around these inlets, but little tidal current in the open waters. Albemarle-Pamlico Sound is an example (Pietrafesa and Janowitz, 1988, and citations therein). Darnell et al. (2012) employed tethered, pressure-logger-equipped ovigerous blue crabs in Beaufort Inlet, where there is a clear tidal signal, and in West Bay in the Albemarle-Pamlico system. While the crabs at the former site swam in concert with ebbing currents (night and day), those in West Bay, where currents (tidal or otherwise) were nil, did not swim but remained on the seabed.

While not described in this manner, Tagatz (1968a) reports a phased post-insemination migration in the St. Johns estuary that has some superficial similarity to that of Chesapeake Bay. Here there are two seasons of down-estuary migration (Phase I, in the Chesapeake terminology). The females migrate to the lower estuary near Jacksonville, about at the limit of salt intrusion, in the spring and in the fall, but do not migrate in summer and winter. Since mating occurs throughout the estuary, the migration distances for individuals vary, and it might be more accurate to describe this Phase I "migration" as females "congregating" in the lower estuary. It is not clear whether the females spawn before or after undertaking this migration, perhaps both, but in any event the broods mature in this reach of the estuary. As the eggs develop, the females migrate the additional 30 km or so to the estuary mouth and into the ocean to hatch.

In Mississippi Sound, Perry and Stuck (1982) report surveys of development of post-insemination female crabs. Recently mated crabs were found in spring through fall, while those with mature ovaries were found throughout the year. There are two immigrations of mature females into Mississippi Sound. In late fall, blue crabs, mainly mature females, migrate from Lakes Borgne and Pontchartrain into the Sound to overwinter. In summer "Gulf" crabs, mature

females that have had previous sponges, move into the Sound. Ovigerous crabs are most abundant July through September (mid- to late-summer). Appearance of sponge crabs in early spring is cited as evidence that these overwintered before spawning.

For the bays of the Gulf of Mexico, the smaller dimensions of these systems compared to Mississippi Sound or Chesapeake Bay means that migration to the estuary inlet, spawning, emigration into the sea, and hatching can be effected in a single process. This is exemplified by two successive one-year studies (1962-63) at Aransas Pass. The first was carried out by Hoese and Jones (1963) using a drop-net sampler in Redfish Bay, just inside the pass. This "bay" is actually shallow grass flats, mainly *Thalassia testudinum*. Blue crabs were taken January through May, with peak abundance in March and April and almost total absence after June. The following year, B. J. Copeland (1965) lowered a net in Aransas Pass three days weekly at the race of ebb and flood to sample macrofauna entering or leaving the bay. *Callinectes*—mostly blue crab—were captured in the ebb samples mainly April through November with peak abundance in April and May, which accords well with the previous year results of Hoese and Jones. A large number of the peak emigrants in April and May were females with sponges. For the Gulf bays, this migration is addressed in the following section, rather than the present, on the basis that it is the ultimate hatching of larvae that is of primary ecological significance.

5.2 Expulsion of larvae to the sea

In early work on Chesapeake Bay, observations of ovigerous females in the lower bay, and the later appearance of megalops in the same region led to the inference that the larvae were hatching and developing here, see, e.g., Hay (1905), Churchill (1919), Truitt (1939), Sandoz and Rogers (1944), Van Engel (1958). The associated hypothesis, that the lower regions of estuaries are nurseries (see Van Engel, 1958, Epifanio, 2007, and citations therein) has not been sustained by observation. In fact, the larvae are carried out of the estuary and develop in the waters of the inner continental shelf (Williams, 1984, Epifanio, 2007, and citations therein). There was growing suspicion that the ocean was involved in the life cycle. Van Engel (1958) noted, for example, "Migration of large numbers of adult females past the Capes to the ocean, and

subsequent appearance of megalops along the ocean beaches, suggest that a substantial amount of spawning may occur outside the Bay." Farther south, in the St. Johns estuary of Florida, Tagatz (1968a) observed that most spawning and hatching took place offshore in the ocean. In Texas, Daugherty (1952) reported that hatching occurs offshore in the Gulf (as much as 10 miles, from indirect evidence). However, only with detailed observations in the last couple of decades of the twentieth century, especially in Chesapeake Bay, Delaware Bay, and Albemarle-Pamlico Sound, did the pieces begin to fall in place.

In the mouth of the Delaware, Dittel and Epifanio (1982) found the greatest concentrations of blue crab larvae at the surface, from which they concluded that the larvae are flushed from the estuary. In the mouth of Chesapeake Bay, direct observations of early stage blue crab larvae were carried by Provenzano et al. (1983) during June – August 1979, in which the water column was sampled vertically with a plankton net at three-hour intervals over 30 hours (encompassing, therefore, two complete semidiurnal tidal cycles and one diurnal). Although first-stage larvae were found generally throughout the water column, they were most abundant in the upper 1-2 m, especially in the neuston (the upper 10-15 cm). Peaks of larvae density occurred at night just after slack on the ebbing tidal current. Provenzano et al. concluded that this was not due to vertical migration of the larvae, but rather to a pulse of new larvae resulting from synchronized hatching. Similar conclusions were reached by Epifanio et al. (1984) based on three years of plankton sampling in the vertical in the mouth of the Delaware.

Hatching at the surface during a high tide clearly maximizes the probability that the hatchlings will be carried out to sea on the subsequent ebbing current. The principal predators of crab larvae in estuaries are young fish*, which are typically most abundant in the brackish reaches of the estuary, declining toward the lower estuary and nearshore coastal zone, and are least abundant offshore (Morgan, 1990, Morgan and Christy, 1995). On the Atlantic coast the predominant planktivores are silversides (*Menidia* spp, *Membras* spp) and anchovies (*Anchoa*

* While many invertebrates are reported to consume crab larvae, they do not appear to represent the same level of predatory impact as planktivorous fish. This may be due to the avoidance ability of crab larvae arising from their shadow response (Tankersley and Forward, 2007). The main invertebrate predators seem to be ctenophores (notably *Mnemiopsis leidyi*) and hydromedusae (notably the cabbagehead, *Stomolophus meleagris*). See Morgan (1992).

mitchilli), and to a lesser extent killifish (*Fundulus* spp), not because of their particular favoritism for crab larvae, but rather because these numerically dominate the young fish species in estuaries (Morgan, 1990). The advantage to hatching just before the current turns to ebb (i.e., on the high tide) is that the larvae's time in the estuary mouth and nearshore zone is minimized, thereby reducing exposure to the abundant planktivores in this region. The ecological value of the nocturnal hatching time is evidently to ensure that the initial efflux of larvae to the shelf takes place in darkness, when the predation of nearshore planktivores will be minimal (Morgan and Christy, 1995, 1997). The larvae of blue crabs are particularly vulnerable to these planktivores because of their color and morphology (Morgan and Christy, 1997).

As remarked above, on the Florida Atlantic coast, the females migrate into the ocean to hatch the eggs (Tagatz, 1968a). In March and April, Tagatz (1968a) found berried crabs mainly within 1.5km near shore, but as the spawning season advanced into late summer, they were found farther offshore (5 – 6 kms). Tagatz found most of the zoeae concentrated in the surface waters. Tagatz (1968a) also notes that many females return to the lower estuary to spawn, and that many "if not all" females spawn twice, either in the same season or over two seasons. Females returning to the estuary were easy to distinguish because their carapaces were dull-colored and encrusted with marine fouling organisms. Later tagging studies (Steele, 1982) established that some of these females also migrate along the coast.

On the Gulf coast of Florida, spawning occurs in the offshore zone near the major estuaries (Steele, 1982). In the 1970's, tagging and recapture experiments revealed an apparent large-scale migration, summarized in Oesterling and Adams (1982) and citations therein (see also Oesterling, 1976, Oesterling and Evink, 1977, Steele, 1982). While males and some females tended to remain in or near their home estuaries, some of the females migrated generally to the north along the peninsula toward the Florida panhandle, and along the panhandle to the west, mainly September through March. (No crabs were recovered beyond Florida but it is possible that a few migrated farther to the west.) A general concentration of mature females seemed to be occurring in the base of the panhandle. Moreover, the only ovigerous females captured were in this region, with new sponges. This movement is interpreted by Oesterling and Adams as post-insemination migration toward a spawning area, analogous to the down-estuary migration of the

mid-Atlantic, but in this case the target spawning area appears to be the Apalachee Bay area of Florida. They hypothesize that the bight of coastline from Panacea to Punta Gorda (below Tampa Bay) is the "spawning ground" for crabs on Florida's Gulf coast, where the freshwater plume of the Apalachicola River entrains and redistributes the zoeae. They state that this hypothesis is confirmed by observations of abundant berried crabs in Apalachee Bay reported by the local crabbers and shrimpers.

Steele (1991) disputes this interpretation, noting that elsewhere female crabs migrate to waters of higher salinity, not lower. From later tagging studies, he confirmed the northward migration, but argues that the crabs are not seeking a spawning area, but rather spawn offshore throughout this migration route, some of the crabs from the estuaries of southwest Florida entering Tampa Bay and contributing to its crab population. He further attributes the apparent congregation in Apalachee Bay to the freshwater flow from Apalachicola Bay acting as a low-salinity barrier to further migration to the west. Moreover, the concentration of these crabs against the Apalachicola plume renders them vulnerable to the high-intensity fishery in this region, which would account for the few migrants found farther to the west.

In Texas, it has been long established that the life cycle of the blue crab does not accord with that of the mid-Atlantic. Most spawning and hatching occurs in the Gulf rather than the lower estuaries (Williams, 1984). Higher salinities are certainly part of the reason for this, at least for the northern bays of Texas. Of the ovigerous crabs taken by Gunter (1950) in his survey of Aransas-Copano Bay and the adjacent Gulf of Mexico, 58% were caught in salinities greater than 30‰. Spawning, over the 1947-50 period of the Texas Game and Fish Commission (TGFC, the predecessor to TPWD) blue crab studies in the Cedar Bayou region (Daugherty, 1952), took place December through October with peak period June – August. Later studies indicate that spawning can occur on the Texas coast year-round, unless meteorology, notably cold winters, interferes. In the 1949-50 data of Daugherty (1952), less than 5% of mature females in the bays (Mesquite, Aransas, San Antonio) carried sponges, and about 16% migrating seaward through Cedar Bayou were berried, implying that the majority of these emigrating to the Gulf had not yet spawned.

In the TGFC Cedar Bayou collections, both directional fish traps and traditional crab pots were installed in the inlet. While the outgoing trap collected mainly (about 70%) mature females, over 80% of which were either unspawned or ovigerous, the crab pots on either side trapped mainly large males, indicating that the females were resolutely migrating without concern for food, compared to the easy diversion of the males for a meal. Sampling in the Gulf immediately outside Cedar Bayou caught few females, so the females emigrating from the inlet quickly moved farther offshore (Daugherty, 1952). Hatching, it follows, occurs offshore in the Gulf of Mexico. In the incoming directional fish traps in Cedar Bayou, nearly 90% of the mature females trapped had already spawned (determined from remnants of eggs on the swimmerets). These females were clearly re-entering the estuary after hatching their brood in the Gulf. Similar studies were performed the following year (1950-51), reported by Simmons and Hoese (1959), in which mature male and female crabs, predominantly sponge crabs, moved through the pass into the Gulf in April – July, and "spent" crabs migrated back into Mesquite Bay May – November.

In the late 1960's, Texas Parks and Wildlife (TPWD) returned to Cedar Bayou, performing a 2.5-year study of migration through the inlet, reported by King (1971). Three platforms spanning the inlet held stationary plankton nets opening toward the sea to capture organisms entering Mesquite Bay. Mature crabs were sampled by directional traps in the inlet, and by upcurrent trawling. Megalops, but no zoeae, were captured in the plankton nets, from which King inferred that zoeal development occurred entirely offshore.

Based upon two years of data from Galveston Bay, More (1969) forwarded a conceptual model of the blue crab life cycle, in which he identified three groups (or cohorts). The first spawned March-April, the second June-July, and the third July-August. The confidence with which one can differentiate these three groups can be questioned. In Lake Pontchartrain, Darnell (1959) encountered a similar complexity in time-series behavior, and was less ambitious in inferring patterns, stating, "As the individuals undergo their complex patterns of migration the different waves are seldom distinguishable from one another… ." Combining More's three groups would imply that ovigerous females in the lower bay migrate to the Gulf throughout the period March – August, which would reasonably agree with the peak spawning period observed in Cedar Bayou.

5.3 Diaspora on the shelf

The fact that newly hatched larvae enter the nearshore ocean raises corollary questions: in what zone(s) of the ocean does development take place, how complete is the development, i.e. what stage(s) is recruited to the estuary, by what mechanism(s) do the larvae, postlarvae or young crabs find their way back to an estuary entrance, and are they returned to their estuary of origin (their natal estuary)?

Observations on both the Atlantic and Gulf coasts have demonstrated that the larval development offshore is complete to the megalop stage (e.g., Smyth, 1980), which requires some three to six weeks depending upon conditions, mainly temperature (see Section 3.3). Zoeae and megalops have been observed in the mid-Atlantic bight generally in the 10-80 km zone offshore, and concentrated in the upper few meters, especially the neuston at night (the upper 10-15 cm, Smyth, 1980, Provenzano et al., 1983, D.F. Johnson, 1985, though Epifanio, 1995, disputed their prevalence in the neuston). After the early summer hatching, zoeae were found most abundant in late summer. Three important studies are: quarterly nocturnal neuston and bongo-net tows of stations from the nearshore to the shelf break from New Jersey to Virginia (Smyth, 1980), a detailed sampling from the mouth of Chesapeake Bay out 30 km on the shelf (McConaugha et al., 1983), and three years of plankton sampling in the mouth of the Delaware by Epifanio et al. (1984). The Smyth (1980) survey shows a substantial pool of larvae offshore to the 1000-m isobath (120-150 km), mainly late-stage zoeae and megalops, except with some early-stage zoeae within the nearshore 30 km in summer. Both of the latter two studies disclosed late-summer peaks in Zoeae I larvae followed in about five weeks by high concentrations of megalops. In the former (McConaugha et al., 1983) few, and in the latter (Epifanio et al., 1984) none of the intermediate stages Zoeae II-VII were collected. Epifanio et al. noted that Zoeae I occurred mainly during ebb currents, and megalops mainly during flood currents, and concluded that the freshly-hatched Zoeae I were transported out of the estuary mouth to the sea, and the megalops were transported into the estuary from the shelf.

In the mid-Atlantic, megalops concentrations are highly variable, and have been collected year-round, but with greatest abundance in summer. Megalops begin to concentrate in the nearshore

zone in summer, reaching maximum abundance in late summer to early fall (Epifanio, 2007). In the beaches alongside the mid-Atlantic inlets, the myriad of megalops in the surf has long been a source of vexation to swimmers, who complain of the bites of "water fleas", in fact the nips of megalops with their miniscule chelae, which produce itching and a rash. Truitt (1939) reports that swimming ceased at a Maryland seaside resort throughout August 1925 due to megalops. Van Engel (1958) notes the numerous complaints of swimmers at the ocean front at Virginia Beach about bites of water fleas. Up to the present, ocean beaches are closed sporadically for high concentrations of megalops (e.g., Hampton Roads *Virginian-Pilot* 6 July 2006). On the Texas coast, Gunter (1950) reports many occurrences of megalops in the surf around Aransas Pass during the warmer months.

Blue crab larvae are planktonic (see Section 2.3) so their movement and distribution are determined by the structure and seasonality of circulation on the inner shelf and nearshore coastal zone. The questions of the zones of development and the mechanism for re-accessing the estuary raised above are therefore addressed through physical oceanography. Without vertical mixing, the zoeae remain confined to the upper layer of the water where they hatched, at least until they develop to a stage with some modest swimming capability (see Section 2.3). Like other planktonic organisms, their distribution is patchy. In the mid-Atlantic coastal zone, the patch dimensions have been measured to range 1 – 2 km. The patches are considered to be the initial result of synchronous hatching by a group of females, then maintained by both physical (hydrodynamic) and biological processes, but the precise mechanisms remain obscure (Natunewicz and Epifanio, 2001, Epifanio and Tilburg, 2008). The most important consequence of this patchiness is to corrupt direct observations of offshore zoeae distribution, which are rare (e.g., Smyth, 1980, Epifanio et al., 1989), with considerable stochastic noise (Weinstein, 1988a, Epifanio, 1995, Garland et al., 2002, Epifanio and Tilburg, 2008). This means that it is mainly left to theory to construct a conceptual model of the transport of larvae in the nearshore environment.

5.3.1 The Atlantic Shelf

The general conceptual model of larval transport on the shelf (nicely summarized by Epifanio, 2007, and by Epifanio and Tilburg, 2008), as with other aspects of research on the blue crab life cycle, is dominated by work on the mid-Atlantic coast. This is comprised of the superposition of two components (Münchow and Garvine, 1993), the first being a nearshore buoyant current fed by the coriolis-turning outflow plumes from estuaries (e.g., Wong and Münchow, 1995), and the second a wind-driven circulation on the inner shelf. The nearshore estuary current is conceived to accomplish longshore advection of larvae expelled or hatched into the inner shelf environment. The wind-driven current(s) provides additional longshore dispersal and an organized seasonal transport that moves the larvae back up the coast in late summer and fall, and ultimately carries them into the nearshore and into the mouths of estuaries.

On the Atlantic seaboard, the first component is a southward- or southwestward-flowing nearshore current ("jet" in some terminologies, e.g. Boicourt, 1982) driven by the outflows from the Hudson, Delaware and Chesapeake, and to a much lesser extent outflows from the Gulf of Maine and the Gulf of St. Lawrence, in turn resulting from the spring freshwater inflows to the estuaries. This current is characterized by lower salinity water and is confined to a relatively narrow nearshore band of 10-20 km width (Epifanio et al., 1989, Wong and Münchow, 1995). The strength, cross-shelf width and length of this current are directly related to the volume of net flow leaving the estuaries (Defant, 1961, esp. Chap. XVI, Münchow and Garvine, 1993, Wong and Münchow, 1995, Simpson, 1997, Hill, 1998). In the late summer, as inflows to the estuaries typically decline, the current narrows and weakens. Normal to the coast, there is a density gradient, arising from the lower nearshore salinities, that induces a cross-shelf gravitational circulation with offshore-directed flow in the upper layer and onshore flow in the lower. This is an extension of the well-known gravitational circulation of an estuary (Ward and Montague, 1996). As nearshore salinities increase with the advance of summer, the shelf-normal salinity gradient decreases, and the associated cross-shelf circulation weakens.

On a larger scale, the currents over the continental shelf set south or southwesterly, generally following bathymetry, fed by the confluent Labrador Current and North Atlantic subpolar gyre

circulation (Loder et al., 1998). Observational studies on the inner shelf of the mid-Atlantic in the mid-twentieth century found this southerly flow to be reinforced in October through March by the prevailing northwesterly* winds of this season, and reversed at intervals during April through September in response to prevailing southwesterly winds, see the summary of Bumpus (1973). Current meter deployments in the second half of the twentieth century indicated a possible, more complex spatial configuration, with a wind-driven north current seaward of the estuary-driven nearshore southward current, and a broad southward current farther offshore, producing a "banded" current regime (Boicourt, 1982, Epifanio et al., 1989, see also Epifanio and Garvine, 2001). Whether this spatial structure obtains or (what is more likely) there are transient nearshore reversals of the prevailing southerly current, the important feature is a wind-driven north-setting current in late summer on the inner shelf of the mid-Atlantic. This was given theoretical support by a simplified dynamic model applied to the shelf configuration around the entrance to Chesapeake Bay by Johnson et al. (1984), to estimate the currents that would result from various scenarios of wind stress vector, stratification, turbulent exchange, and longshore water-level gradient. The southerly (i.e., northward) wind stress typical of summer was shown to drive a northerly current within 25-50 km of the coastline, reversing the large-scale southerly current, of speed sufficient to return larvae to the bay region.

The general sketch of the conceptual model is as follows. The newly hatched larvae are injected into the southward nearshore buoyant current. Over their 30-50 day development period to megalops, this nearshore current can transport the zoeae 100-300 km down the coast. Over multiple generations, this downcoast transport would result in a depletion of the crab population, most quickly in the northernmost estuaries, unless there is some mechanism for the retention and/or return of larvae to the region offshore from the natal estuary. This mechanism is conceived to be the wind-driven northerly current on the inner shelf that occurs, perhaps intermittently, in late summer and flows counter to the prevailing current. At least some of the larvae are postulated to be transported offshore out of the coastal current by turbulent mixing, by cross-shelf advection driven by the coast-normal gradient in salinity (provided it maintains its

* The reader is reminded that the direction convention for current is that *to* which the current flows, while the convention for wind is the direction *from* which the wind blows. A north (or northerly) wind flows to the south, in the direction of a south (or southerly) current.

strength, which has come into doubt from recent field observations, see below), and/or by Ekman transport forced by prevailing south or southwest winds of summer (Natunewicz et al., 2001). These larvae would then be entrained into the northward-flowing current to be carried back up the shelf. Wind is also conceived to be the mechanism that carries the larvae back into the nearshore, including the mouths of estuaries.

For this wind-driven component, there are two schools of thought, distinguished by the rôle postulated for Ekman transport relative to other forcings in the nearshore environment. A useful historical marker in the evolution of the perception of Ekman-layer dynamics is the workshop on larval transport through inlets convened in Ocean Springs, Mississippi, by the Waterways Experiment Station of the U.S. Army Corps of Engineers in 1985, published later as a *Symposium* volume of the American Fisheries Society (Weinstein, 1988b). These proceedings represent the status of understanding of estuary-shelf exchange in the life cycle of catadromous organisms as exemplified by a cross section of workers on the American Pacific, Atlantic and Gulf of Mexico coasts. Of the thirteen published reports in this volume, only two proposed Ekman transport as a major factor in the transport of larvae in the nearshore shelf. Within the next decade, as represented by the survey articles of Epifanio (1995), and Epifanio and Garvine (2001), Ekman dynamics was embraced by a number of the researchers on the blue-crab life cycle on the Atlantic. The paper by Roughgarden et al. (1988) seems to have been particularly influential.

The theoretical basis of Ekman-layer dynamics is conceptually straightforward. Wind stress (τ_x, τ_y) applied to the surface of the ocean accelerates the underlying water. The stress diminishes with depth, and vanishes at some level h below the surface. Integrating the current velocity (u,v) from this depth to the surface gives the component volume transports

$$U_E = \int_{-h}^{0} u\, dz \qquad V_E = \int_{-h}^{0} v\, dz \tag{6}$$

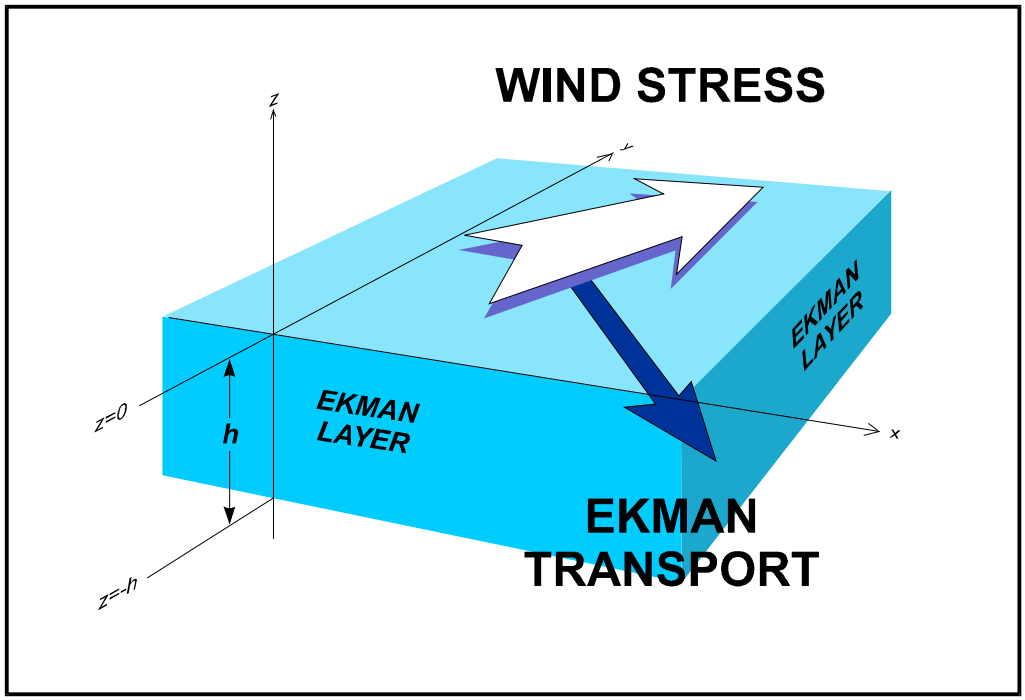


Figure 16 - Diagram of Ekman transport driven by wind stress at the ocean surface (northern hemisphere)

(Actually, the dimensions of these transports at this stage of calculation are [L^2/T], flow per unit width, pending a later integration.) The equations of motion, assuming steady-state equilibrium and no additional forcing other than the rotation of the earth, and similarly integrated over the same layer, may be written:

$$-f V_E = \frac{1}{\rho} \tau_x \qquad\qquad f U_E = \frac{1}{\rho} \tau_y \qquad\qquad (7)$$

Here the *x*- and *y*-components are conventionally taken to be eastward and northward, resp., ρ is water density, *f* is the coriolis parameter, and (U_E, V_E) is the transport in this layer (the Ekman transport). This is the Ekman layer, though more generally this term refers to the surface boundary layer in which both friction and rotation are important. The physical meaning of (7) is that the Ekman transport is directed normal to the direction of wind stress, to the right in the northern hemisphere, see Figure 16. Spatial variations in wind direction translate to spatial variations in Ekman transport. For example, convergence in low-level wind induces divergence

in the Ekman transport and *vice versa*, which in turn induces upwelling (Ekman suction) and downwelling (Ekman pumping), respectively. The theoretical depth of the Ekman layer in the open ocean outside of the equatorial belt ranges 10-100 m. Equation (7) is singular at the equator where $f \rightarrow 0$.

The distinction between the two schools of thought is the mechanics of the transport of the late-stage zoeae and megalops from the inner shelf waters to the region of the estuary mouth, after either (1) remaining in the region offshore from the estuary due to being shielded from downstream advection (in a "null" zone, see below), or (2) being transported to the region offshore by the north-setting currents of late summer. One view is that megalops are carried across the nearshore and into the estuary by an influx of water volume* driven by the direct response to onshore (south- or southeast) wind events, notably in advance of cyclones and/or frontal passages (see, e.g., Austin and Lentz, 1999). The other view is that megalops are carried to the estuaries by Ekman transport associated with north winds following passage of cyclones or fronts. Both conceptual models agree in the major determinants of the movement on the shelf, *viz*. upcoast transport with northerly currents, transport to the estuary region by cross-shelf water movement, and the function of midlatitude meteorological disturbances in driving this cross-shelf transport.

Other transport mechanisms have been proposed to account for the return of late-stage zoeae and megalops to the estuary. The onshore flow at depth associated with the buoyant nearshore plume has been suggested, as has selective tidal stream transport. However, field observations disclosed that the larvae remained in the surface layer (but not necessarily the neuston) throughout their development (Epifanio, 1995, and citations therein), thereby rendering dubious both hypotheses. Even where megalops were present in sufficient numbers at depth to take advantage of the onshore transport in the lower layer, the rate of movement was too slow to explain the influx of megalops into the estuary (Epifanio et al., 1989), and, besides, the deeper water is frequently too cold for development or even tolerance of megalops (Epifanio, 1995,

* In the literature, the term "inflow" is often used to refer to the influx of a substantial volume of water into the estuary from any source, including the sea. It has become the convention in Texas to reserve "inflow" specifically for freshwater.

Epifanio and Garvine, 2001). Thus, wind-driven transport has become the leading theory, either through Ekman-layer dynamics, or through direct wind stress.

Ekman-layer dynamics, deriving from the magisterial analyses of V. W. Ekman (1905, 1928, 1932) on the mechanics of oceanic boundary layers, is an elegant theoretical device that has been spectacularly successful in qualitatively explicating the relation of wind stress to surface currents in the open ocean and to the major zones of divergence (upwelling) and convergence (downwelling). Details of the modern theory are given by Gill (1982), Pedlosky (1982), Lykossov (2001), Vallis (2006) and others. The simple theory of (6) and (7) is the purest form of an Ekman layer, but conditions for which (7) is applicable are so rare as to prohibit direct validation of the theory, a fact that impels the frequent caution of dynamicists (e.g. Gill, 1982, Vallis, 2006, Dyke, 2007).

Equation (7) is in fact a display of mathematical legerdemain. First, the derivation of (7) requires strong assumptions: steady flow, only two forces operating (coriolis and wind stress), in equilibrium, and a homogeneous ocean of infinite depth. This implies the neglect of other forces (notably water-level gradients, buoyancy, stratification and Langmuir circulations), dynamic time variations (due to accelerations, and surface and internal waves, see Lentz and Fewlings, 2012), and the effect of a bottom. Finite depth can be accommodated fairly easily (and was addressed by Ekman, 1905), in which case a bottom Ekman layer results, where the current just above the bed is directed to the left of the interior current (in the northern hemisphere). Water-level gradients can be accommodated through the assumption of geostrophic flow, in which the flow in the frictional Ekman layer is ageostrophic, but the force balance is more complex, see Gill (1982) and Vallis (2006).

Second, (7) contains an unspecified variable, namely the depth h over which (6) is integrated. This layer depth is strongly dependent upon the specific properties of vertical turbulence and its mathematical form (e.g., Csanady, 2001, Lykossov, 2001). Third, one must be careful in specifying the stress direction in (7). Strictly, this applies exactly at or very near the water surface (technically, within the constant-stress sublayer, see Lykossov, 2001). Wind data from an observing station anemometer at even a standard height (10 m) will depart in direction from

the surface stress. More importantly, the wind at geostrophic/gradient level is directed to the right of the wind at the surface, so use of synoptic wind climatologies constructed from pressure data will substantially overestimate the rotation of Ekman transport from north.

In shoaling water over the shelf, the simplifying assumptions of Ekman dynamics* become even less defensible than in the open ocean, especially in the nearshore and inner shelf (as anticipated and addressed in Ekman's 1905 treatment, see also Beer, 1997). The nearshore zone is especially complex, with simultaneous operation of buoyancy plumes, tides, turbulence and mixing, and rotation effects (e.g., Simpson, 1997). As depth diminishes, the wind-driven current tends to the direction of the wind stress. For example, although the mechanics of the model of Johnson et al. (1984) would accommodate Ekman dynamics, the other processes in the model suppressed the *cum sole* turning of the current from the wind direction and exhibited a closer correspondence between directions of wind and current (D.R. Johnson, 1985).

The recent review and synthesis of Lentz and Fewings (2012) present scale analyses of cross-shelf and along-shelf momentum budgets including most of the terms neglected in (7). On the inner shelf, where the surface and bottom boundary layers are expected to merge, the Ekman effects are relatively unimportant, and the wind-driven surface currents follow the direction of wind stress (see also Hearn, 2008), though greatly modified by wave processes and nearshore water-level set-up. This theoretical configuration was not found, however, in the detailed hydrographic surveys off the New Jersey coast reported by Garvine (2004). Instead, the surface and bottom boundary layers maintained their separation into the nearshore, and the water column was stratified over this entire range. Dzwonkowski et al. (2009) examine the seasonal variation in drivers of cross-shelf flows, finding Ekman domination under quiescent summer south-westerly winds, but direct cross-shelf wind-stress forcing during other seasons (including the late

* One also must differentiate Ekman dynamics on the eastern boundary of the ocean (the examples given by Roughgarden et al., 1988) from the western boundary, exemplified by the mid-Atlantic. On the eastern boundaries, the approximations of Ekman transport are better satisfied than the western boundaries: the longshore winds are steadier, the coastlines are morphologically simpler, and water depths generally increase more steeply away from the coast. Ekman-transport-induced upwelling is better established, and, indeed these coastlines are well known for their high productivity in both the northern and southern hemispheres. An additional factor that contributes to the complexity of the western coastline is the westward propagation of planetary-scale disturbances from the interior of the ocean, a process to which the eastern coastline is immune, see Hill (1982).

summer and early fall). In the Delaware estuary buoyancy current, field observations of Münchow and Garvine (1993) and Wong and Münchow (1995) confirm the baroclinic circulation generated by the density gradients in the plume, especially the cross-shelf circulation. Their field data are complex, with simultaneous tidal, buoyancy and wind-stress forcing. Their approximate separation of the tidal and buoyant components yields a wind-driven component that appears consistent with Ekman dynamics. *NB*, their data were measured in May and June. (Moreover, their field data fail to validate a rigorous application of the Princeton Ocean Model to the coupled estuary-shelf circulation.) Tracings of particle movement on the shelf (both with drogues and monitoring of larvae patches) have been generally confusing. Epifanio (2007) suggests that the problem may be a mismatch between the spatio-temporal scales upon which transport operates and the scales of measurement.

Recent research has identified what may be an alternative return/retention mechanism to the natal estuary region besides the complex shelf-transport trajectory described above. Field studies in the mid-Atlantic have shown that the buoyant coastal plume driven by outflows from the estuaries weakens downcoast more quickly than first thought, and in fact there are regions of low transport just upcoast from the mouths of the major estuaries. These have been referred to as "null" zones, because those larvae entering this region are not transported farther downcoast, but are effectively retained (Tilburg et al., 2007). Detailed larval sampling along transects crossing the offshore edge of the buoyant plume from the Delaware showed that the larvae are in fact concentrated at the surface along the frontal boundary of the plume (Tilburg et al., 2009). These null zones may represent regions in which the zoeae develop to the megalop stage and remain available to re-enter the estuary. It is noteworthy that McConaugha (1998) reported a segregated distribution of zeoae I southeast from the entrance to Chesapeake Bay, and megalops to the east-northeast (his Figure 2). McConaugha (1988) interpreted these distributions as two limbs of a cyclonic circulation around the mouth of the bay. However, they are consistent with the null-zone notions of Tilburg et al. (2007), the former corresponding to the outflow plume from the bay, and the latter to the null zone.

The circulation over the shelf of the south-Atlantic bight differs in some respects from the mid-Atlantic. The shelf is narrower (10-20 km), except off Georgia where it widens to over 100 km,

the outer shelf is directly influenced by the Gulf Stream, and the inner-shelf currents basically track the seasonal winds, setting north in summer (driven by south winds) and south to southwest in early fall (driven by north to northeast winds), see, e.g., Bumpus (1973), Blanton et al. (2003). There is a nearshore buoyant plume forced by discharges of the Savannah, Pee Dee, and Cape Fear rivers, among others, which is typically less than 10 km in width, and less well-defined and more transient than its mid-Atlantic counterpart (Boicourt et al., 1998). This coastal current is dependent upon wind as well as discharge, being extended by north-wind stress, and opposed and disrupted by south-wind stress, through both direct stress and cross-shelf Ekman transport. Edwards et al. (2006) report an extensive study of shelf circulation using drifters, which is particularly relevant to estimating the movement of plankton. For the hatching and grow-out period for blue crab larvae (i.e., summer), both field data and a numerical model displayed movement up the coast, with most drifters exhibiting offshore meandering, presumably driven by late summer frontal passages. This meandering resulted in a concentration 30-50 km offshore from Georgia and is interpreted by Edwards et al. as evidencing retention. (More than 80% of the drifters remained in shelf waters, only a few being entrained into the Gulf Stream.)

5.3.2 The Gulf of Mexico Shelf

In the Gulf of Mexico, delineation of the general circulation has seen considerable advances in the past quarter century, especially benefiting from technological advances in data-acquisition equipment, satellite imagery, and numerical analysis on the digital computer. What is revealed is a complex circulation driven principally by wind stress and the dynamics of the Loop Current, especially separation and subsequent trajectories of vortices (rings). Recent surveys are given by Boicourt et al. (1998), Nowlin et al. (1998), Olacoaga (2010), Schmitz (2003) and Sturges and Lugo-Fernandez (2005). The wind climatology can be succinctly summarized as easterly, essentially the trades, veering* southeasterly in the northwestern Gulf, and interrupted by north winds associated with midlatitude disturbances (e.g., Rhodes et al., 1989, Morey et al., 2005).

* Veering is a clockwise turning of the wind, in contradistinction to backing, which is counterclockwise.

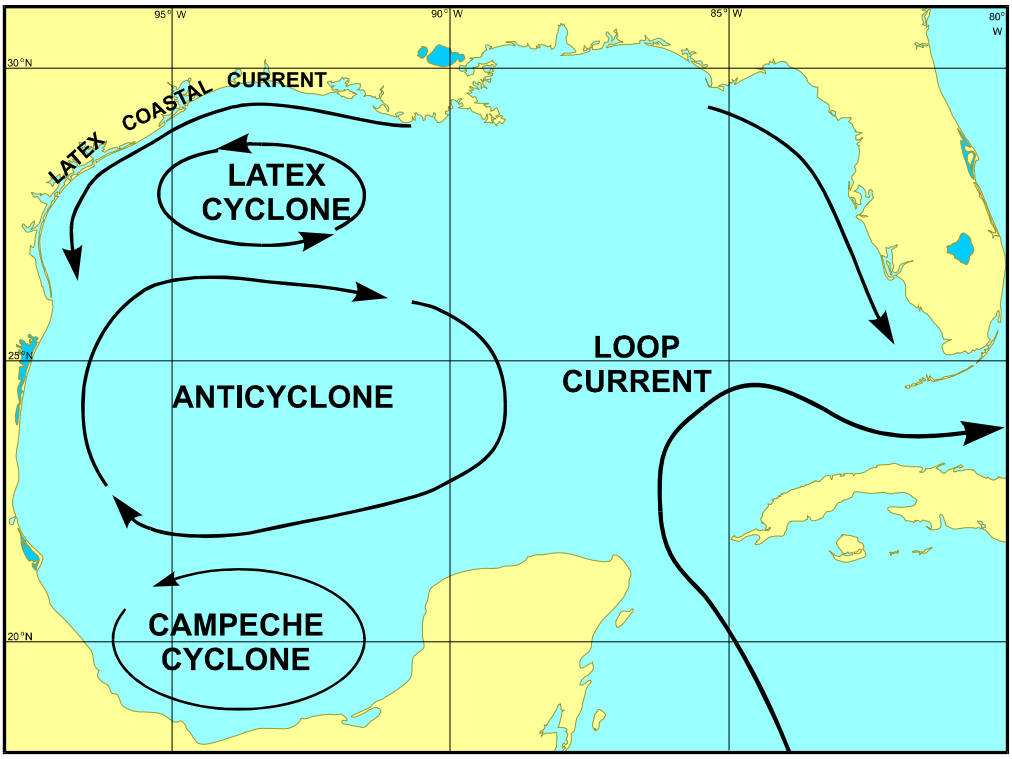


Figure 17a - Schematic of surface currents in Gulf of Mexico, nonsummer conditions

Over the Gulf, north winds following cold-air outbreaks veer quickly to the east (e.g., Walker, 1996), so that in the winter months, the prevailing winds are northeasterly.

The Mississippi is the predominant source of freshwater discharge to the Gulf. The surface area of the plume, and hence its susceptibility to wind-stress forcing, is a strong function of stratification (Wright and Coleman, 1971, Walker, 1996). Its plume typically curves to the west, facilitated by the prevailing easterly winds, but under various combinations of wind and river flow, can lie to the east (Morey et al., 2003). An extreme example was the Great Flood of 1993 in which the plume set to the east, was entrained into the Loop Current and was carried to the east coast of the U.S. (Walker et al., 1994). However, the Mississippi flow is not a major driver of the coastal current in the Gulf. Rather, the wind has a dominating effect on the distribution and size of the plume (Walker, 1996).

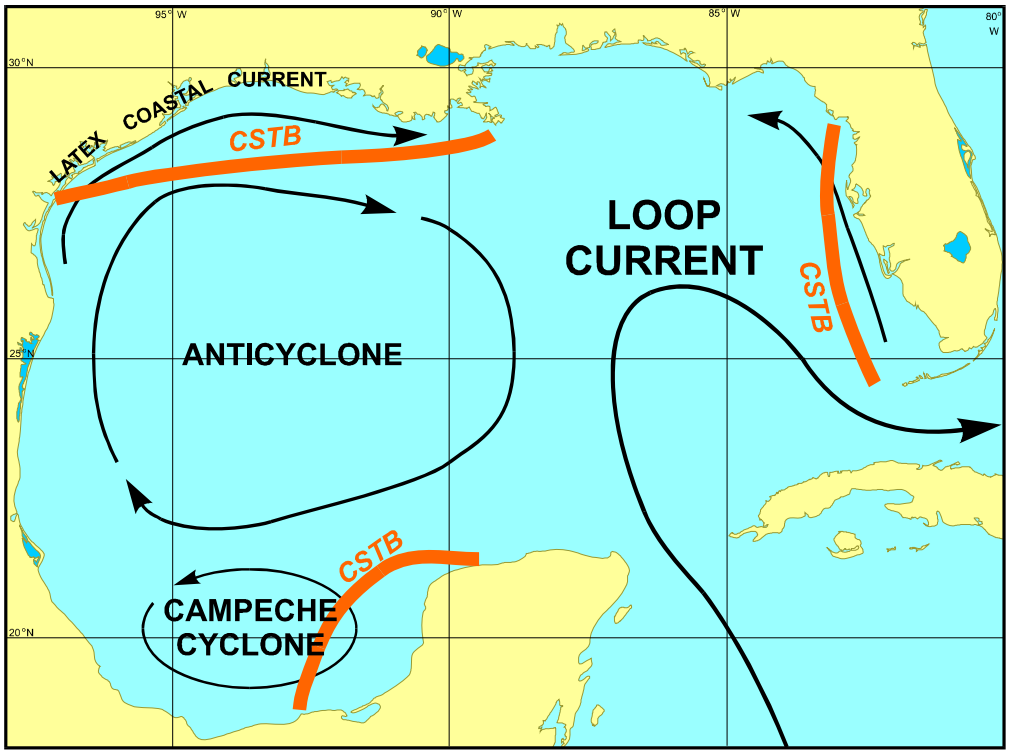


Figure 17b - Schematic of surface currents in Gulf of Mexico, summer conditions. CSTB denotes cross-shelf transport barrier, see text.

The elements of the circulation of surface waters are sketched in Figure 17, drawn from the work of Cochrane and Kelly (1986), Morey et al. (2003, 2005), Cho et al. (1998), Nowlin et al. (1998), Nowlin et al. (2005), Sturges and Kenyon (2008). Circulation in the open waters is dominated by an anticyclone in the western Gulf and by the configuration of the Loop Current in the eastern. It is the shelf circulations, however, that are of direct relevance to the fate of blue crab larvae hatched in the nearshore and inner shelf, and are addressed below. Figure 17 must be qualified. It depicts only the generalized circulations. It cannot display the day-to-day variations in currents, even reversals, tracking the changes in winds. Johnson (2005) presents animations (as Quick-Time™ files) of drifter trajectories that dramatically show the effect of wind on surface currents. Nor does Fig. 17 depict the complex secondary circulations associated with the shedding and movement of rings from the Loop Current, many of which maintain their integrity for months.

Circulation over the shelf in the eastern Gulf of Mexico is transient and essentially wind-driven. A north-setting current during June through August over the wide west Florida shelf, Fig. 17b, is inferred from ship-drift reports (USWB and USNHO, 1959, updated in Sturges, 1993), has been measured by moored current meters and has appeared in numerical circulation models (Weisberg et al., 2005). This is also consistent with the northward migration of blue crabs observed by Oesterling and Adams (1982) and Steele (1992). During October through May, the nearshore current sets generally to the south, Fig. 17a.

The northeastern shelf currents, off Alabama and the Florida panhandle, are much more variable, responding to both wind events and intrusions of rings from the Loop Current (due to the narrowness of the shelf), see Sturges et al. (2001), and Hamilton and Lee (2005). The variability of currents in the northerneastern Gulf was illustrated in the 1960's by drift bottles released monthly from a station on the shelf break south of Pensacola. These were recovered on the Gulf coast predominantly to the east for April – July and to the west for August – October (Ichiye et al., 1973), though in almost every month some bottles were recovered from the Texas coast to the east coast of Florida. Two decades later, the number of drifters employed has increased two orders of magnitude, and remote positioning allows their paths to be monitored, but the variety of movement is just as bewildering, as evidenced by any "spaghetti" plot of drifter trajectories (e.g., Sturges et al., 2001), or, for example, the animations of Johnson (2005).

A recent discovery of pertinence to larval transport is that there is a "forbidden zone" on the south Florida coast extending from above Tampa Bay south to the Keys, essentially within the 50-m isobath, that appears to be immune to drifters released in the Gulf (Yang et al., 1999, see also Beron-Vera and Olascoaga, 2009). It is thought to be a manifestation of the distribution of lagrangian coherent structures (LCS). The LCS is a locus of accumulation of fluid particles, arising from nonlinear advection in some mysterious way, that acts like a material surface (analogous to a Taylor column), hence impeding exchange. Delineation of the regions of LCS's in the Gulf is determined by lagrangian simulation, presented by Olacoaga (2010), and zones free of LCS's are diagnostic of a "forbidden zone". The boundary of such a zone, where LCS's are dense, has been named a cross-shelf transport barrier (CSTB, Olacoaga, 2010). The Florida shelf CSTB appears to be a year-round phenomenon with maximum intensity in the third quarter of

the year, see Fig. 17b. It is noteworthy that the region within this CSTB includes the migratory paths of female blue crabs reported by Oesterling and Adams (1982). Perhaps this barrier assists the crabs in their open-water migration by preventing their loss to the offshore regions of the Gulf. Interestingly, the simulation of Olacoaga (2010) also revealed a CSTB-protected region along the Lousiana-Texas coast from the Mississippi delta to the Coastal Bend, as well as one adjacent to Yucatan, also shown in Fig. 17b. Olacoaga (2010) hypothesizes that the limited offshore exchange in these regions makes them especially susceptible to red tide blooms.

In the northwestern Gulf of Mexico, throughout most of the year, generally October through June, the Lousiana-Texas (LATEX) coastal current sets west then southwest down the coast paralleling the isobaths, Fig.17a. In late summer, July through August, it reverses, setting northeast along the south Texas coast, then east along the east Texas coast, see Fig. 17b. Its speed is about 5 km/day, but varies a factor of two or more about this mean. As noted in Section 5.2, blue crabs hatch mainly May through August. The reversing coastal current therefore provides a potential retention process, the early spawn (May – June) being transported to the south then returned with the reversed current. The later spawn (July – August) would be first transported to the north, then returned in September – October after the fall reversal of the coastal current. The coastal current is considered to be mainly wind-driven (Smith, 1978), its reversal being due to the summer winds turning southeasterly, though recent research is uncovering a much greater contribution from Loop Current eddies than previously thought (Ohlmann et al., 2001). River flows discharging from the estuaries do not appear to contribute as much to the inshore current as on the mid-Atlantic coast. Smith (1978) studied current meter measurements from 10 km offshore and found reversals of longshore current in summer to be taking place at intervals of one to two weeks, superposed on the larger-scale prevailing current.

As on the east U.S. coast, the developed larvae must be transported to the region of estuary mouths in order to be capable of entering these system. This requires some hydrodynamic mechanism of cross-shelf exchange. Shaw et al. (1985) hypothesized that larvae carried by the coastal current are intercepted by cross-shelf currents entering estuaries and drawn into the estuary as they pass. This hypothesis was framed specifically for Gulf menhaden (*Brevoortia patronus*), but the process would apply generally to the planktonic life stage of any organism

spawned on the inner shelf, including blue crabs. Based upon extensive analysis of current-meter records in Main Pass, the entrance to Mobile Bay, Wiseman et al. (1988) determined that it is the onshore (i.e., north-south) wind stress that is mainly responsible for exchange between the bay and the Gulf, and that this process would satisfy the hypothetical larval transport forwarded by Shaw et al. This is in contradistinction to the invocation of Ekman stress for the same process in the mid-Atlantic (see Section 5.3.1 above).

5.3.3 Summary

This brief survey of the blue crab larva's sojourn on the nearshore and shelves has now grown larva-like to mimick the meandering of larvae themselves. But the book is not yet closed on this review of the transport of larvae to the estuary mouth. Much that is known about the timing of the magalops' appearance at the estuary mouth is based upon observations of their settlement within the estuary, which is the next stage of blue-crab migration and is addressed in the next section.

The immediate conclusions about the transport of blue crab larvae are:

(1) Larvae are hatched in the mouths of estuaries or offshore, and are potentially susceptible to being entrained into the coastal current system. On the mid-Atlantic the inshore current is driven by discharges to the coastal zone of freshwater inflows to major estuaries. On the Texas coast, the inshore current is mainly wind-driven, locally reinforced by freshwater discharge. These larvae, organized into patches of high density, are then advected down the coast. Generally, this would represent a net loss of larvae from the natal reach of the coastal zone. On the mid-Atlantic, many of these would be transported offshore at Cape Hatteras. In the northwestern Gulf, the downcoast estuaries may benefit from larval transport from Louisiana.

(2) At least some of the larvae carried in the coastal current (1) will be transported offshore. On the mid-Atlantic shelf, these larvae will be returned as late-stage larvae to the region of the natal estuary by late-summer northward currents located farther

offshore than the inshore buoyant current. On the Texas coast, those larvae that remain in the coastal current are probably returned by the seasonal reversal of the coastal current, though perhaps not to the region of the natal estuary.

(3) The most probable mechanism for transport of late-stage larvae and megalops to the estuary mouth is large volumes of shelf water driven by winds, especially associated with synoptic-scale storm systems. On the mid-Atlantic, those that occur in late summer and fall, when the larvae are offshore, are most important. On the Gulf coast, there is a longer spawning and larval development season than in the temperate mid-Atlantic. There is also a well-developed seabreeze that may also provide on onshore transport mechanismin the absence of frontal passages.

(4) While Ekman transport may be a factor in the volume transport of (3) on the mid-Atlantic, which would imply a north wind forcing, this remains a qualitative explanation, for which direct current response to wind stress may be equally plausible. On the northern and western Gulf of Mexico coasts, direct wind stress appears the more likely mechanism.

(5) There remains much mystery about the trajectory of larvae in the nearshore and shelf environments. Many aspects of the present conceptual models must be regarded as provisional, at best. As Epifanio (2007) remarks, with regard to the conceptual models applicable to the mid-Atlantic, they "lack rigor, and it is difficult to test the models in any quantitative way." This is even more true for the Texas coast, where there has been much less observational research on the development, transport and distribution of larvae and megalops.

5.4 Invasion of the megalops

Eventually, blue crab megalops "reinvade" the lower reach of the estuaries from the sea, usually in pulses of high density. Relative to the estuary, the megalop is considered the recruiting stage for blue crab (though there are occasional reports of early-stage juveniles being caught offshore). Once inside the estuary, the megalops are dispersed into shallower areas in which they colonize the bed, referred to as settlement (e.g., Scheltema, 1974, Forward et al., 2001). Here they molt

and metamorphose into the juvenile crab. The megalop stage is morphologically intermediate between larvae (i.e., zoeae) and crabs. Because of their swimming ability (see Section 2.3), megalops have more control over their movement than zoeae. Since they are subject to dispersal by currents and turbulence, but have ability for directed movement to desired habitats, they are ecologically intermediate between planktonic and benthic.

5.4.1 Immigration

Controversy surrounded this stage of the blue crab migration during the last two decades of the twentieth century, some of which lingers to the present. The patchiness of megalop distribution led to low densities in some collections (e.g., Dudley and Judy, 1971, who sampled May – November out 13 km on the North Carolina shelf, but took very few megalops, Epifanio et al., 1984, Brookins and Epifanio, 1985), leading some investigators to question whether megalops recruited to the estuary, but instead metamorphosed in nearshore waters whereupon the early juveniles invaded the estuary (Johnson 1985, Epifanio, 1988, McConaugha, 1988). Observations accumulated of coherency between the abundances of megalops and early juveniles in nursery areas. Orth and van Montfrans (1987), for example, reported a high association between the settlement of megalops and the density of early-instar crabs in grassbeds (*Spartina*, *Zostera* and *Ruppia*) in lower Chesapeake Bay. The interannual variation in juveniles tracked the same variation in megalop density, suggesting that it is the megalop supply that controls the abundance of young juveniles. Some physiological evidence for the reinvasion hypothesis was provided by the advancing of intermolt-to-premolt stage with distance into the estuary. Metcalf and Lipcius (1992) reported that the proportion of megalops in pre-molt stage increased with position at which they were caught, from offshore, into the estuary, and up into the upstream regions.

In the Florida Atlantic coast, Tagatz (1968a) collected relatively few megalops in the inlet or lower reach of the St Johns estuary, and few first or second instar juveniles (2-3 mm), and hypothesized that the metamorphosis to the first crab stage occurs mainly offshore. He offers no information on settlement of megalops, but observes that early stage juveniles (<10 mm) appear in the lower 40 km of the estuary in high-density “waves”, predominantly 6-9 mm, which is

consistent with the hypothesis that metamorphosis occurs offshore and early-juvenile crabs enter the estuary. Steele (1982) summarizes the sampling results of Tagatz, but does not appear to accept this hypothesis.

Adkins (1972a, 1982) reported that megalops were found in the Louisiana estuaries throughout the year, with peaks in February and November. Weekly samples in Whiskey Pass (one of the inlets to Terrebonne Bay) averaged over 1969-72 showed little seasonal variation apart from low numbers in December and January.

On the Texas coast, in the 1950-51 studies in Cedar Bayou, Simmons and Hoese (1959) observed "millions" of postlarval crabs migrating through the inlet in February and March, and noted their odd absence during May – August, despite spawning and hatching in the Gulf during this period. More (1969) summarized studies of plankton samples in the Texas inlets conducted by the Texas Parks and Wildlife Department (TPWD) during the period 1963-65, and identified two coastwide peaks of megalop immigration in spring and a smaller peak in late November. These samples were taken monthly, however, and an examination of the data shows the coastal averages to be distorted by individual large and small numbers. The "spring peak," for example, is driven by a single sample in Cedar Bayou whose concentration is five times the next largest (Matagorda Entrance Channel) measured during the entire study. The three-group (cohort) schema proposed by More (1969) for Galveston Bay (see 5.2 above) leads to a prediction of megalops entering the bay year-round (Group 1: April-June, Group 2: July-September, Group 3: October-March).

In the late 1960's, Texas Parks and Wildlife (TPWD) returned to Cedar Bayou, performing a 2.5-year study of migration through the inlet, reported by King (1971). Three platforms spanning the inlet held stationary plankton nets opening toward the sea to capture organisms entering Mesquite Bay. Megalop abundance fluctuated, with inconsistencies between the variations of the first and second years. King noted the pulse-like nature of megalop concentration, "waves" in his terminology. The first year exhibited a single peak in February-March, and the second year, three peaks in January-March, May-June (the largest) and October. There was no correlation between megalop abundance and the light/dark cycle, lunar phase, tide range, or wind

speed. There was, however, a positive correlation between abundance and salinity, which may simply reflect the entry of megalops on an incoming tide.

Lochmann et al. (1995) sampled *Callinectes* megalops in the center of the Matagorda Entrance Channel during the period April – August 1987. They used 335 μm plankton nets that were deployed closed and opened only while at a prescribed sample depth, profiles thereby being obtained at 2-hr intervals over 24 hours, on sampling runs in April, May, July and August. Megalops were found to be most abundant on the flooding tide (as determined from current measurements) and at night, the variation with tidal current being more pronounced. No variation with salinity was observed. (This year 1987 exhibited relatively high freshwater inflow, with peak monthly inflow in June, see Ward, 2010a.)

5.4.2 Mechanism

Another aspect of megalop reinvasion that was controversial during the last two decades of the twentieth century was its mechanism. Proposed mechanisms included inflowing tidal-mean (residual) currents at depth, wind-driven surface currents, tidally synchronized vertical migration, i.e. selective flood transport (SFT), and indirect wind-forced exchange (Epifanio 1988, 1995, McConaugha, 1988). Field studies in the lower reaches of the mid-Atlantic estuaries (e.g., Epifanio et al., 1984, Brookins and Epifanio, 1985, Little and Epifanio, 1991) indicated that megalops tended to be more numerous in the water column on the tidal flood, compared to the ebb, suggesting SFT (see Section 4.1.2). But most of these studies were confounded by the small numbers of megalops collected. An exception to this statement is the rigorous field work of Olmi (1994) in the York estuary in 1988-90. Olmi's data clearly portray a close relation between nocturnal flooding current and abundance in the water column. Although concentrations on the bottom were not measured, from study of their vertical distribution over time, he suggests that megalops rather quickly fall out of the water column at slack before ebb and ascend from the bed during flood. This is consistent with the rôle of fluid turbulence in stimulating vertical migration, see Section 4.1.2.

A key point at issue was the vertical distribution of megalops. Over the shelf and in the estuary mouth, field observations of vertical distribution of blue crab megalops established that they are located preferentially within the surface layer, particularly but not exclusively the neuston (Smyth, 1980, Provenzano et al., 1983, D.F. Johnson, 1985, Epifanio, 1995). This fact would appear to gainsay any mechanism of selective tidal current transport or transport by the bottom-layer inflow of gravitational circulation, since either would require a vertical migration. Thus researchers were led to a surface-transport mechanism. The wind was the usual suspect, but it was doubted that a wind-driven current, at least under normal prevailing winds, would be sufficient to overcome the freshwater-driven surface outflow from an estuary.

It was noted (e.g., Sulkin and Epifanio, 1986) that megalops were mostly—but not exclusively—concentrated in the surface layer in the vicinity of the estuary mouth, and did appear in lower layers and near the bottom, albeit in reduced numbers (see especially the data of Smyth, 1980, and D.F. Johnson, 1985). This re-admitted the possibility that SFT might be a mechanism for ingress to the estuary.

There are conflicting reports on diurnal variation of megalop concentrations, arising mainly from where the observations are made. Although some response of megalops to light (phototaxis) is exhibited in laboratory tests, there is disagreement in the literature as to whether it is positive (attractive) or negative (repellent), the majority indicating positive (see Section 4.1.1). There is also a pronounced circadian rhythm observed in the laboratory in which megalops swim upward to the surface during the time of daylight, and downward at nighttime. On the shelf, field observation would seem to confirm this, the higher concentration of megalops occurring during daylight (see Forward and Rittschof, 1994, Forward et al., 1995). This, however, is in contradiction to field observations in the lower reaches of estuaries, which report that megalops aggregate in greater abundance in the surface layer during nighttime (e.g., Sulkin, 1984, Luckenbach and Orth, 1992, Epifanio, 2007, who suggests that the field results may be an artifact due to limited nighttime field data from shelf waters). This conflicting behavior in estuary and shelf waters was verified in the laboratory by Forward and Rittschof (1994), who posit that megalop presence at the surface offshore facilitates transport to the estuary by wind, but once in the estuary the positive swimming response to light is reversed by chemical cues

specific to estuaries. Forward et al. (1997) substantiated this by more detailed experiments identifying specific chemical cues.

Within the estuary, vertical distribution of megalops in the water column becomes more homogeneous, due to the intensity of turbulence and the shallower depths compared to offshore (see McConaugha, 1988, and citations therein). Within the lower Delaware, Little and Epifanio (1991) found no significant difference between surface and bottom megalop concentrations. The upstream movement of megalops is now generally accepted to be selective flood transport. In waters characteristic of estuaries (though not necessarily in the physical bounds of an estuary), this selective flood transport (SFT) behavior becomes more complex. The migration to the surface at night and to depth during the day (Forward and Rittschof, 1994) is compounded with migration to the surface on flooding currents and to depth on ebbing (Epifanio, 2007). Therefore, after entering the estuary the megalops will be found in the water column, perhaps near the surface, on nocturnal flooding currents and on the bottom or at depth otherwise (Epifanio et al., 1994, De Vries et al., 1994). In the 16-month study of Mense and Wenner (1989) in tidal creeks around Charleston Harbon in 1986-87, megalops and early juvenile crabs occurred mainly in nocturnal surface samples and in daylight bottom samples. Their vertical distribution was reported to be consistent with the selective flood transport behavior observed in the mid-Atlantic estuaries.

Upward migration during (nocturnal) flooding tides, and downward migration during ebbing tides takes advantage of both the inward flooding current and the net upstream density current at depth. Selective flood transport is reviewed in Section 4.1.2 above, where it is remarked that two properties of estuary hydrography are necessary for selective tidal stream transport (STST) to operate: a horizontal gradient in salinity that can be advected by tidal currents, and the occurrence of flood current during a sufficient proportion of the night. The inflows into the mid-Atlantic estuaries usually ensure the former, and the semidiurnal tides ensure that the major portion of one flood cycle will occur at night.

In lagoonal estuaries, typical of those on the Gulf of Mexico coast, including Texas, exchange with the sea occurs through narrow inlets. While it is probable that something analogous to SFT

occurs in the bay as a mechanism for directed movement through the estuary, it is not clear that it operates within the inlet *per se*. A net influx of megalops can result from the transport of nearshore waters through the inlet on tidal flood with their high abundance concentrations, and the transport of bay waters, now with lower abundance concentrations due to mixing, out to sea on the succeeding tidal ebb, throughout which the megalops are simply carried as passive particles. In the megalop profiles of Lochmann et al. (1995) from the Matagorda Entrance Channel, vertical structure of megalop abundance was highly variable, its center of mass ranging randomly from near-surface to near-bottom with no correlation with either tidal current or time of day. Since the rise and fall of the center of mass did not exhibit the expected association with flood and ebb (respectively) of the tidal current, Lochmann et al. judged the data equivocal as to whether SFT was the invasion mechanism.

5.4.3 Settlement

Observations of settlement of megalops have confirmed their rôle as the main recruitment stage of the blue crab (e.g., Orth and van Montfrans, 1987). The swimming ability of megalops (Section 2.3) means that they have some ability to select or avoid settlement sites. The primary settlement regions in the mid-Atlantic estuaries are beds of submerged aquatic vegetation, preferentially seagrass beds (Orth and van Montfrans, 1987). Hines (2007) comments that the relative unimportance of salt marshes in Chesapeake Bay for settlement may be a simple consequence of the relative lack of salt marsh in the estuaries. He also notes that the limited salt marshes found on the central eastern shore of the bay exhibit the greatest production of blue crabs in the system. The value of seagrass habitat for food and shelter (Wilson et al., 1990, De Vries et al., 1994) is evidently enhanced by its degree of patchiness (see Hines, 2007 and citations therein), the smaller patches having much higher survival of crabs compared to larger, unfragmented seagrass beds.

In the Gulf of Mexico estuaries megalops generally settle throughout the year (Rabalais et al., 1995, Morgan et al., 1996, Guillory et al., 2001b, Minello et al., 2008). Marshes are the primary settling habitats, though seagrass beds where available are important (Thomas et al., 1990). Sites

were chosen by Morgan et al. (1996) in Mobile Bay and the adjacent Mississippi Sound to evaluate the relative effectiveness of vegetated versus nonvegetated, and seagrass versus marsh grass. Higher settlement rates were measured on vegetated sites, of which the settlement rates for marsh grass differed by several factors (either direction) from those of seagrass sites, though the data were so variable that this rate difference was not statistically significant.

A primary mechanism by which megalops direct their movement toward settlement sites is detection of odors. Forward et al. (2003c) performed careful laboratory observations of megalops swimming in a flume, and found that they swim toward odors characteristic of sea grass (*Zostera marina*) and salt marsh cordgrass (*Spartina alterniflora*), and away from odors of the predatory fiddler crabs (*Uca pugilator*) and grass shrimp (*Palaeomonetes pugio*). Crabs were also observed to swim away from odors of ammonium, though the reason is not clear. This might be a behavioral response to avoid low dissolved oxygen, which in estuaries is frequently associated with high ammonia concentrations (Tankersley and Wieber, 2000). Also, ammonia (the sum of ammonium ion NH_4^+ and NH_3) is a source of intoxication, and the rejection of ammonia through the gills can compromise the function of gills in osmoregulation (e.g., Romano and Zeng, 2012). Forward et al. (2003c) found also that these swimming behaviors were enhanced as the current speed diminished (i.e., approach slack water). This is consistent with the hydromechanics of dilution, in that the odors would be more concentrated in low-current conditions.

As reviewed in Section 3.3, the duration of the megalop stage is plastic, potentially ranging one to several months. The only certain fact is that the metamorphosis molt occurs shortly after settlement. This suggests that the megalop stage can be sustained as necessary for the megalop to find a satisfactory settlement site, whereupon something triggers molting. (For other crab species, there is a time limit beyond which metamorphosis must occur, but it is unknown whether this applies to the blue crab, see Forward et al., 2001.) As noted above, upon entering the estuary, the megalop is in intermolt stage, but as it moves further up the estuary, it advances through its various pre-molt stages. It is not clear whether proximity to suitable habitat dictates molting, or the molt stage dictates seeking a suitable habitat. Molting has been discovered to occur preferentially in daylight hours (Forward et al., 1996), but this is considered to be a

consequence of the suppression of vertical swimming during the day in estuarine waters, since the megalops are on the bottom anyway (Forward et al., 2001).

In the 1990s, evidence began to emerge that estuarine water, compared to offshore water, can accelerate metamorphosis of the megalops into the first crab stage (Wolcott and De Vries, 1994). Later laboratory work demonstrated that this acceleration to metamorphosis was in response to a complex of chemical cues, such as eelgrass (*Zostera marina*) exudates and humic acid, derived from wetland or terrestrial runoff and characteristic of upper-estuary waters (Forward et al., 1994, Forward et al., 1996, Forward et al., 2001, Epifanio, 2007). Essentially equivalent reductions in time to metamorphosis were exhibited by the three seagrasses, *Z. marina*, *Ruppia maritima*, and *Halodule wrightii*, and an even greater reduction by *Spartina alterniflora* (Forward et al., 1996). A similar reduction in time to metamorphosis is attributed to *Phragmites australis* (cited in Forward et al., 2001, but apparently never published). Some macroalgae reduce time to metamorphosis, e.g. *Ulva lactuca* but not *Gracilaria* (Brumbaugh and McConaugha, 1995). Time to metamorphosis is unaffected by a number of vegetation species, but no species is known that lengthens this time (Forward et al., 2001, and citations therein). Ammonia, though a chemical typically associated with estuaries, was determined to have the opposite effect, namely delaying metamorphosis (Forward et al., 2001), c*f*. the avoidance response to ammonia, discussed above.

It appears that a megalop in pre-molt may be more susceptible to the above chemical cues and it has been suggested that this is a stimulus to settle (Brumbaugh and McConaugha, 1995, Welch et al., 1997). Hasek and Rabalais (2001b) discovered that time to metamorphosis was substantially shorter, about a factor of two, for megalops collected during a pulse event versus those collected during low-level non-pulse settlement, for both plankton tows and artificial substrates (see Section 5.4.4 below).

The above notwithstanding, settlement may not be as directed a migration as it might appear. While there are evidently chemical cues that attract the megalops, an unknown proportion of the megalops do not encounter primary habitat and instead settle elsewhere. One of the chief attributes of seagrass beds is structure, and some alternative settling habitats are structured as

well, such as saltgrass marshes, oyster reefs, or debris on the seabed (Lipcius et al., 2007). Olmi et al. (1990) found considerable heterogeneity in both space and time, and inconsistency in the settlement habitat of megalops between seagrasses, plankton, and artificial structured habitat. Unstructured habitat, i.e., flat and open, is considered to present too much risk of predation for young instars. However, it is likely some megalops settle in unsatisfactory regions and perish.

5.4.4 Data from artificial-substrate collectors

Artificial substrates (synthetic-fiber "hogs-hair" air-conditioning filters) were first used in 1985 for blue crab megalop sampling at the Virginia Institue of Marine Science (Goodrich et al., 1989, van Montfrans et al., 1990) and have been widely used since. With these devices, megalops are sampled by random encounter, and are retained due to their "clinging" (thigmotactic), not by any particular attraction of this substrate for settlement. The chief advantage of this methodology is that it avoids the sparse-sample problem that plagues traditional plankton tows from a boat. In principle, a time series can be generated at whatever temporal resolution is practical for servicing the collectors. The disadvantage is that the samplers may not be measuring the settling process *per se*. Lipcius et al. (1990) found that artificial substrate collections were correlated with megalop abundance in the plankton, but not with settlement in natural habitats. On other hand, in the work of Olmi et al. (1990), artificial substrate data were not correlated with plankton, while plankton density and settlement in grassbeds were correlated (but these researchers note that these statistics are based on a single day of data and may not be reflective of longer-period associations). The apparent consensus among researchers is that the megalop substrate data are related to planktonic concentrations (Rabalais et al., 1995).

In the late 1990's, three studies were performed in the York estuary (lower Chesapeake Bay), two of which employed artificial substrates and one, stationary plankton nets. These three studies, conducted at the same location over about the same period, each developed a daily-resolution time series of megalop abundance over multiple years. The most important and fundamental conclusion from these three studies is that the episodic "pulse-event" behavior of megalop abundance suggested by plankton surveys is confirmed by the detailed time series.

Comparison of their results is instructive, however, in illustrating how substantial variation in megalop abundance arises, even with intensive daily sampling, and how different analyses with differing emphasis can lead to disparate conclusions about similar time series.

Sampling daily with artificial substrates during the late summer to early winter over four years in the York estuary (lower Chesapeake Bay), van Montfrans et al. (1990) determined the "settlement" time signal to be sustained periods (a few weeks) of low levels with imbedded pulse events of 1-3 days duration, shown in Figure 18. There was no year-to-year consistency in timing or magnitudes. However, these investigators noted an apparent association of megalop pulses with full moons, as exhibited in Fig. 18.

Goodrich et al. (1989) used the 1985-87 data from this project to evaluate causal connections to wind. They found 16 apparently stochastic pulses of high megalop concentration, of which 12 were associated with atidal high-water episodes at the pier that they interpret as wind events. From a separate analysis of a 32-year record of July-November Chesapeake water-levels with tides removed, Goodrich et al. found an average annual frequency of 10 high-water events in the five months of recruitment (July – November), a sufficient frequency, they concluded, to effect a substantial cumulative influx of megalops. These were assumed to be wind-driven events, moreover to be associated with synoptic disturbances and/or tropical storms. This is different from the smaller wind stress associated with normal prevailing winds.

There remains a question of the nature of the wind event, and whether the influx to the estuary is driven by Ekman transport (requiring northeasterly winds on the mid-Atlantic coast) or the direct stress of wind (requiring east or southeast winds). It is unfortunate that Goodrich et al. did not specifically compare their volume anomaly data to a time series of speed/direction of wind, to better characterize the nature of the meteorological event driving the response (and to better establish that these are indeed wind-driven). As noted above, van Montfrans et al. (1990) presented a later analysis of the 1985-88 data, in which they disclose a high association of the pulse events with the third lunar quarter, at and after full moons, but not with (astronomical) tides. The inference that megalops preferentially settle under moonlit conditions is, as noted by

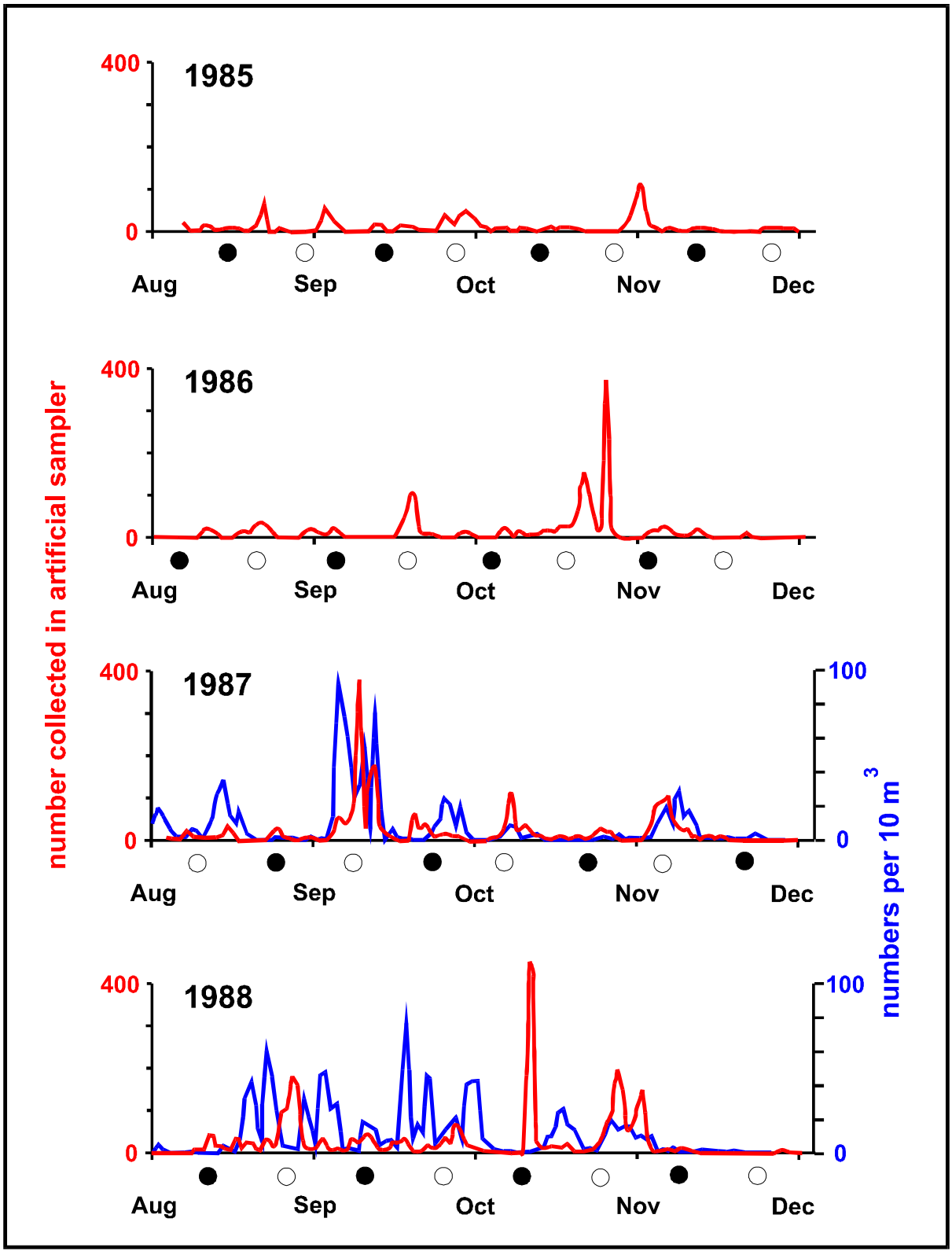


Figure 18 - Time histories of daily megalop collections on artificial substrates (red) and plankton nets (blue) in York Estuary, lower Chesapeake Bay, showing association with lunar phase. Redrawn from van Montfrans et al. (1990) and Olmi (1995).

van Montfrans et al., "counterintuitive," appearing ecologically detrimental as predation would be greatest. Though two authors are common to the Goodrich et al. and van Montfrans et al. studies, they do not reconcile the apparent conflict in causal rôles of wind events versus lunar phase.

During the period 1987-89, Olmi (1995) performed a dense series of plankton samples in the same area of the York, using stationary plankton nets deployed nightly on or about the time of maximum flood current, over the calendar period of recruitment (July – November). Two of his study years overlap with the data sets of van Montfrans et al. (1990). These are superposed on the plot of Fig. 18. Frequently, the two time series are consistent, but in much of the record they are spectacularly inconsistent. Olmi determined a significant association of pulses with wind stress directed to the west for all three years (i.e., a strong negative correlation between pulse and latitudinal component of wind stress). Association with lunar phase was weak: a number of pulses occurred during the new- or full-moon quarters, but there were also pulses at other points in the lunar calendar.

Olmi repeated the atidal (subtidal, in Olmi's terminology) volume calculations of Goodrich et al. (1989), and found a significant negative correlation ($|r| < 0.5$) with eastward wind stress. However, there was no compelling association between megalop pulses and atidal volume. In a multivariate regression, east-west wind stress was the single most important variable but the explained variance in megalop abundance varied from year to year. A weak correlation of abundance with north-south wind proved to be an artifact arising from the co-association between the two wind components. This implies that Ekman forcing is a minor factor compared to the effect of direct (local) wind stress. Olmi suggested that the apparent relationship of megalop pulses to the phase of the moon is due more to the added transport afforded by spring tides (in association with selective flood transport).

This most pregnant application of artificial substrates to megalop recruitment was a coordinated study by the Blue Crab Recruitment Group, a loose affiliation of academic and federal agencies, carried out at six sites on the Atlantic and five sites on the Gulf of Mexico coasts, summarized in

Table 7
Deployment sites for coordinated artificial-substrate monitoring
by the Blue Crab Recruitment Group, see text

Site	*Estuary*	*Monitored*	*Relevant citations*
Broadkill River	Delaware Bay	1989-92	Little and Epifanio (1991) Jones and Epifanio (1995)
Tangier Sound	Chesapeake Bay	1989-91	van Montfrans et al. (1995)
VIMS, York River	Chesapeake Bay	1989-92	van Montfrans et al. (1990, 95)
Middle Bay, NC	Pamlico Sound	1992	Mense et al. (1995)
Banks Channel, NC	inside Masonboro Inlet	1990-92	Mense et al. (1995)
South shore	Charleston Harbor, SC	1989-92	Boylan and Wenner (1993)
Fowl River, west shore	Mobile Bay	1991	Rabalais et al. (1995)
Fort Gaines Dauphin Is	Mobile Bay	1990-91	Rabalais et al. (1995)
Belle Fountaine Beach	Mississippi Sound	1991-92	Perry et al. (1995)
LUMCON	Terrebonne Bay	1990-91	Rabalais et al. (1995), Hasek and Rabalais (2001a)
Galveston USCG	Galveston Bay	1991-92	Rabalais et al. (1995)

Table 7. Replicate substrates were deployed and monitored during the recruitment season (July – November) over the period 1989-92. Consistent equipment and protocols were observed at all sites (Metcalf et al, 1995). Results are summarized for the Atlantic coast by van Montfrans et al. (1995) and for the Gulf coast by Rabalais et al. (1995), with additional analyses presented by van Montfrans et al. (1990), Little and Epifanio (1991), Boylan and Wenner (1993), Blanton et al. (1995), Jones and Epifanio (1995), Perry et al. (1995), Morgan et al. (1996), Hasek and Rabalais (2001a). The principal conclusions reported are:

(1) The megalop influx can be characterized as a low quasi-steady daily settlement with superposed episodic pulses.
(2) The pulses account for at least 50% of total July-November settlement at a site (the remainder being the steady daily settlement). The pulses are generally incoherent across years at a site, and incoherent across sites in a given year, though there are occasional pulses that occur synchronously at multiple sites. The lack of coherence between

Mississippi Sound and Mobile Bay (sites separated by only 60 km) is particularly notable.

(3) Correlation with lunar phase was exhibited at the York River and Charleston Harbor sites, where a clear 15-day cycle in megalop abundance emerged, after all results were standardized to a lunar month (day 1 = new moon). No clear relationships with lunar phase were found at the remaining sites on the Atlantic or the Gulf coasts.

(4) On the Gulf coast, in Terrebonne Bay (Hasek and Rabalais, 2001a), Mississippi Sound and Mobile Bay (Morgan et al., 1996), a well-defined association between the lunar-declination cycle and megalop settlement was found, *viz*. pulses occurring during small-declination (equatorial) tides.

(5) No statistical relationship was found between wind direction or wind speed and megalopal settlement at most of the sampling sites. While in specific years, an apparent relation appeared, mainly to onshore-directed wind, this relation was not manifest over all years of data. The effect of onshore winds, when strong, on settlement pulses was particularly notable on the northern Gulf of Mexico (Morgan et al., 1996, Hasek and Rabalais, 2001a).

(5) The rate of settlement in the Gulf of Mexico estuaries was about two orders of magnitude greater than in the Atlantic estuaries.

With respect to Conclusion (1), it is interesting to note that the genetic analyses of Kordos and Burton (1993) on megalops and blue crabs from the Texas coast yielded substantial heterogeneity in allelic frequencies, and discordance between the megalops and crabs, even in proximate samples. As a hypothesis to explain this, Kordos and Burton proposed that "sporadic major recruitment events occur against a background of low continuous recruitment, with the major pulses having the greatest impact on allelic frequencies."

Example data, from the Hatteras and Galveston sites, are shown in Figures 19 and 20, resp., illustrating the episodic nature of the megalop pulses. The lunar signal at the York River and Charleston Harbor sites showed megalop maxima roughly centered on the first and third

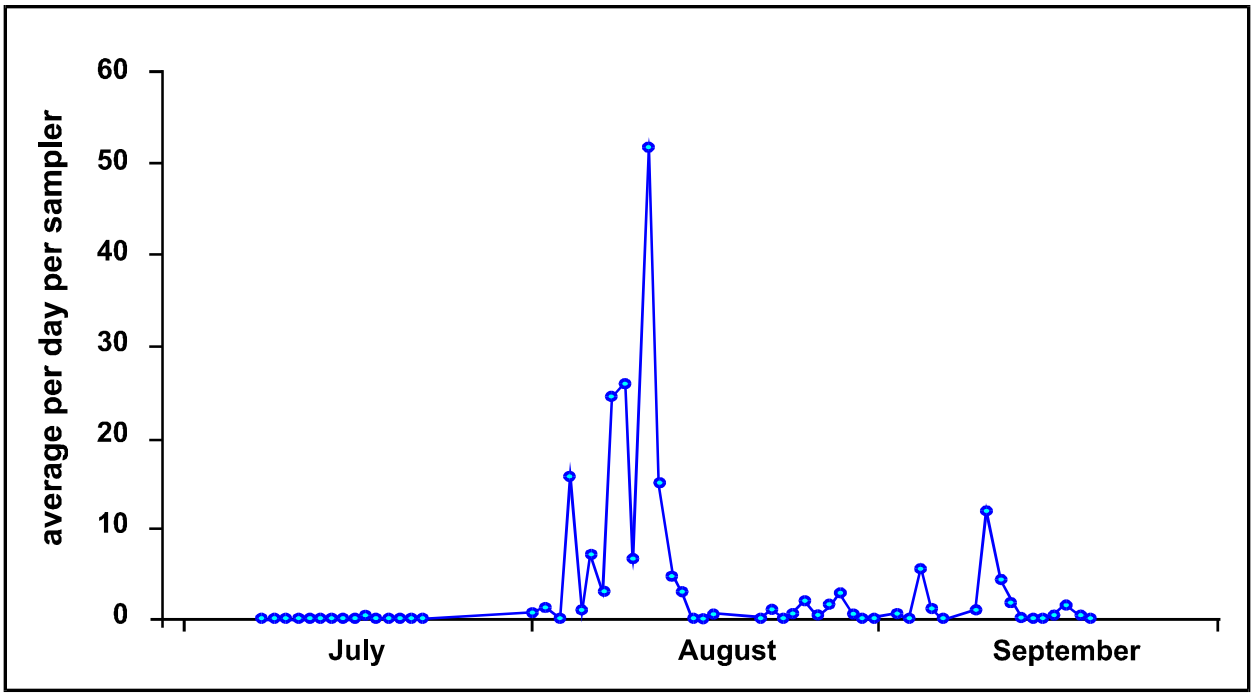


Figure 19 - Times series of megalop data from artificial substrates at Hatteras Inlet Coast Guard Station, data of Mense et al. (1995) replotted

quarters, the former being more consistent year-to-year (Metcalf et al., 1995, Boylan and Wenner, 1993). (There are therefore minima — in fact, zero at Charleston — at new and full moons.) There was no clear association of megalop settling with full moon events, even at the York River site. An additional site on the Georgia coast in the Duplin River was equipped with samplers (Wrona et al., 1995), but several samplers were lost to the swift tidal currents, and the data collection, covering only a few months, was disappointing. Nonetheless, the limited data are generally consistent with the conclusions above. More than half of the total settlement (in the limited period of data collection) occurred on a single day.

In addition to the two sites listed in Table 7, Morgan et al. (1996) monitored megalop settlement at one other site in upper Mobile Bay and two sites in eastern Mississippi Sound. These researchers correctly identified the lunar declinational cycle (in contrast to lunar phase, i.e. spring-neap cycle) as the primary lunar control on tidal range in the northern Gulf of Mexico

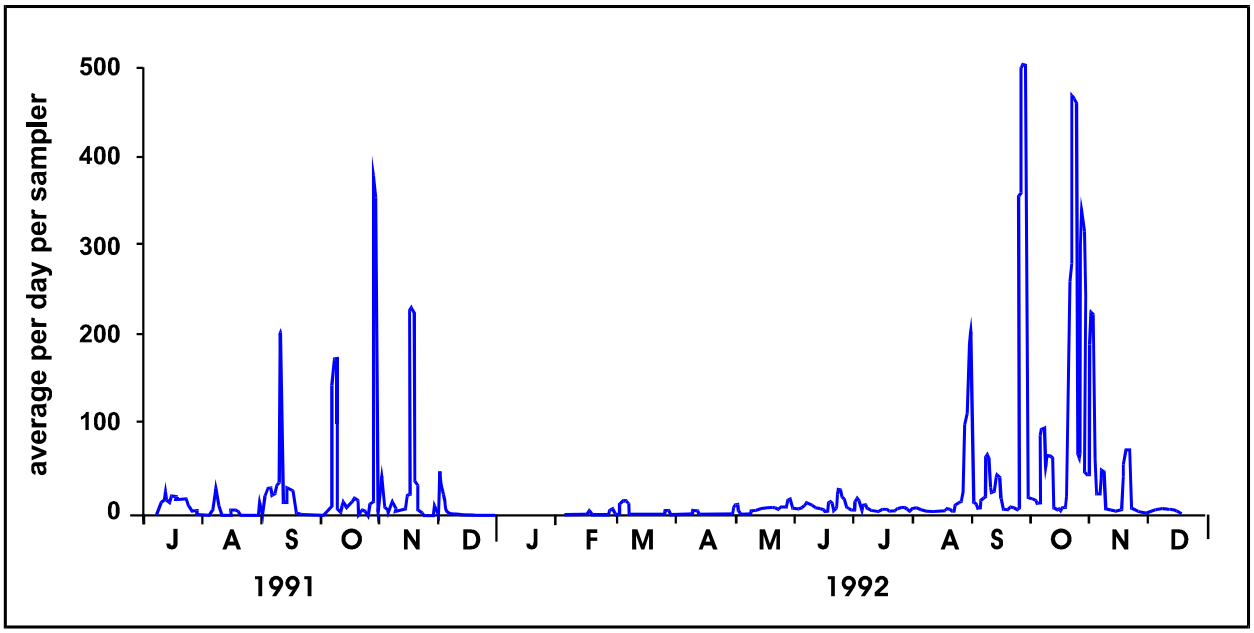


Figure 20 - Times series of megalop data from artificial substrates at Galveston Coast Guard Station, data of Rabalais et al. (1995) replotted

(see, e.g., Ward, 2010b). They found that pulses of settlement were strongly associated with onshore (south) winds, when these winds were strong, and with small declination tides. Winds parallel to the coast (i.e., east-west) were unrelated to pulse events, implying that Ekman drift does not make a substantial contribution to megalop transport into the estuary. Pulses were correlated with the phase of the moon only when lunar phase happened to be correlated with lunar declination. (The two slowly drift in and out of phase, see Ward and Montague, 1996.) There was no consistent difference between settlement at night and day. With distance up the estuary, settlement declined, while later molt stages became proportionately larger. Relatively few megalops were found to settle in the head of estuary. These researchers suggest that megalops prefer the higher salinities of the lower estuary.

Conclusion (5) above, from the Blue Crab Recruitment Group artificial substrate projects on the Atlantic and Gulf coasts, presents a conundrum (Heck and Coen, 1995). The measured megalop settling rates in the Gulf states (including Texas) were found to be one-to-two orders-of-magnitude greater than those measured in the Atlantic states, based upon identical sampling

protocols. Yet several studies of juvenile abundance in seagrass habitat in both regions, using the same sampling methodology (e.g., Thomas et al., 1990), indicated similar abundance values in both the Atlantic and Gulf estuaries. (To which one can add that the crab harvests on the mid-Atlantic greatly exceed those on the Gulf, though the lack of effort data makes such comparison hazardous.) How can these two facts be reconciled? Heck and Coen (1995) hypothesized that the young juveniles in the Gulf of Mexico settling habitats were decimated soon after metamorphosis by a greater intensity of predation. They speculate that the higher predation intensity might result from a greater diversity of predators in the Gulf of Mexico and a more stable seasonality (i.e., year-round predation). The predation hypothesis was verified by tethering studies on both coasts (Heck and Spitzer, 2001). In 1997 and 1998, the megalop settlement studies were repeated in Alabama (Heck et al., 2001, Spitzer et al., 2003), and though the settlement rates were lower than those found earlier (perhaps due to hurricanes), they were still at least an order of magnitude greater than those of the mid-Atlantic. In addition, the mortality remained high: within a few days after a pulse of settlement, the abundance of young juveniles receded to background levels, so that there was no correlation between large settlement events and post-settlement juvenile abundance. As noted in Section 4.4 above, this is consistent with density-dependent mortality, studied by Moksnes et al. (2003), which implies that the juvenile population is self-regulating.

Garvine et al. (1997) formulated a mathematical equivalent of the mid-Atlantic conceptual model of the blue crab growth and transport on the shelf, which included functional forms for grow out and mortality. The key to this model is the input field of current velocity (i.e., speed and direction), for which Garvine estimated currents based upon the known shelf circulation (Section 5.3), neglecting tides and variation in longshore current. "Settlement" in the model occurs when larvae aspire to the megalop stage at the entrance of the estuary. This model roughly simulated the four years of megalop data from the Broadkill (Table 7), which gave some credence to the underlying conceptual model. Tilburg et al. (2008b) coupled the circulation model application of Whitney and Garvine (2005, 2006) with an extended version of the Garvine et al. (1997) transport model of larval crabs. This circulation model is a variant of the Princeton Ocean Model, and was implemented for Delaware Bay and much of the adjacent shelf, 110 km upcoast

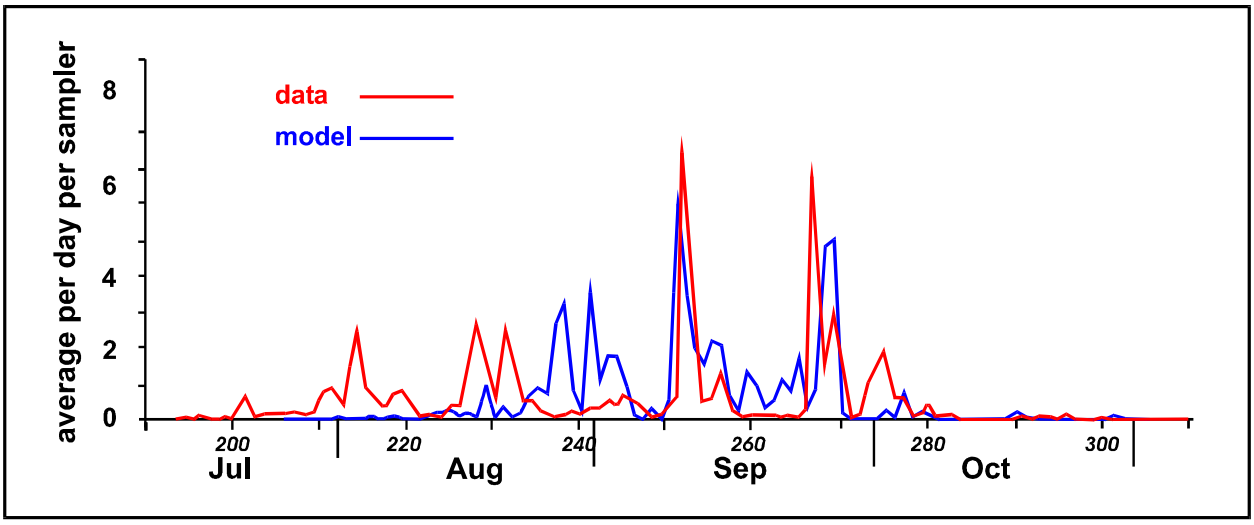


Figure 21 - Observed (red) and modeled (blue) imes series of megalop data from artificial substrates at Broadkill station, Delaware Bay, see Table 7. From Garvine et al. (1997) and Tilburg et al. (2008b) replotted

and 230 km downcoast, out to the 100-m isobath, see Whitney and Garvine (2005, 2006). A constant rate of egg release over the spawning season was specified as a model input. Model results were compared to the artificial substrate results from the 1989-92 Broadkill station in the Delaware (Table 7). An example from the four years of simulation is shown in Figure 21. While the model could not be described as validated, the results are encouraging, in that the model displays pulse settlement events that show some similarity to the observed time series. (Figure 21 is neither the best nor the worst of the four years simulated.)

One of the several weaknesses of the model application enumerated by Tilburg (2008b) was the assumed constant hatching rate. To operate the model with realistic hatching data, field observations were needed. Tilburg et al. (2008a) conducted field studies of Phase II migration of ovigerous females in the Delaware, from the brooding grounds in the lower estuary, through the mouth, into the hatching grounds of the coastal ocean. The egg stage was used to estimate timing of larval release for each crab. With egg stage as a predictor, a time series of larval hatching was developed. This showed a release of larvae in pulses into the nearshore from June – October with peaks in July and August. The model was then used to simulate the dispersal of larvae in the nearshore shelf and the subsequent "settlement" under two scenarios: a best-fit time

function to the projected hatching data, and a constant rate of larval release. The two scenarios produced nearly the same pulsed temporal pattern of megalop settlement. This implies that this settlement time pattern is the result of offshore physical processes, not the details of the supply of first-stage larvae. (The magnitude of the larval-hatching pulses did influence the simulated magnitudes of megalop settling pulses, but it is the pattern, not its specific magnitude, that is of concern here.)

The attraction of being able to generate a temporally detailed time series of megalop concentrations with a fraction of the labor-intensity required of frequent plankton tows has fueled a growing popularity of artificial-substrate collectors. Forward et al. (2004a) presented results from a seven-year (during 1993-2002) deployment of collectors moored in the Newport River estuary. While a definite association with neap tides was found, Forward et al. regard this as a coincidental consequence of the neap tides generally coinciding with tidal flooding events in darkness, a combination that favors the transport of the megalops. No relation was exhibited between settlement events and either cross-shore or longshore winds. Ogburn et al. (2009) employed artifical-substrate data from the same general area of the Newport estuary entrance for the period 2004-06, finding positive correlations of settlement in the estuary with winds favoring onshore Ekman transport, onshore winds, and the duration of nighttime tidal floods. Which mechanism was predominant varied, however. Hurricanes, when they occurred, were associated with the highest abundances.

A recently reported study, by Eggleston et al. (2010), is based upon ten years of deployment of artificial-substrate collectors in the Pamlico-Albemarle system (Croatan-Albemarle-Pamlico Estuarine System, CAPES) at as many as ten stations simultaneously. The substrates were deployed daily during the late summer to mid-fall, typically August – October. Although large numbers of megalops were measured at Hatteras and Oregon inlets, they did not appear to disperse through the CAPES system under normal hydrometeorology, though tropical storms and hurricanes apparently achieve effective dispersal. Settlement at inshore stations was sensitive to the particular storm tracks. Generally, the researchers conclude that tropical storms and hurricanes are important for settlement through the CAPES. Under other conditions, the settlement at Hatteras and Oregon was highly correlated with northeasterly winds, to which

Eggleston et al. attribute Ekman transport into the inlets. However, the southern inlets (Ocracoke and Drum) logged much lower settlement rates, even though these would be expected to experience even greater Ekman transport under these wind conditions. Several hypotheses are offered for this "recruitment shadow".

Another recent study Bishop et al. (2010) conducted on the Georgia coast employed passive megalop collectors to sample settlement in marshes. They found that winds providing Ekman transport into the coast, i.e., winds directed to the SW, were unable to account for the settlement events as well as onshore-directed wind just prior to the settlement event.

It is indubitable that passive collectors represent a minor revolution in measurement of megalopal transport into an estuary. They are inexpensive, physically robust, and convenient. They are impervious to the operational problems that plague electrometric instruments, and provide a temporal resolution limited only by the frequency of service that the user is able to maintain. But they also have a major limitation, in that they measure the integrated number of megalops that intersect the collector surface during deployment. This is a number that varies with the dimensions of the collector, its exposure to currents, the details of the fabric, and geometrical configuration of the substrate. To cross-compare the results of two samplers, it is mandatory that they be of identical construction, and be deployed and serviced using exactly the same procedure. This, indeed, was the motivation behind the protocols established for the Blue Crab Recruitment Group (Metcalf et al, 1995). Even at this, however, the measurement cannot be related to a physical density because the volume of water sampled is unknown. This is in contrast to the standard plankton net deployment, which includes a flow-meter measurement of the volume of water passing through the net structure. The passive collector is, at best, an index to megalopal flux, but without a calibration relation, it is not an absolute measurement.

At present, the aritifical-substrate passive collector is a promising methodology that requires additional research and development. There are indications in the literature that artificial-substrate data is intrinsically noisy, in that replicate collectors are needed at a site to ensure "statistical efficiency", or to "stabilize variance" (e.g., Metcalf et al, 1995). These statistics need additional study, and reporting of the data needs better statistical characterization. Cylindrical

collectors would appear to offer an advantage over planar collectors in presenting the same cross section to the current independent of its direction, but the effectiveness of this cross section (i.e., the distribution of the angle of flow intersection with the curved surface) is an unknown function of size. There may also be a nonlinear response to currents due to higher speeds purging megalops from the collector. Finally, more studies are required to quantify exactly what property is measured by an artificial substrate. Its dimensions are the flux of megalops, i.e., numbers per unit area per unit time, but the transfer per unit time is through some unknown, and possibly curvilinear, surface. A true cartesian flux could be divided by the normal current speed to obtain density. This is in fact measured by a conventional plankton net. This is suggestive that the collector measurement is related to the planktonic density of megalops. However, the comparison of plankton density of Omni (1995) with collector data of van Montfrans et al. (1990) in the York, shown in Fig. 18, is a glaring demonstration that the measurement question has not been answered satisfactorily. Whether the megalop collector measurement in the water column bears any relation to actual settlement on habitat substrates likewise remains unresolved.

5.5 Recruitment and the rise through the ranks

5.5.1 Early juveniles

Megalops are now generally accepted as the stage of the blue crab that recruits to the estuary. At metamorphosis they are inducted into the benthos. As they age, the early juvenile crabs undergo further "processing" by the ecosystem resulting in variations in abundance and dispersion, until the survivors achieve a size sufficient to be recruited into the pelagic population, during which they migrate throughout the extent of the estuary, especially into the upper reaches. Although the beginning and end points of this phase of the crab life cycle are well known, the intermediate stages, which may include at least one more migration, are only now being detailed by observation. Suction sampling, i.e., pumping out a drop net, is the favored methodology for sampling these early, and very small, juveniles, see, e.g., Zimmerman and Minello (1984), Orth and van Montfrans (1987), Rozas and Minello (1997).

In Chesapeake Bay, from the data of Orth and van Montfrans (1987) and Pile et al. (1996), juveniles less than about 4.3 mm (first and second instars, see Fig. 12) appear in the grassbeds and in unvegetated marsh creeks in the lower reach of the estuary during the period August-December, peaking in September, with densities in grassbed habitat an order of magnitude greater than in creek habitat. Orth and van Montfrans (1987) performed neuston tows to quantify the megalop concentration at the same stations, whose year-to-year magnitudes were found to be coherent with those of the early juveniles in both habitats. Of course, the megalop supply does not *per se* account for the difference in population of grassbeds versus marsh creeks. This is attributed to active selection by the megalops (see 5.4, above), passive settling due to the friction-element drag of seagrasses on currents, and differential predation in the two habitats (see also Pardieck et al., 1999).

With time, juveniles about 7.5-11 mm (fifth or sixth instars, see Fig. 12) appear in the marsh creeks, evidently migrating from the seagrass beds. After they exceed about 16-20 mm (ninth or tenth instars, Fig. 12), they are found preferentially in shallow unvegetated habitats. Apparently, these juveniles are of sufficient size that the benefits of larger prey to be found in the open areas of the estuary bed outweigh the risks of predation. At this stage, they vacate the primary nurseries, and disperse many tens of kilometers mainly into the upper reaches of the estuary (Hines et al., 1995, Pile et al., 1996). While less than about 70 mm, they still seek protective cover from predation, mainly cannibalism by larger crabs (Hines and Ruiz, 1995), such as grassbeds and detritus, and lacking this, shallow nearshore habitat such as the fringe of salt marshes and muddy ponds. As the crabs grow, they occupy progressively deeper waters.

A similar set of processes operates in the Albermarle-Pamlico system, but the dispersal from the primary nursery habitats apparently occurs somewhat earlier in the crab's development. Here early juveniles (first – second instar) are found in the seagrass beds behind the barrier island, mainly adjacent to the inlets through which the megalops enter, then after about a month third-fifth instars appear on the opposite shore some 50 km distant (Etherington and Eggleston, 2000, Blackmon and Eggleston, 2001). The crabs appear to accomplish this by swimming to enter the water column then being carried by currents. There are some early provisional indications in the Chesapeake that SFT may be involved (Blackmon and Eggleston, 2001). In CAPES, significant

tidal currents occur only within a few kilometers of the inlets in the Outer Banks, otherwise circulation in the system is wind-driven. Etherington and Eggleston (2003) determined that the dispersal was effected by seasonal wind events. Forward et al. (2004b) studied the CAPES juveniles and found an endogenous circadian swimming rhythm in which the crabs were active at night, which would minimize predation during dispersal. Using mark-recapture methods, Etherington et al. (2003) determined that the first and second instar population behind the barrier island suffered significant reductions, about equally due to mortality (mainly predation) and emigration. Further studies of the juveniles in seagrass beds adjacent to Oregon Inlet (Reyns and Eggleston, 2004) disclosed that the juveniles in the plankton were first instar, and their density was best explained by the density of early juveniles in the seagrass beds. Here planktonic dispersion was initiated at an even earlier stage of the juveniles development, and was a clear response to increasing density of juvenile blue crabs in the seagrass bed. This dispersal as a pathway from the nursery beds to the inland shore of CAPES was basically confirmed by plankton transects (surface and bottom) across the open waters, in which the juveniles were dominated by first instars (Reyns et al., 2006). This study also found the presence of megalops in the same samples across the Sound (Reyns et al., 2007), suggesting that the range of megalop settling within CAPES inferred from passive collectors may be underestimated.

The movement of early-stage juveniles from the primary nursery habitats has been termed "secondary dispersal" and is considered to be essentially planktonic, whether tidal (such as in the Cheasapeake and Delaware) or nontidal (as in the Pamlico-Albemarle). Lipcius et al. (2007) propose a revised conceptual model (evidently based on work up to about 2005) in which megalops are conceived to colonize primary nursery habitat, but many of the newly metamorphosed first-instar crabs, and perhaps other early instars, are forced to emigrate elsewhere in the estuary due to high densities, comprising secondary dispersal. Consonant with the earlier conceptual model, later juveniles, from the fifth to the tenth instars, are considered to migrate to other nursery habitat better matched to their size, both structured and unstructured. The attraction of unstructured shallow bottoms for older juveniles may be greater density of infauna, notably mussels and clams.

Mense and Wenner (1989) studied megalops and early stage juveniles in tidal creeks around Charleston Harbon in 1986-87. Megalops and early stage juveniles were distributed through the estuary, but megalops were more numerous in the lower polyhaline station, while early-stage and other juveniles became more numerous with distance up the estuary. Juvenile (mean CW 15 mm) densities were found to be much greater in unstructured sandy-mud habitats than structured marsh or shell-hash. The first, late-summer samples of Williams et al. (1990) in Perdido Bay in the Gulf of Mexico were predominantly juveniles less than 5 mm, which then shifted to 5-10 mm in October and November, then greater than 10 mm in winter, probably reflecting growth of the late-summer cohort. In Mobile Bay, post-settlement dispersal is considered to be limited by predation, especially of small juveniles (Heck et al., 2001).

5.5.2 Late juveniles and adults

Norse (1977) and Williams (1984) note the wide range of habitats used by *Callinectes*, including seagrass beds, marshes, mud and sand bottoms, rock substrates, wood detritus and mangroves, from which Lipcius et al. (2007) conclude that *C. sapidus* "exhibits no preference for a specific habitat type." Adkins (1972a) remarks that the blue crab "occupies almost all available habitats in coastal Louisiana" from freshwater to marine salinity. Similarly, Sánchez and Raz-Guzman (1997) found blue crabs to be "distributed throughout the lagoon [Laguna de Términos, in the southwestern Gulf of Mexico] independently of a particular habitat type". Peterson and Turner (1994), using flume nets in a Louisiana marsh, determined that blue crabs were much more abundant at and around the marsh edge than in the interior of the marsh. Minello (1999) presents a valuable compilation of measured densities of estuarine species, including the blue crab, in various habitat types in the bays of Texas and Lousiana (excepting the chenier plain), showing the highest densities in *Spartina alterniflora* marsh edge, followed by submerged aquatic vegetation, about six times the density of shallow nonvegetated bay bottom. Minello and Rozas (2002) and Minello et al. (2008) also found the edges of marshes to be the preferred habitat for juvenile blue crab, their abundance declining about 50% within 5 m into the marsh from the edge and 1 m out from the edge in the adjacent water. Their data were predominantly juveniles less than 15 mm, mainly 5-10 mm. Densities in shallow (< 1 m) unvegetated open water versus salt

marsh were comparable, with somewhat higher densities in the shallow water for the smaller juveniles. The larger juveniles favored the marsh habitat, and integrated over all sizes, the marsh was found to have about four times the standing crop of open shallow water. Later, similar results were found in St. Andrews Sound on the Florida panhandle (Rozas et al., 2012).

In the work of Heck et al. (2001) in Mobile Bay, late juveniles were found in similar densities in the secondary habitats as observed on the mid-Atlantic. Adkins (1972a) reported crabs less than 50 mm in the marshes and bayous in upper Vermilion Bay (Louisiana), and as these crabs attained sizes of 80-85 mm, they moved into the bays and larger bayous. Williams et al. (1990) reported juvenile habitat selection behind Ono Island, part of the barrier system of Perdido Bay, Alabama. Substantially higher densities were found in grass bed habitat (*Halodule wrightii*) than unvegetated sand bottom.

While salt marsh is generally the preferred habitat in Texas as elsewhere on the northern Gulf of Mexico, there does not seem to be systematic movement from structured to unstructured habitat as the crabs age, but rather a vacillation between the two habitat types. Zimmerman and Minello (1994) and Minello et al. (2008) found generally similar presences in vegetated and unvegetated areas for crabs ranging 20 mm to 50 mm. In both of these studies, there was a tendency for higher abundance of early juveniles in the unvegetated habitat, reversing in the 20-30 mm sizes. The better size resolution of Minello et al. indicates that juveniles < 10 mm (the first five instars, see Fig. 12) preferred unstructured shallow water to marsh vegetation, this preference reversing above 10 mm. In West Bay, of the Galveston system, Trent et al. (1975) found higher densities of blue crabs in *Spartina* marsh than in adjacent boat canals and open bay. These data were taken by trawl, so it is likely the crabs exceeded 20 mm. It appeared that the crabs were migrating into the marsh areas at night, then returning to the boat canals during the day. None of the observations precludes a movement into bays and bayous around sizes of 80 mm, as observed in Louisiana.

As the crabs approach maturity, they become widely dispersed through the estuary, especially males, which range from the upper reaches to the mouth, though with higher concentrations in the former. Though late juveniles abandon the sheltered shallows for deeper, unstructured

habitats, they continue to return to the shallows at the most dangerous times of their life cycle, when they molt (Section 3.1, Wolcott and Hines, 1990). In most estuaries, these shallows are found in the upper reaches of the system, which also occur in zones of lower salinity. Hines et al. (1987) observed pre-molt males moving upstream and post-molt males moving downstream in the Rhode estuary. They suggest that the males were seeking lower salinity for molting. The same type of sorting, males into shallow waters in the upper estuary, and females in deeper waters in the lower estuary was observed by Ramach et al. (2009) in an embayment within the Onslow Bay bight, North Carolina. Salinities are near-oceanic and homogeneous, so the partitioning cannot be due to salinity preferences.

In Charleston Harbor, the distribution of juveniles by salinity shows a largely homogeneous frequency from 0 to 21‰, with little difference between males and females (Archambault et al., 1990). Mature crabs are more prevalent in salinities 21-35‰, and, interestingly, the size distributions are very similar for males and females. While this might suggest that the divergence of male and female populations upon maturity of the mid-Atlantic is not exhibited in the South Atlantic, the logistics of the trawling of Archambault et al. (1990) precluded sampling in the shallow regions of the estuary, so the contribution of this part of the population is unknown. It is likely, however, that the mature and market-size crabs are concentrated where the trawling was performed, and likewise the inference that mature crabs also migrate to the higher salinity regions of the estuary.

As fall water temperatures drop with the approach of winter in the mid-Atlantic, both males and immature females move to the deeper sections of the upper and central estuary to overwinter (Aguilar et al., 2005, Hines, 2007). Often the males disappear from the upper reach habitats, moving into the open bay (Hines et al., 1987). In Weeks Bay, a secondary estuary of Mobile Bay, McClintock et al. (1993) focused on unvegetated habitats, and found little predictable seasonality in the crab population, but rather “long periods of relative stable abundance” punctuated by sporadic peaks. Juveniles were dominated by males, but adult males were found only near the mouth of the bay, suggesting that they migrate into Mobile Bay.

Typically in the mid-Atlantic, subadult and adult male crabs do not engage in long-distance migration, but rather limit their movement to normal meandering for foraging or avoidance. They tend to stay in their home estuaries, though a minority (about 1%) of tagged females have turned up in adjacent systems (Hines, 2007). An analysis of historic 1925-48 tagging data in the Chesapeake (Miller, 2003) shows that males moved an average of 9.9 ± 16.4 n.m. (18.3 ± 30.4 km) from point of release to point of recapture. The largest seasonal movement occurred in fall, averaging 17.3 ± 23.3 n.m (32.0 ± 43.2 km). In comparison, females were found to average 32.3 ± 35.5 n.m (59.8 ± 65.7 km). After mating, the females begin their spawning migration (Section 5.1). If the seasons of the spawning migration are averaged separately, rather than being combined with foraging, the distances are much greater, 41.5 ± 43.5 n.m. (76.9 ± 80.6 km) in summer and 47.6 ±34.5 (88.2 ± 63.9 km) in fall, which includes selective tidal stream transport.

In tagging studies in the St. Johns estuary (Florida), Tagatz (1968a) discovered that a substantial portion of males also migrate downstream over the course of the year, some migrating several tens of kilometers. In fact, about 2% of the males migrated south to other watercourses via the Intracoastal Waterway, and to the ocean, mainly in the fall and early winter. In Texas, as noted earlier, Daugherty (1952) observed both male and female crabs emigrating through Cedar Bayou, females outnumbering the males about 2 to 1. Daugherty (1952) interprets the occurrence of large males in the inlet to be from a "static population" in the area, rather than a migration.

The greatest reported distance found in this brief literature survey was one of the crabs tagged in upper Chesapeake Bay by Aguilar et al. (2005), later captured in Flagler Beach, Florida, 1040 km down the coast. Two of the tagged releases of Tagatz (1968a) out of more than 11,500 in the St. Johns estuary were retrieved over 500 km away, apparently following the Intracoastal Waterway. Two tagged crabs released in the eastern Gulf of Mexico were retrieved 500 km up the western coast of Florida (Oesterling and Evink, 1977, Oesterling and Adams, 1982).

A recent discovery of concentrations of blue crabs in shoals lying 20-30 km offshore from Atchafalaya Bay and Terrebonne Bay in the Gulf of Mexico (Gelpi et al., 2009, Condrey and Gelpi, 2010) raises questions about the life cycle of the blue crab. The first question is whether the rôle of offshore habitat has been properly considered. These 3-6 m shoals, relict barrier

islands, were found to be extensively used for spawning and pre-spawning foraging by mature females. Salinity during trawling ranged 25-35‰. The size of the crabs reported ranged 110-182 mm. Only 1% of the crabs was male, and about 0.5% of the females had recently mated. This population of crabs spawns at least from April through October. From the observations and analyses of Gelpi et al. (2009, see also Condrey and Gelpi, 2010) it appears that these crabs were spawning continuously, producing and hatching a new sponge every 21 days. This translates to production of seven or more sponges over the spawning season. While an implication of this remarkable discovery is that mating of blue crabs can take place in waters other than estuaries, the question is raised as to how the 90% of the females that were either inseminated or ovigerous had been impregnated with such a small representation of males. A likely explanation for their presence on these shoals is that they are émigrés from the estuaries on their seaward migration to hatch.

The effect of storm events on the movement of crabs on the shelf has generally not been adequately addressed. It is safe to assume that these crabs are largely carried by prevailing currents. However, storm winds have a greater disruptive potential, not only in generating locally intense currents, but also in the accompanying wave action, which becomes particularly intense in nearshore shoal water. There is anecdotal information suggesting that wind-tide currents are strong enough to sweep mature crabs along and beach them. Van Engel (1982), for example, reports that in February 1964, dead female blue crabs by the thousands washed up on the ocean beach at Virginia Beach. Their shells were chalky, having been smoothly abraded, apparently by being dragged over the sediments by currents. He noted that similar abrasions on dead crabs were reported by crab dredgers after a mid-Atlantic storm in March 1969.

6. THE BLUE CRAB IN SAN ANTONIO BAY

6.1 Data sources

Texas Parks and Wildlife Department (TPWD), or its predecessor agency (Texas Game and Fish Commission, TGFC, née Texas Game, Fish and Oyster Commission), has collected biological and hydrographic data in the Texas bays since the nineteenth century, and in the Coastal Bend bays certainly since the 1940's, perhaps earlier. The failure of the blue crab fishery in Aransas Bay in 1945-46 led the TGFC to institute a blue crab investigation focusing on the Mesquite Bay region (Daugherty, 1952). Sampling stations were monitored in Aransas, Mesquite and San Antonio Bays as well as in Cedar Bayou. Nearly two decades later, in the late 1960's, B.D. King conducted a major investigation of migration through Cedar Bayou (King, 1971). The San Antonio Bay Freshwater Inflow Study was undertaken jointly by TPWD and Texas Water Development Board in the early 1970's, co-directed by Ray Childress and B.D. King, and reported in Childress et al. (1975).

These studies were all special-purpose, with specific objectives, for which sampling strategies were devised and sampling carried out for limited time periods. To evaluate the longer-term, large-scale variation of the abundance of specific organisms like the blue crab requires an established, consistent sampling program, with a continuing commitment in staff and equipment. The Coastal Fisheries monitoring program of TPWD provides quantitative data on abundance of various aquatic species in the Texas bays and Gulf of Mexico nearshore zone, using standard biological collection gear and consistent protocols, which enables comparisons from bay to bay, and over an extended period of time. Details of the gear used and protocols observed are given in TPWD (1999). This is the data set employed in the analyses presented in this report, in particular collections by otter trawl. Some analyses address the individual trawl events, but most aggregate and average the data to better exhibit patterns in space or time.

Uniformity in TPWD data collection procedures for routine monitoring (in contrast to special-purpose research projects like those listed above) has been enforced coastwide since the 1970's,

and digital logging of the data has been carried out since about 1975 (varying from bay to bay and with the type of gear).*

In this evaluation, the focus is upon gears that allow estimation of the volume of water sampled, so that organism density may be calculated. Gill nets and similar passive devices do not satisfy this condition (unless equipped with a recording flowmeter). Both trawl and bag seine entail well-defined movement of a known cross section through the water, so the catch data may be converted to density, either areal or volumetric. The necessary arithmetic is given in Appendix F. In this study, volumetric density is used exclusively, though numerical results for otter trawl may be converted to areal density by multiplying by the effective height of the trawl opening (0.5 m). Both bag seine and otter trawl data have become available for all of the bays since the mid-1980's (though for most of the bays, the record begins somewhat earlier than this). Trawl data is of greater interest in the present context because this gear measures the abundance of the larger blue crabs in the open waters of the bay, so it targets the late juveniles and adults. Bag seine, in contrast, typically samples smaller juveniles in the nearshore shallows. (Moreover, data from the two types of gear are not comparable, apart from their different targeted life stages, because their sampling efficiencies are different.)

6.2 General assessment of blue crab abundance

In Table 8, the average biomass density for the twenty-year period 1986-2005 for each of the major bay systems of Texas is tabulated, for both bag seine and otter trawl. Biomass was obtained by first converting carapace width of each crab measured to crab mass using the Pullen-Trent relation (Table 1), then determining the total biomass for all crabs in each sample (bag-seine pull or trawl tow) as the total crab count in that sample multiplied by the average biomass

* The earliest use of the then new-fangled high-speed digital computer for analysis of standard biological collections by TPWD that this writer has been able to locate is the San Antonio Bay Freshwater Inflow Study (Childress et al., 1975). Trawl and bag seine data, along with water chemistry and physical observations were entered on custom coding sheets and keypunched by TWDB staff in Austin. Unfortunately, over the years, with changes in computer systems and in data-storage technology, the punched cards and the later digital files from this effort appear to have been lost.

Table 8
1986-2005 average biomass density of seined and trawled blue crabs
in TPWD Coastal Fisheries collections by major bay system, in mg/m^3

estuary	*bag seine*	*otter trawl*	*estuary*	*bag seine*	*otter trawl*
Sabine Lake	118	103	Aransas-Copano	74	101
Galveston Bay	147	66	Corpus Christi	117	43
East Matagorda	136	81	Upper Laguna	80	74
Matagorda	45	52	Lower Laguna	73	112
San Antonio	71	147	*average over all bays*	96	86

of the crabs measured (because widths are measured for a subsample when the number of crabs caught is large). This gives biomass in grams for the crabs in each sample. This was converted to a density by dividing by the volume of water intercepted by the sampling gear.* As described in Appendix F, for the trawl this is the volume intercepted by the area of the trawl opening times the distance that the trawl is towed. For the bag seine, this is approximately the surface area across which the seine is pulled times the average water depth. Both bay seine and trawl data are given in Table 8. Data for bays other than San Antonio are from Sutton and Wagner (2007).

An inspection of Table 8 identifies several interesting facts about the distribution of blue crabs on the Texas coast. There is no down-coast decline in otter-trawl crab abundance from the less saline to more saline bays. In fact, both sections of the Laguna Madre exhibit higher abundances than Galveston and Matagorda Bays, and the Lower Laguna higher than Sabine Lake. There seems to be a substantial depression in abundance in Matagorda Bay, evident in both the bag seine and the trawl data. As measured by otter trawl, blue crabs are more abundant in San Antonio Bay, by a substantial margin, than any other bay.

* This conversion to density is really less than it might appear to be, because in effect it applies a constant multiplier to the enumeration data, or, in the case of the trawl, the enumeration per unit time of towing, and therefore does not alter any statistical relations that might be uncovered about abundance variation or its relation to external factors. Its advantage is that it converts the dimensions of count or mass per sample event to a physical quantity.

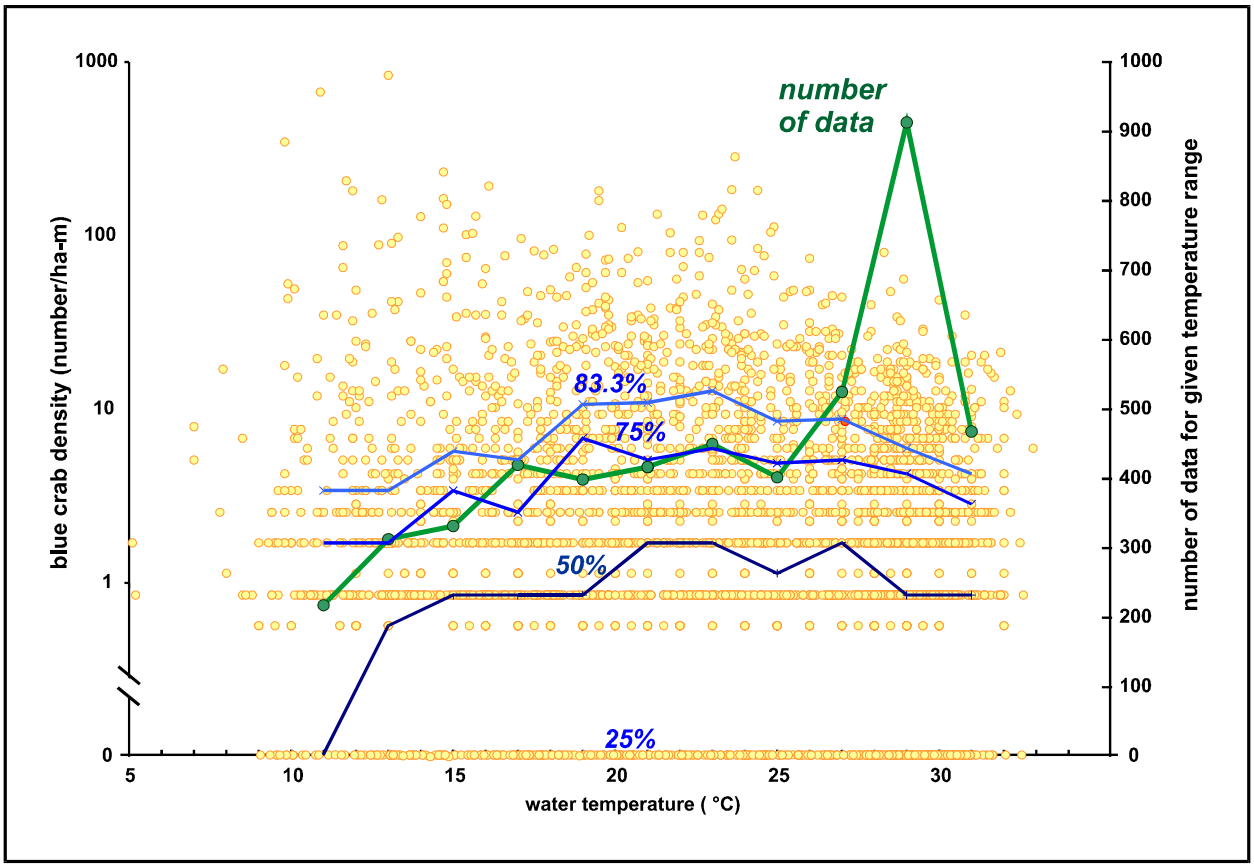


Figure 22 - Blue crab density for all 1982-2008 otter-trawl samples from San Antonio Bay vs concurrent water temperature (small filled circles), quantile values (lines) based on 2-degree bins, see text. Density values plotted on logarithmic axis, except for values below 0.5.

The obvious first analysis is to examine the relation between crab abundance, as measured by volumetric density, and primary environmental parameters. Figures 22 and 23 display the individual trawl values of blue-crab density from San Antonio Bay (the entire area depicted in Figure 25, below) in which selected quantile values for increments (bins) of 2° temperature and 1 ‰ salinity are shown as lines. Density is given in numbers per hectare-meter (ha-m), which happens to be within about 15% of the number of crabs per hour of towing. The selected quantiles are 16.7% (lower hexile), 25% (lower quartile), 50% (median), 75% (upper quantile), and 83.3% (upper hexile). (The outer hexiles enclose 68% of the data, so are the nonparametric analog to standard deviation bands.) These can be interpreted as the probabilities of

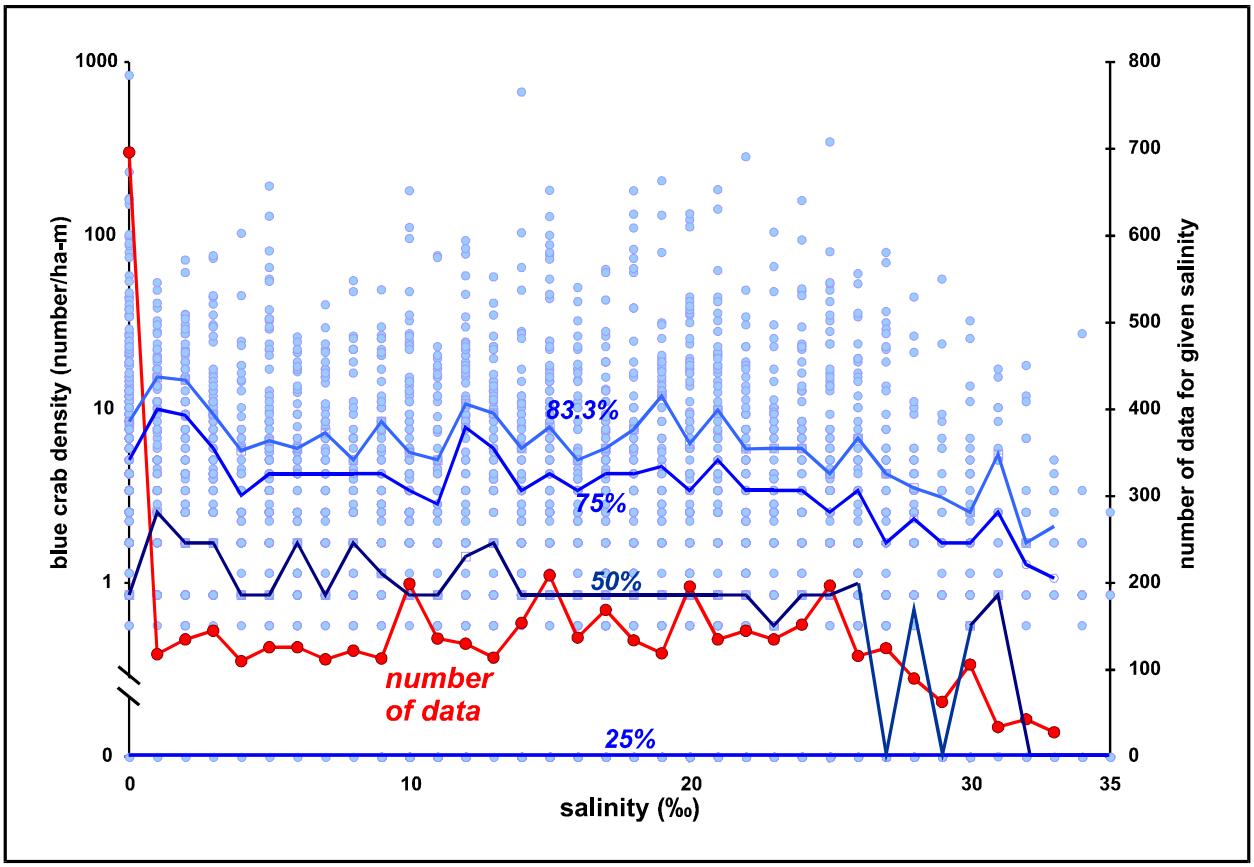


Figure 23 - Blue crab density for all 1982-2008 otter-trawl samples from San Antonio Bay vs concurrent salinity (small filled circles), quantile values (lines) based on 1-part-per-thousand bins, see text. Density values plotted on logarithmic axis, except for values below 0.5.

encountering a crab density no greater than the corresponding density value. Each graph plots over 5000 data points, but because the environmental parameters are reported at discrete values and the smaller values of blue-crab density are also discrete (corresponding to small numbers of crabs), many data points plot on top of each other. The utility of the quantile lines is to better indicate the clustering of data, which is masked by the overplotting.

Several conclusions are immediate from inspection of these figures. The measurements are heavily positive skewed, the bulk involving capture of less than five crabs. An alternate demonstration of the high skew in the blue crab data is presented in Figure 24, which plots the probability of catching a given number or less of crabs, from 0 to 5, in the TPWD otter trawl as a

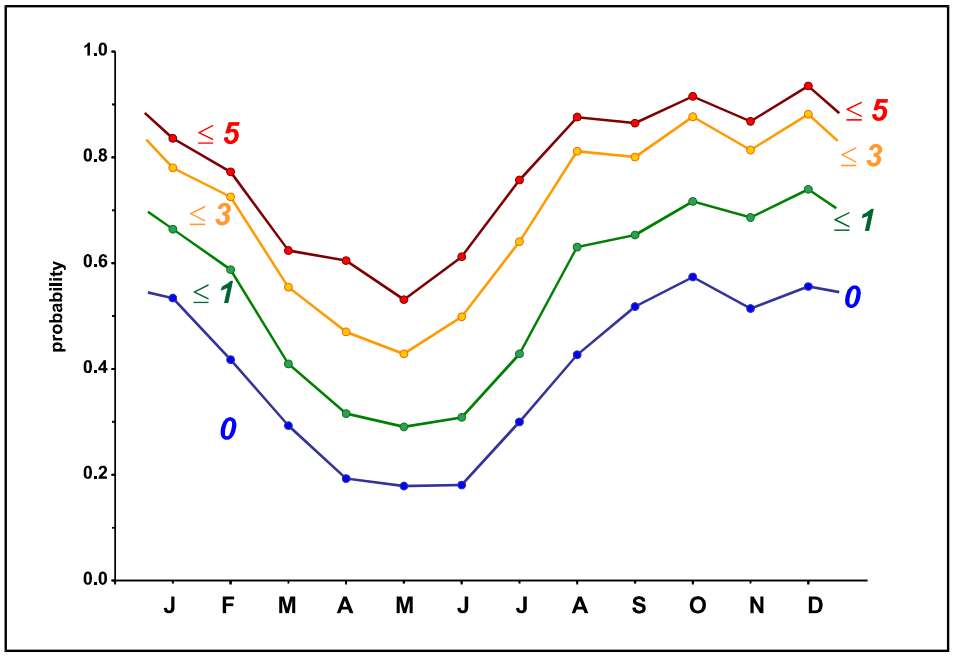


Figure 24 - Probability of catching the indicated number of blue crabs in the TPWD otter trawl, from data of 1982-2008

function of season. If the blue-crab density data are plotted on a linear ordinate in Figs. 22 and 23, the graph would be unreadable. The logarithmic ordinate spreads the small values out to better display their distribution. The lower hexile and lower quartile are zero over the range of temperature and salinity. More importantly, within the variability of the quantile lines, there is no clear trend with either salinity or temperature.

The problem with using this kind of display to detect changes in response of blue crabs to salinity or temperature is that the data are not uniformly sampled, hence all values of temperature and salinity are not equiprobable. To a certain extent, this could be compensated by averaging the data over each salinity/temperature bin, but the extreme skewness of the data would mean that any salinity/temperature combinations that are infrequently sampled would be biased toward lower values of average density. Note, for example, that over half of the temperature data is in the range 23-35°C, the remainder spread over the much larger range 0-23°C. For salinity only 20% of the data were taken in salinities over 23 ‰, which would imply a bias to lower density in the higher salinities.

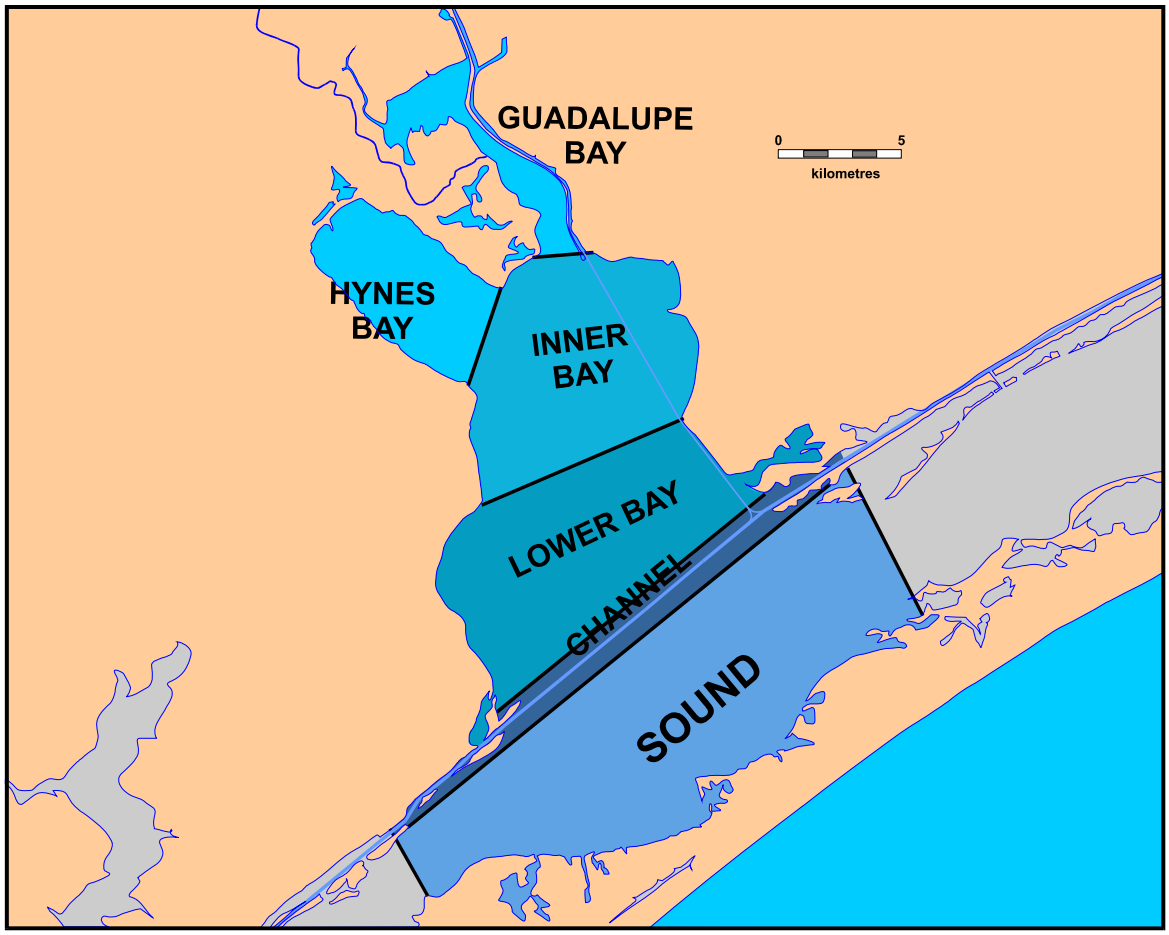


Figure 25 - Segmentation of San Antonio Bay for analysis of blue crab distribution. Channel segment is ± 1 km from axis of Gulf Intracoastal Waterway.

6.3 Geographical and seasonal variation of blue crabs in San Antonio Bay

To better delineate the distribution of crabs within San Antonio Bay, the bay was subdivided into the six segments shown in Figure 25. The distribution by segment, and by temperature or salinity are tabulated in Tables 9 and 10, resp. These tables also give the number of data points within each segment/parameter-range bin going into the average. It should be emphasized that these are the numbers of trawl events occurring in each bin, and have no relation to the number of crabs caught. These tables indicate a higher abundance of crabs in and around the GIWW, except perhaps in higher salinity (> 25 ‰). There seem to be higher abundances in the

Table 9
Average densities of trawled blue-crab in number/ha-m, in incremental temperature ranges, and number of trawl events for San Antonio Bay segments shown in Fig. 25. Entry omitted when number of trawls < 20.

temperature range (°C):	*Guadalupe*	*Hynes*	*Inner*	*Lower*	*Channel*	*Sound*
			(a) average densities, number/ha-m			
0-4.9						
5.0-9.9			19.0	153.1		2.3
10-14.9		26.5	35.8	85.6	258.8	26.8
15-19.9	9.0	42.8	63.4	52.1	79.5	32.2
20-24.9	19.0	52.0	72.9	70.2	117.3	36.9
25-29.9	21.0	30.6	34.0	39.2	44.6	18.4
30-34.9	16.5	11.7	53.1	26.7	16.5	12.2
			(b) number of data in above averages			
0-4.9						
5.0-9.9			32	24		32
10-14.9		61	192	190	49	178
15-19.9	22	70	227	250	76	337
20-24.9	40	97	278	265	83	321
25-29.9	54	141	390	425	103	510
30-34.9	23	42	1423	162	23	134

Lower Bay and Channel segments under cooler temperatures. No clear variation of abundance with salinity is evident in any of the segments. Though the highest abundance in the system was measured in the Channel under very low salinities (< 5 ‰), this was also based on a relatively small number of data points.

Since these data are averaged over the entire record, seasonal variations are suppressed. A substantial seasonal variation would be expected from the life cycle of the blue crab. Some indication of this was given by Fig. 24. Although the peaks in abundance are not reflected, there is an increased probability of catching more than five crabs during the March - June period. (Figure 24 plots the probability p of catching N or less crabs. The probability of catching more

Table 10
Average densities of trawled blue-crab in number/ha-m, in incremental salinity ranges, and in San Antonio Bay segments shown in Fig. 25. Entry omitted when number of data < 20.

salinity range (‰):	*Guadalupe*	*Hynes*	*Inner*	*Lower*	*Channel*	*Sound*
			(a) average densities, number/ha-m			
0-4.9	17.2	33.8	42.5	61.2	309.5	50.3
5.0-9.9		21.6	49.9	36.0	37.8	33.5
10-14.9		47.9	54.0	61.4	59.9	22.2
15-19.9		40.8	47.5	69.9	78.8	26.9
20-24.9		36.0	52.5	46.8	105.7	28.8
25-29.9			50.6	66.0	39.9	16.4
30-34.9			16.8	12.5		13.7
			(b) number of data in above averages			
0-4.9	144	182	401	278	45	155
5.0-9.9		83	238	202	27	103
10-14.9		83	194	211	65	173
15-19.9		43	162	216	71	270
20-24.9		20	148	222	68	304
25-29.9			62	140	52	325
30-34.9			22	47		151

than N is $1 - p$.) A better depiction is Figure 26, showing the annual variation of 1982-2008 monthly means of blue crab density and carapace width. Median width is also plotted, which tracks the mean width rather closely. More detail on seasonal variation in size statistics is shown in Figure 27, which includes means ± standard deviation, and medians, quartiles and outer hexiles for each month.

From an inspection of Fig. 26, there are four divisions of the year suggested. In the first, December – March, there is a marked increase in abundance while the mean size is more or less stable around 60 mm (median 50 mm). Crabs hatched in the July-August period would be attaining a size of around 60 mm during this period, cf. Fig. 6. This would also correspond to the approximate size range in which crabs move out of the marshes and shallows into the bays and bayous (see Section 5.5.2 above) where they could be trawled. Recruitment of a size range more

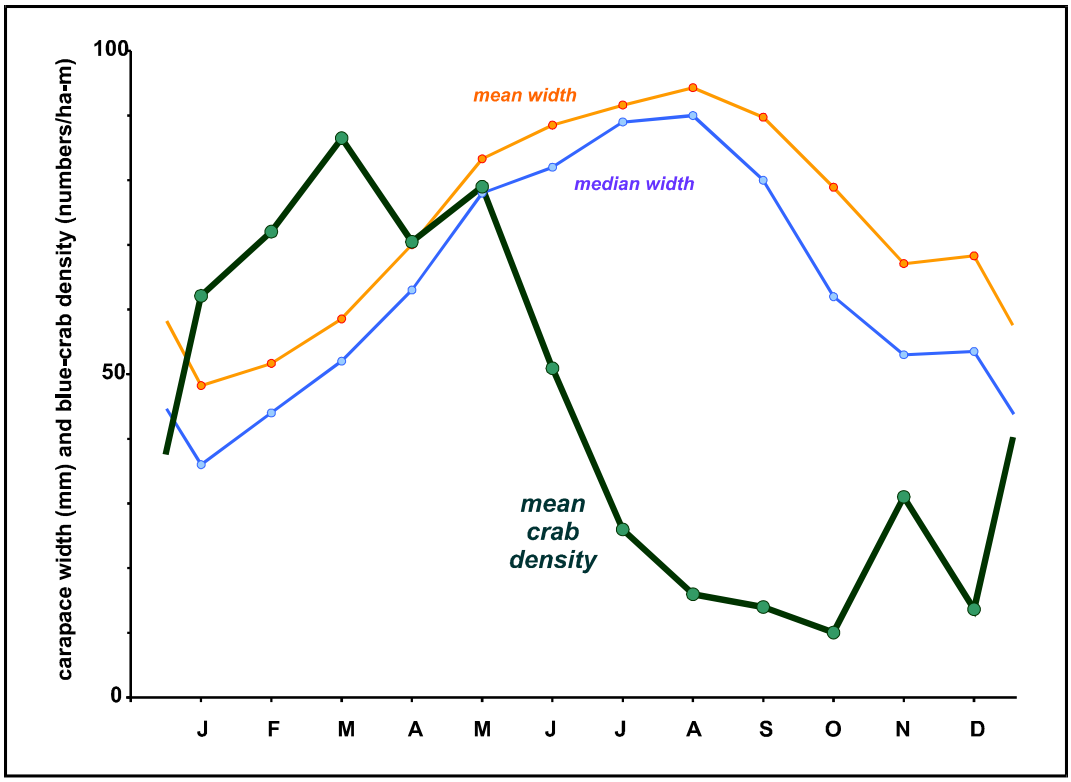


Figure 26 - Monthly mean variation of blue-crab density and carapace width, from TPWD 1982-2008 otter-trawl data

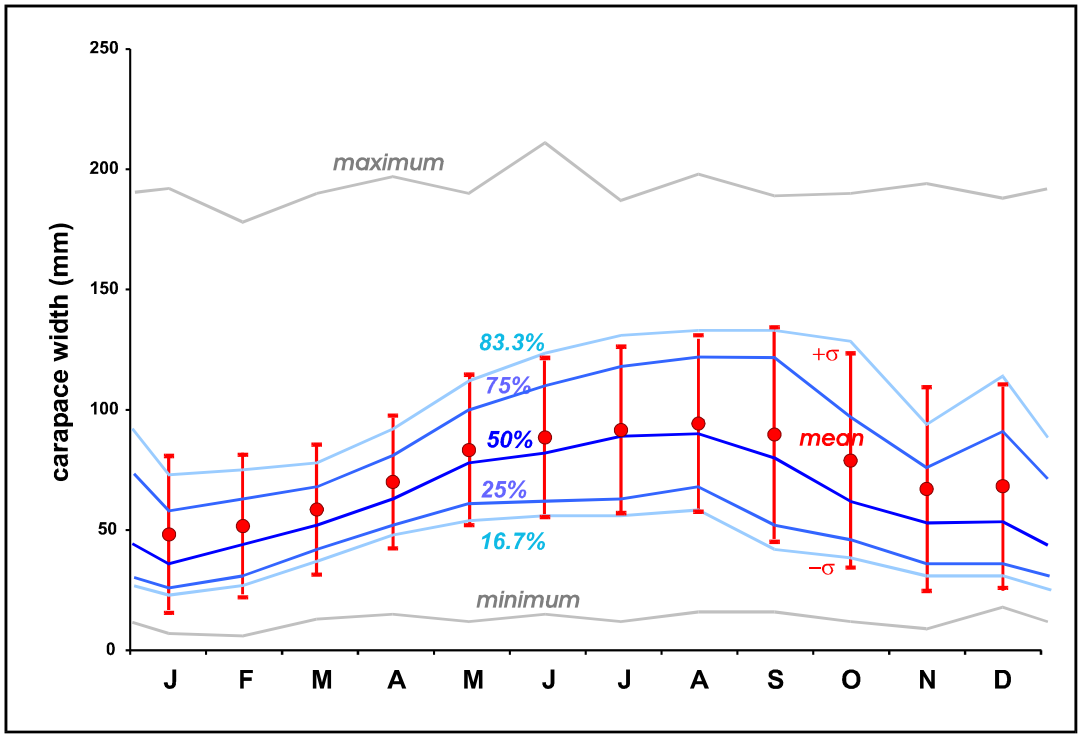


Figure 27 - Statistics of blue-crab size from TPWD 1982-2008 otter-trawl data

or median of the distribution, as indicated by Fig. 26. The second period is March – May, during which the crab density is more or less stable while the mean size increases from about 60 to 90 mm. This could result from grow-out of the existing population so that the sizes shift upward with no change in abundance. The third, and longest period is May – September, during which there is a monotonic decline in density by nearly a factor of ten, while the mean and median sizes are relatively constant around 90 mm. One scenario that would entail this result is a loss of crabs of sizes evenly distributed about 90 mm. Certainly, part of this could be migration to the sea as well as harvesting, but this would involve mainly crabs larger than this median size (cf. Fig. 13). The loss of crabs smaller than median might be simply due to a combination of predation and grow-out to larger sizes. The fourth period is September – December, during which abundance, though variable, exhibits no systematic decrease or increase, while the mean and median shift downward to smaller sizes. A continued loss of larger sizes, an addition of smaller sizes or both, would achieve this result. The early hatchers (late-spring to early-summer hatching) would be attaining sizes in the 40-50 mm range around this time, cf. Fig. 6. While most would be vacillating between marsh and unvegetated shallows, it seems likely that many would be accessible to the otter trawl.

We can conclude that Figs. 26 and 27 are consistent with the picture of blue crab migration and grow-out that has emerged from this literature review. This division into a rising limb, a stable high density, a falling limb, and a stable low density is of course the characteristics of an annual pulse in abundance. Using Fig. 26 to identify the calendar periods associated with each limb of the pulse offers a basis for conjecturing the underlying processes.

The segmentation of Fig. 25 was used to display the spatial aspects of the monthly variation of blue-crab distribution in San Antonio Bay. Table 11 presents the monthly abundances averaged over the 1982-2008 period for each of these six segments of the bay. In addition, the Guadalupe Bay, Hynes Bay and Inner Bay segments have been combined into a more regional depiction, named Upper Bay, and the Channel and Sound segments were similarly combined into Outer Bay. The same data are displayed graphically in Fig. 28 for the six geographical segments and in Fig. 29 for the regional segments. (The averages over the entirety of San Antonio Bay listed in

Table 11
Mean monthly densities (nos/ha-m) of blue-crab, 1982-2008 trawl, by bay segment, see Fig. 25. Upper Bay aggregates Guadalupe, Hynes & Inner Bay. Outer Bay aggregates Channel & Sound.

	Jan	*Feb*	*Mar*	*Apr*	*May*	*Jun*
Guadalupe	7.4	4.1	22.0	20.7	23.7	27.6
Hynes	13.1	58.2	104.6	49.8	64.9	47.5
Inner Bay	33.6	65.2	102.0	84.8	111.9	65.0
Upper Bay	27.3	56.8	94.1	70.2	91.7	57.6
Lower Bay	149.0	66.3	96.0	97.9	101.2	61.1
Channel	178.3	260.3	120.1	154.0	130.2	80.1
Sound	18.7	35.7	62.5	37.3	36.2	28.2
Outer Bay	43.0	90.7	72.4	53.0	49.8	37.0
San Antonio Bay	62.1	72.0	86.5	70.5	79.0	50.9

	Jul	*Aug*	*Sep*	*Oct*	*Nov*	*Dec*
Guadalupe	19.9	24.6	7.7	10.4	8.4	6.9
Hynes	37.0	16.6	8.8	9.4	19.9	3.8
Inner Bay	29.1	22.3	18.8	8.8	10.7	15.5
Upper Bay	29.6	21.2	15.2	9.1	12.9	11.9
Lower Bay	30.1	16.0	13.6	10.9	10.9	21.5
Channel	29.2	23.1	22.0	24.9	128.5	17.0
Sound	17.1	6.7	11.0	6.8	36.6	7.9
Outer Bay	19.4	10.1	13.0	10.4	60.1	9.7
San Antonio Bay	26.0	16.0	14.0	10.0	31.0	13.6

the last row of Table 11 are shown in Fig. 26.) While this data is noisy, it does not show a clear sequential progression of blue-crab density variation from one segment to the next, as might have been anticipated from a slow migration into or out of the estuary. Instead, the variation in density in all six segments is generally coherent, excepting the occasional positive or negative excursions in individual data points. This suggests that the crabs enter or leave the estuary population sufficiently quickly that on a monthly time resolution they are synchronous. All six regions exhibit the four periods of annual variation identified above: a pronounced increase in

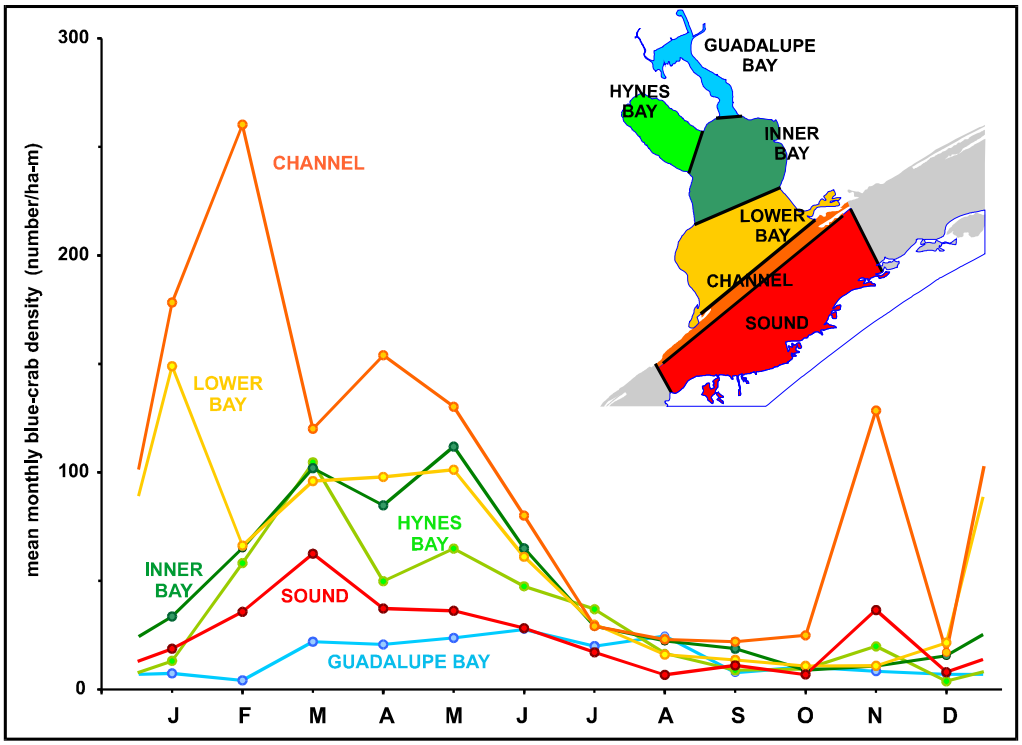


Figure 28 - Average monthly blue-crab density in 1982-2008 otter trawl, distributed into segments of Fig. 24, see also Table 11.

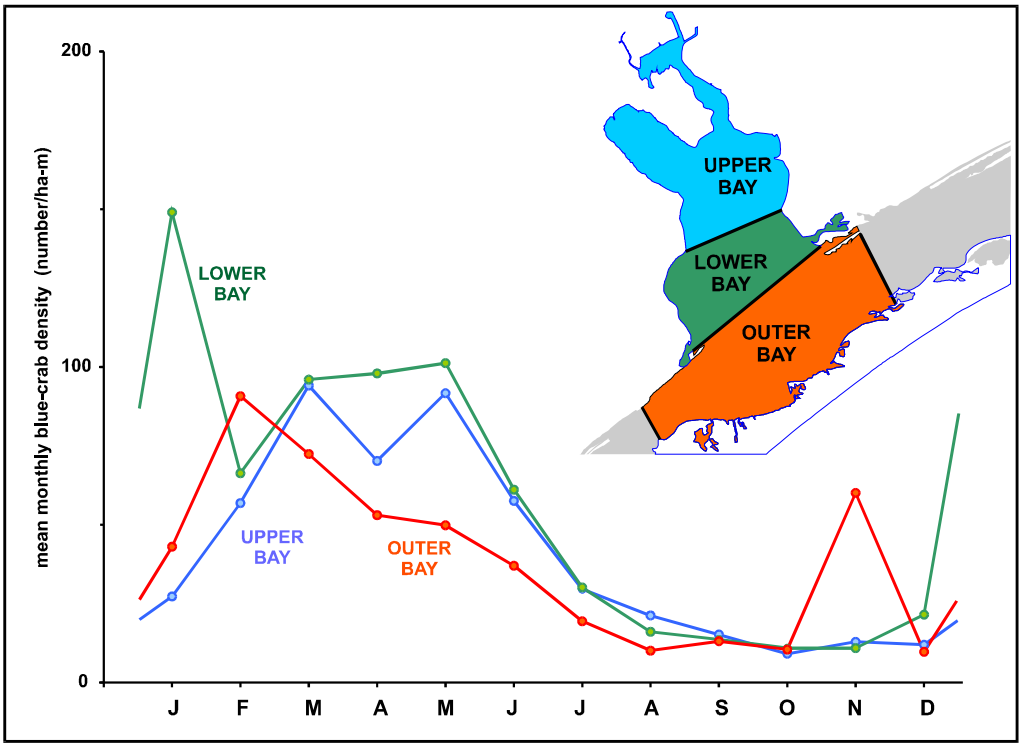


Figure 29 - Same as Figure 28, except aggregating data over larger "regional" segments. Upper Bay combines Guadalupe Bay, Hynes Bay and Inner Bay, and Outer Bay combines Channel and Sound.

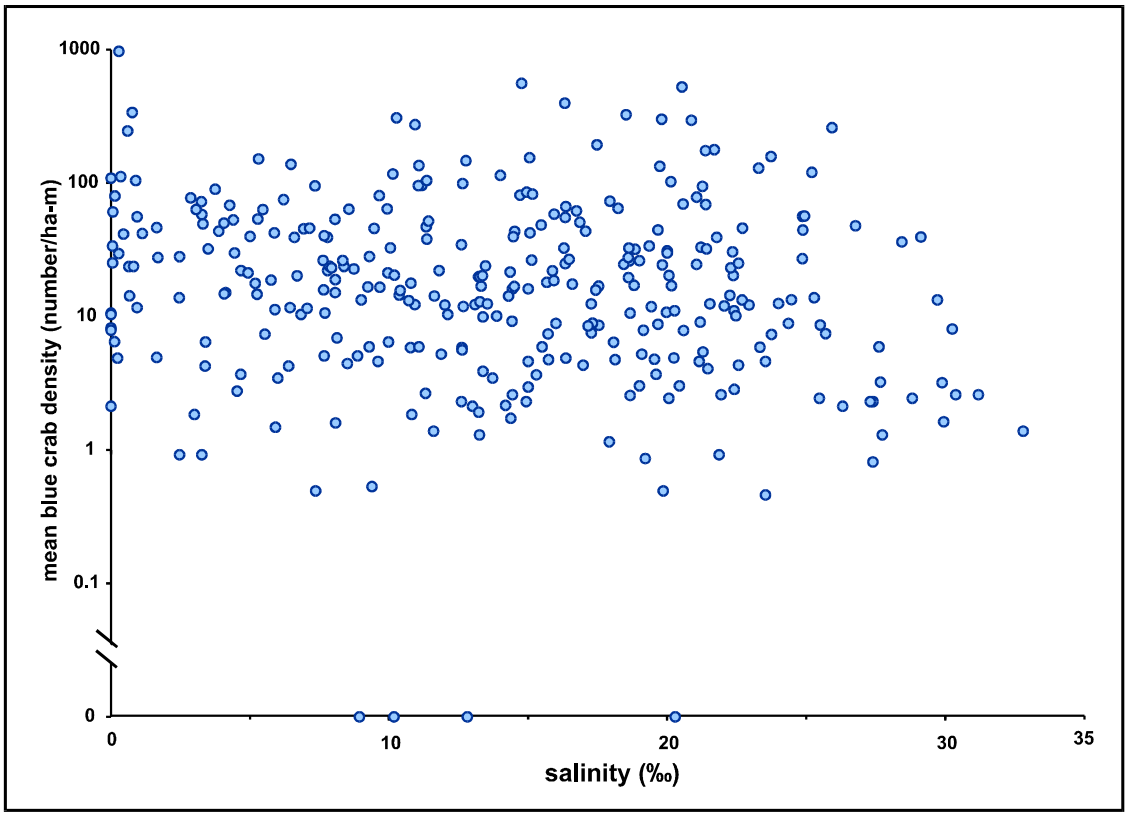


Figure 30 - Monthly-mean bay-average blue crab density versus corresponding averaged salinity, from 1982-2008 otter-trawl data. Densities greater than 0.1 no/ha-m logarithmically transformed.

abundance during December – March, a period of variable but stable density in March – May, a large-scale decline in abundance over the period May – September, and another period of variable but stable density during September – December. Figure 28 also shows that the Channel segment typically has the highest abundance in the system, and Guadalupe Bay the lowest. Aggregation into the three "regions" shown in Fig. 29 (see also Table 11) suppresses some of the variability, and reinforces the general synchrony of variation across the bay. The four divisions of the annual cycle as described above are manifested in this depiction as well.

6.4 Dependency on salinity and inflow

The monthly averaging of course suppresses much of the variance in the trawl event data, and might be expected to better reveal underlying behavior, such as Fig. 26 *et seq*. above. The

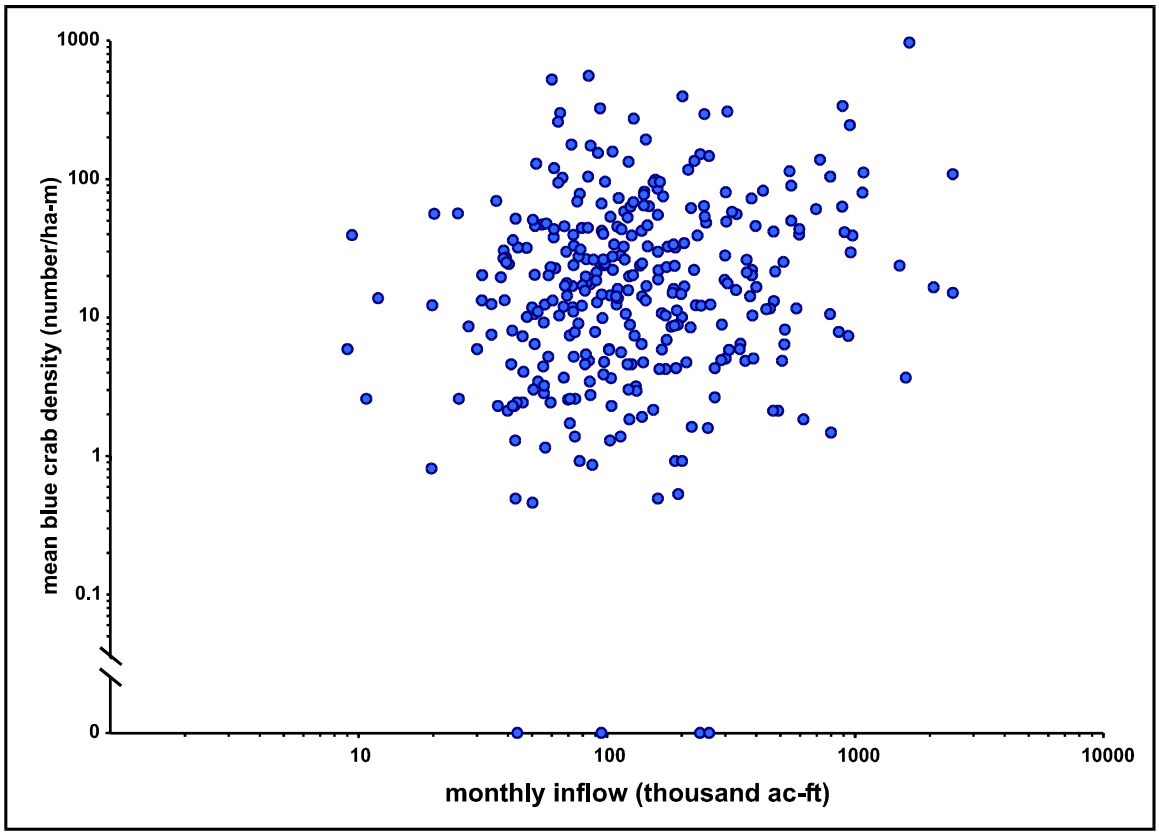


Figure 31 - Monthly-mean bay-average blue crab density versus corresponding mean inflow, from 1982-2008 otter-trawl data. Densities greater than 0.1 no/ha-m and flows logarithmically transformed.

monthly density data are still skewed positive, dominated by small values, but, unlike the individual trawl-event data (Figs. 22 and 23), there are few months with exactly zero mean density. Re-examining the variation with salinity, displayed in Figure 30, in which the ordinate again has been logarithmically transformed to spread the small values of density, we find it to be no better than that of the individual trawl-event data, showing negligible correlation.

An argument can be made (e.g., Montagna et al., 2011) that freshwater inflow provides several mechanisms that could plausibly increase the abundance of blue crabs, besides moderating salinity, and therefore it is warranted to seek a direct relation between abundance and inflow. Since any response to inflow would be an integrated relation, presumably this would be better exposed by examining the behavior of monthly averaged organism density versus monthly

Table 12
Linear correlation of blue-crab density versus independent variable of salinity or inflow, in which blue-crab data is lagged behind independent variable by increments of one month

Lag	*correlation with:*		*Lag*	*correlation with:*	
(mos)	*salinity*	*inflow*	*(mos)*	*salinity*	*inflow*
0	-0.08	-0.13	7	-0.09	0.22
1	-0.02	-0.25	8	-0.11	0.26
2	0.08	-0.31	9	-0.14	0.24
3	0.07	-0.31	10	-0.12	0.15
4	0.08	-0.20	11	-0.08	0.03
5	0.04	-0.07	12	-0.04	-0.14
6	-0.03	0.09			

averaged inflow. As might be expected, the monthly mean inflow also proves to have high positive skew. To exhibit their direct correlation, Figure 31 displays the 1982-2008 monthly-mean data, with both axes log-transformed to spread out the small values of the variables. As might be judged from this figure, the correlation proves to be negligible.

A lagged response behind inflow is frequently exhibited in aquatic environments, so this was explored by lagging the monthly organism density behind the monthly inflow for values up to a year. The results are shown in Table 12. (Salinity was included as an independent variable as well, though a lagged response of more than a month would warrant skepticism. As it turns out, there is little correlation, independent of the lag.) For inflow, the maximum absolute value of correlation occurs with the two and three months lag, but this is negative, i.e., low densities are correlated with high inflows. The highest positive correlation occurs at an eight-month lag. These correlations are barely noteworthy, explaining less than 10% of the variance. Poor correlation between blue crab abundance and both salinity and freshwater inflow into San Antonio Bay has been found in other studies using the TPWD fisheries data (Hamlin, 2005, Mark Fisher, TPWD, pers. comm., 2010, GSA-BBEST, 2011, Tony Smith, RPS-Espey, pers. comm. 2011).

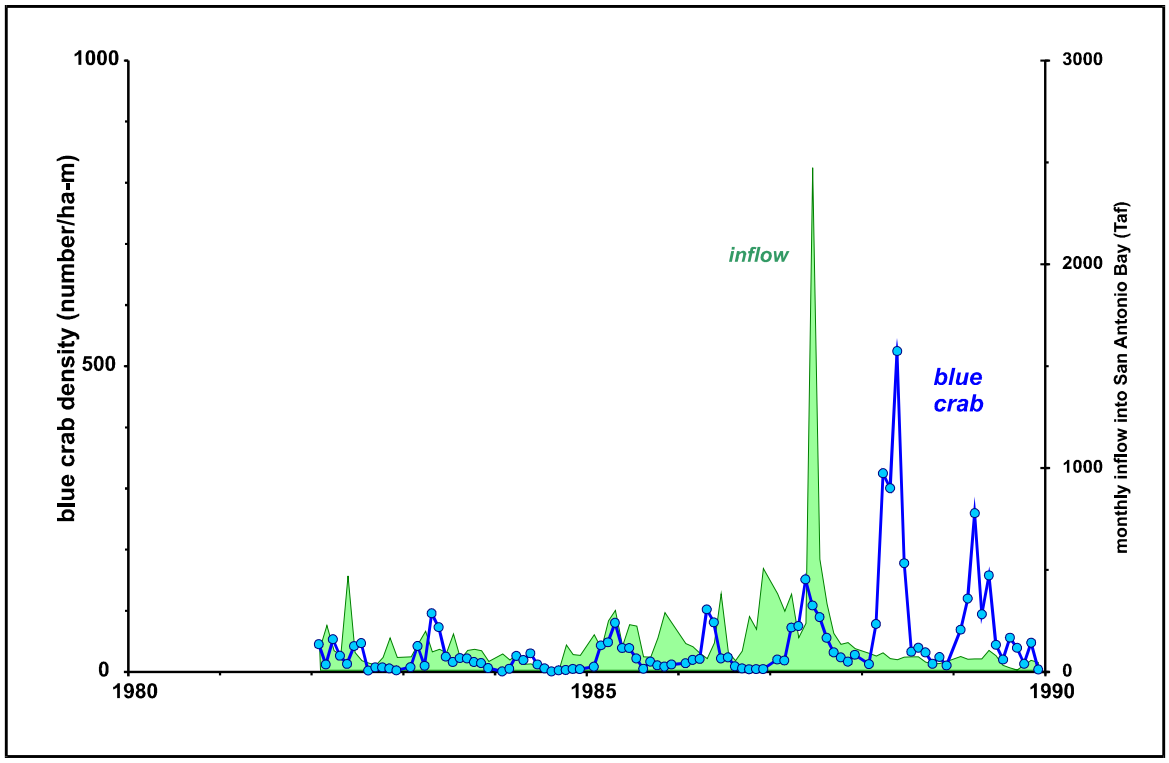


Figure 32a - Time series of blue crab density in San Antonio Bay, 1982-1989

Additional insight into the poor mathematical association of blue crabs in San Antonio Bay with either salinity or inflow may be provided by inspection of the time series of the individual monthly values of organism density shown in Figure 32. There is a clear seasonal pulse in abundance that varies in magnitude from year to year. However, the timing of the pulse fluctuates between years. Moreover, many pulses have multiple maxima, and occasionally there is a second seasonal pulse in the fall. This variability accounts for the frequently conflicting results on the seasonal pattern of blue crab abundance from short-term field studies. For example, Gunter (1950) reported the greatest abundance of blue crabs to occur in spring based upon a two-year study, while Daugherty (1952) in one year of study found the abundance of crabs to be maximal in the period April –July and very low in September –February, and More (1969) determined two seasons of maximal density, April – July and September – October, in his two-year study.

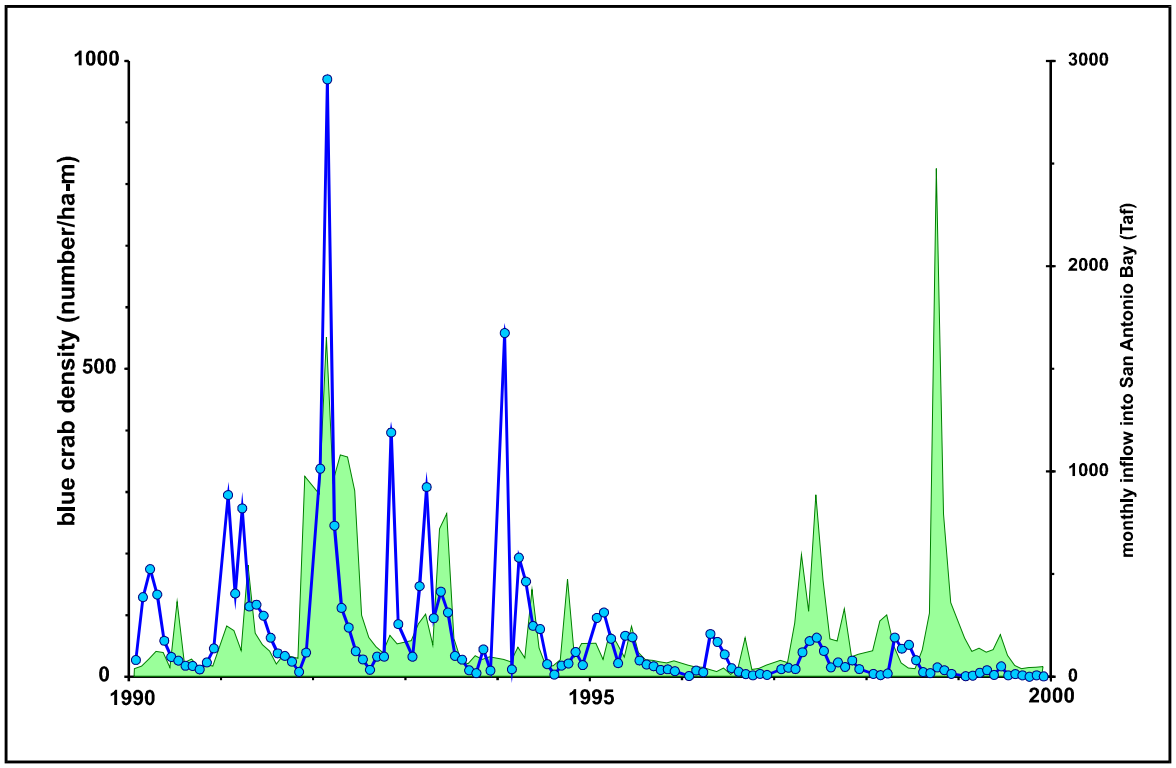


Figure 32b - Time series of blue crab density in San Antonio Bay, 1990-1999

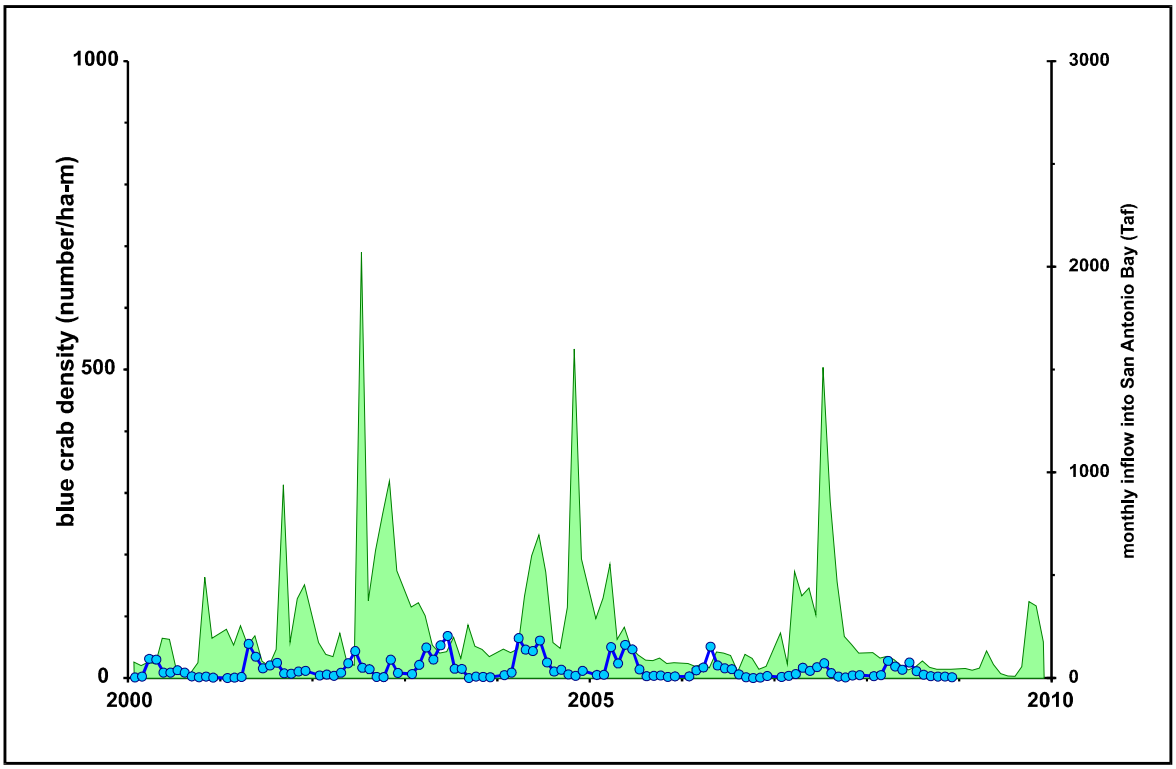


Figure 32c - Time series of blue crab density in San Antonio Bay, 2000-2008

This kind of variability would certainly erode correlation with monthly salinity, e.g. Fig. 30, but this may be a result of applying linear methods to what is much more complex behavior. With respect to inflow, also plotted in Fig. 32, while there are occasional pulses of flow that align with or lead pulses of blue crabs, there are also prominent pulses of either variable that have no corresponding pulse with the other. Any relation of blue crab abundance to inflow must be subtle and involve other variables and/or time relations, whose explication will require more sophisticated methods of analysis than employed here.

6.5 Trends and external controls

Since the mid-1980's, a declining trend has been manifested in both the numbers and size, *a fortiori* in total biomass, of blue crabs in the Texas bays (Osborn et al., 1992, Hammerschmidt et al., 1998, Chocair et al., 2006, Sutton and Wagner, 2007). This is exemplified by the least-squares regression of annual biomass (see Section 6.2) averaged over the Texas bays versus year, shown in Figure 33. Over the period depicted, there is a 70% reduction in biomass. On a bay-to-bay basis, the trend is noisier, as shown in Figure 34, and is not evident in either Sabine Lake or Matagorda Bay (which exhibits depressed abundance over the *entire* 20-year period). For San Antonio Bay, and indeed the other Coastal Bend bays, the declining trend is clearly evident.

The Texas coast is not alone in this problem. Similar declining trends have been observed elsewhere on the Gulf of Mexico and on the Atlantic coasts as well (Stagg and Whilden, 1997, Lee and Frischer, 2004, Pelton and Goldsborough, 2008, Zohar et al., 2011). The causes are considered complex and mysterious, and it would be premature to conclude that some large-scale factor is at work everywhere (though that cannot be precluded either). Among the hypothetical causal factors are overfishing, poor water quality, predation, disease and parasitism, habitat loss, and, generally, people.

These are classified as "external controls" in contrast to the response of the organism itself to its environment, e.g., to salinity or temperature. External controls can be imposed on a bay system, or on an entire region, such as the Texas coast, or, indeed, the entire Atlantic seaboard including

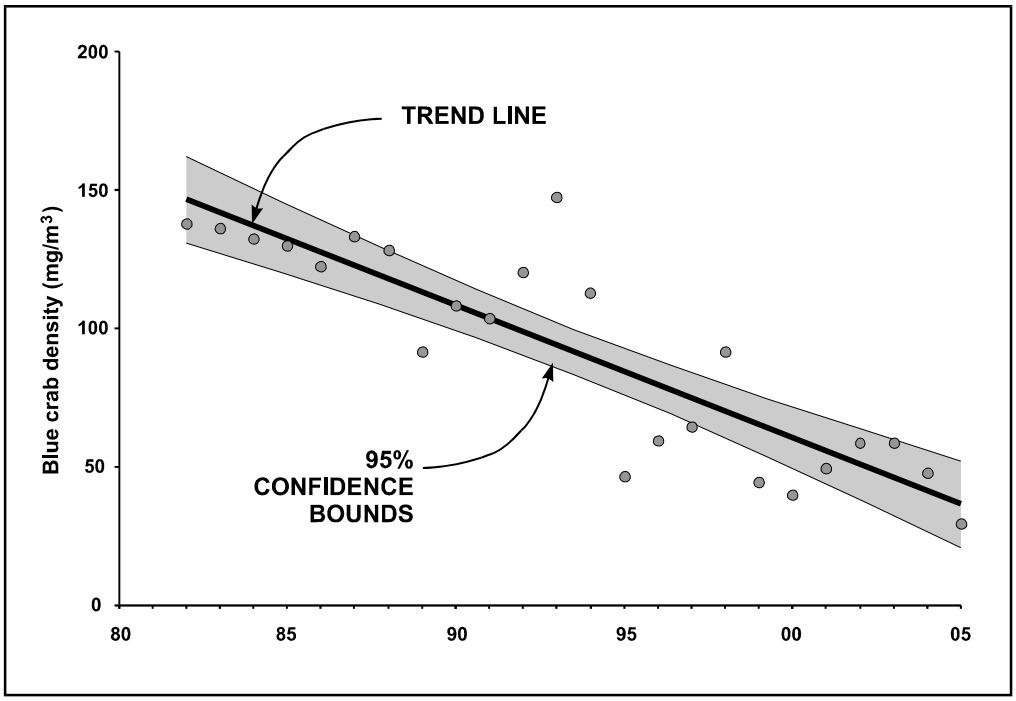


Figure 33 - Annual blue crab biomass, collected in TWPD otter trawl samples 1982-2005, averaged over all bays, showing regression line versus year with 95% confidence band on regression

the Gulf of Mexico. One such external factor that may influence San Antonio Bay is the status of Cedar Bayou, the nearest inlet to the bay. A time line of Cedar Bayou was developed for this project to determine the extent to which its status could be an explanatory variable for fluctuations in blue crab abundance. As reported in Ward (2010b), since 1982, the beginning of the period of analysis for the TPWD blue-crab data, Cedar Bayou has been either closed or only marginally open (as defined in Ward, 2010b), and therefore unlikely to have significantly affected the variations of blue crab abundance in the bay. There are two minor exceptions to this statement. In 1988 the inlet was dredged by TPWD to an unknown cross section, but shortly reclosed after the dredging. After a later dredging project in 1995, the inlet was reported to have been open until around 1997, but again there is no quantitative data on the size of the inlet, either after being dredged or in the two-year period before it was reported closed. Inspection of Fig. 32a shows a substantial peak of about 500 number/ha-m in spring of 1988. No information is available as to the exact date of dredging, but it was probably in the summer, after this peak in

abundance. In any event, it is difficult to ascribe this peak solely to Cedar Bayou, noting (see Fig. 32b) the even more substantial peaks that occurred in the early 1990's when the inlet was closed. Moreover, though the inlet was reported open in 1995-97, after the 1995 dredging, crab abundances are modest.

While a least-squares trend line can certainly be fitted to the blue crab data from San Antonio Bay of Fig. 34, their variation can be just as accurately modeled by a step function with transition from high abundance to low abundance around 1995. Both mean density and variance decrease markedly at this point in time. The same kind of step behavior obtains in the other Coastal Bend bays. This raises the question of whether some process fundamental to the blue crab population underwent a shift at this time.

Sanchez-Rubio et al. (2011a) used post-1967 fishery-independent trawl data from Louisiana and Mississippi to identify two periods in which there seemed to be a significant difference in blue crab abundance, the periods being further associated with climate-related hydrological regimes of the Mississippi and adjacent rivers. The first period 1973-94 was wet, with high rainfall and river inflow. This period also evidenced high abundances of blue crab. The second period 1997-2005 was dry with low river inflows, during which abundances of blue crab were low. The rainfall and river flow conditions, which differentiated the two periods, were in turn linked to the control of large-scale climate modes (Sanchez-Rubio et al., 2011b). The former proved to be dominated by the cold phase of the Atlantic multidecadal oscillation (AMO).

The fact that a drop in abundance in Louisiana occurs at about the same time as in South Texas is intriguing. However, it is not clear that hydroclimatology can explain the decline in San Antonio Bay, for the simple reason that the estuary inflows are not that different during the two periods (Fig. 32). However, as noted by Sanchez-Rubio et al. (2011a), the 1973-94 cold-AMO period was also associated with strong onshore (south) winds, in contrast to the 1997-2005 period. Indeed, these researchers found blue crab abundance to be significantly correlated with onshore wind momentum. We note that in the case of the lower Texas coast, this would suggest that the difference in abundance may be keyed to megalop supply, rather than hydrology.

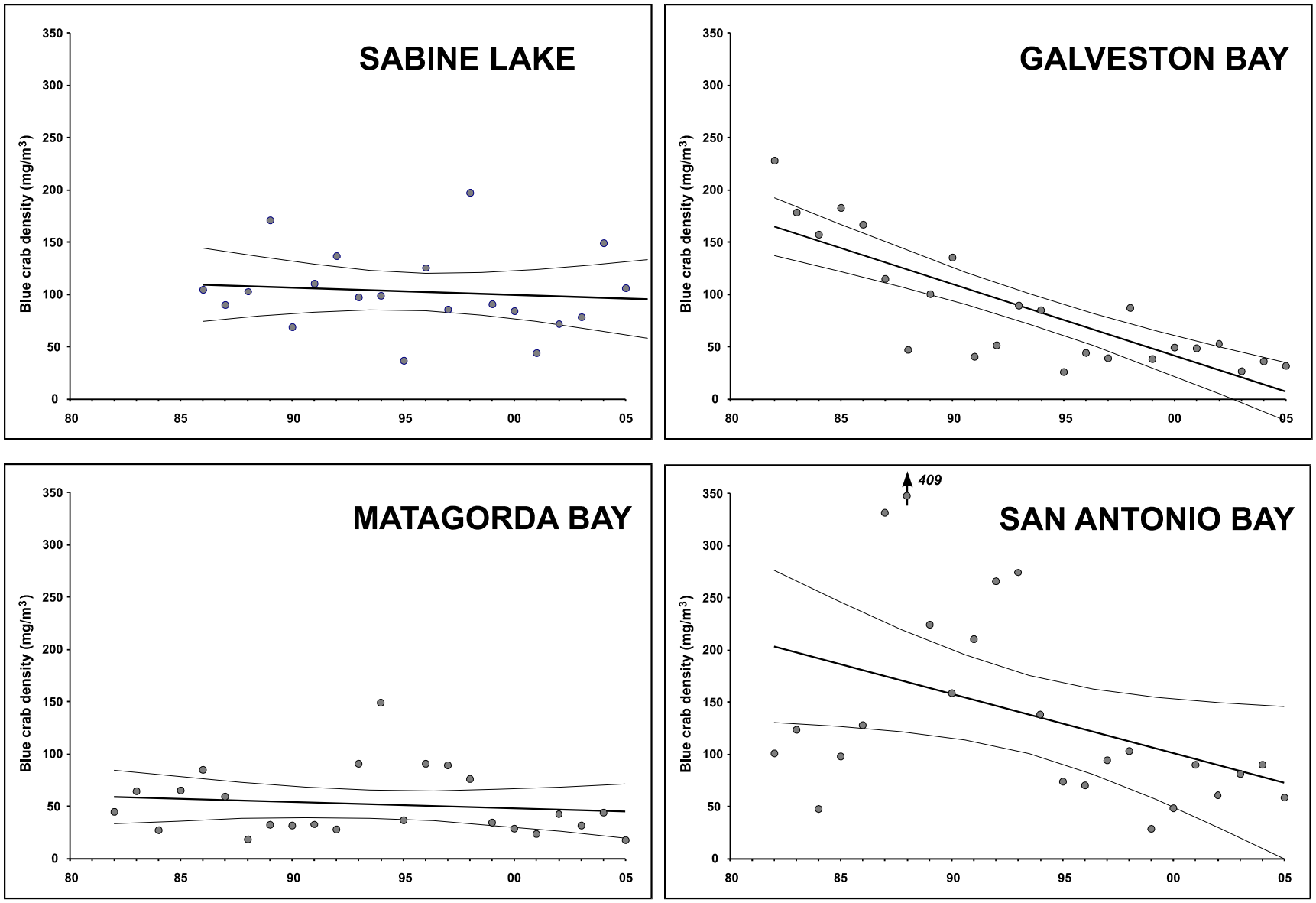


Figure 34 - Time trends in annual otter-trawl biomass for each major bay, 1982-2005, with 95% confidence bounds on regression

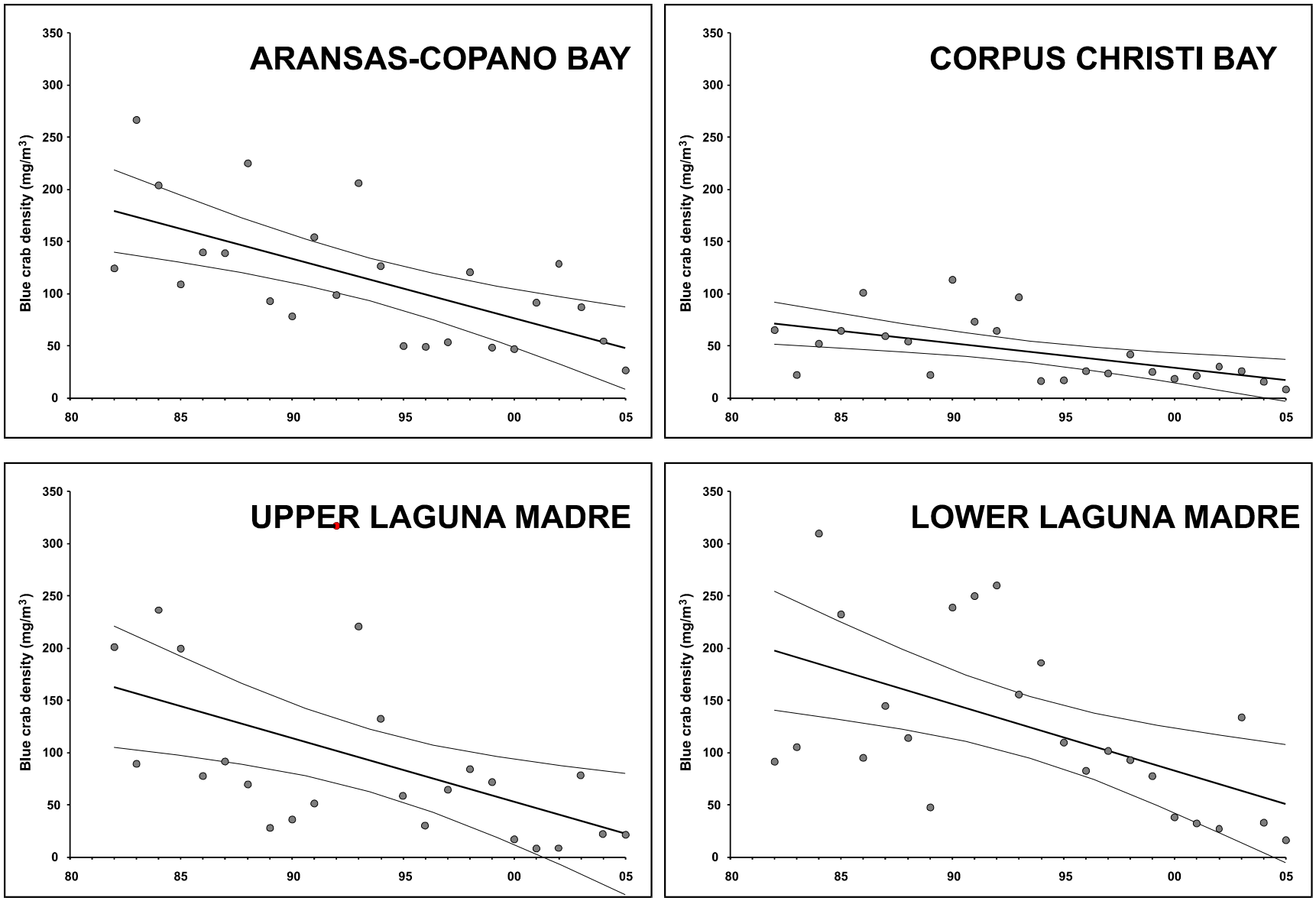


Figure 34 - Continued

7. SUMMARY AND CRITIQUE: THE BLUE CRAB CURRICULUM VITAE

According to Lipcius et al. (2007), the abundance of blue crab in an estuary is governed by four factors: (1) the size of the spawning stock; (2) larval and postlarval (i.e., megalop) survival; (3) postlarval settlement success, and resulting young juvenile recruitment in the primary nursery habitat; (4) dispersion, survival and growth of juveniles in the secondary nursery habitats. These are, of course, the successive stages in the development of blue crabs, starting with the volume of larvae hatched, the subsequent history of developing larvae and postlarvae, the influx of postlarvae into the estuary from the ocean and their ultimate recruitment into the blue-crab population. It is also, in effect, a statement of mass balance, that the totality of crabs in the estuary is given by the number initially hatched at sea less the number of larvae lost to all sources of mortality, less the postlarvae similarly lost, times the fraction of postlarvae that actually enter the estuary, less the number of postlarvae and early juveniles lost within the estuary boundaries. At first blush, such a simple statement of the problem as that by Lipcius et al. might lead to a state of euphoria, that the problem itself is simple and capable of a facile solution. Upon closer consideration of the individual terms in the blue-crab mass balance and the information that is needed to quantify each of these, that euphoria deflates to utter despair. An intermediate position is argued here based on the foregoing review, a position of either cautious euphoria or hopeful despair.

The basic facts of the life cycle of the blue crab can be succinctly summarized thusly:

(1) Zoeae (larvae) are hatched so as to be injected into nearshore waters of the inner continental shelf. They remain at or near the surface and are distributed in heterogeneous patches that, as plankton, are moved by shelf currents.
(2) Over a 1-2 month period, the zoeae develop through seven stages while being transported over the continental shelf, then metamorphose into megalops (post-larvae). Depending upon nearshore and shelf currents, zoeae and megalops can be dispersed many tens of kilometers along the coast, and from the coast out several tens of kilometers.

(3) During or shortly after attaining the megalop stage, some of these are transported by cross-shelf currents back into the nearshore zone, where a portion of these may be subject to transport into the mouths of estuaries. The megalop stage can range 2 weeks to 3 months in duration, so there is considerable opportunity for transport at this stage of development.

(4) The megalops enter the estuary as irregularly timed pulses of high density. Once within an estuary, the megalops are carried into nursery habitats, where they settle and metamorphose into the first juvenile crab stage. Despite their planktonic character, this is a directed migration, effected by a combination of vertical movement between bed and water column and horizontal transport by being carried by currents.

(5) During their early growth stages (the first five or so instars), some juveniles migrate further up the estuary, presumably by selectively entering the water column during favorable currents, where they populate additional nursery habitat. This continued dispersion is apparently density forced, i.e. undertaken to locate better food and habitat, and to avoid predation, especially cannibalism when areal densities are high.

(6) Crabs develop through approximately twenty stages, over one to three years depending upon conditions, during which they occupy deeper and less structured habitat, and migrate throughout the reaches of the estuary. Blue crabs are osmoregulators that survive — even thrive — in a wide range of salinity.

(7) Upon maturity, mating occurs, generally in the shallower reaches of the estuary. Females usually mate once, acquiring a lifetime supply of semen.

(8) The inseminated females begin a seaward migration, while males continue forage-meandering. This leads to a spatial partitioning between the two sexes in the estuary, the females increasing in abundance in the lower reaches of the estuary closer to the mouth, while in the upper reaches males become predominant. Movement is a combination of riding favorable currents, swimming and walking on the seabed.

(9) Ovigerous females migrate to the sea, where they spawn and ultimately hatch their broods, either in the estuary mouth or in the nearshore waters. They are

capable of spawning several broods from stored sperm, and may return to the lower estuary to forage for food during this process.

These elements of the blue-crab life cycle, drawn from the review presented in previous sections, apply throughout its range and are more-or-less independent of the coastal ocean and estuary. However, specific aspects of these elements vary substantially among estuaries, depending mainly upon regional climatology, hydromechanics and biology of the shelf environment, and the morphology of the estuary.

The chief climatological variable that controls the blue crab life cycle is water temperature. Temperature influences mating, spawning, egg development, zoeal development, intermolt duration and growth rate (as exemplified by Fig. 6), and a number of underlying metabolic functions. Apart from controlling the timing of major steps in the crab life cycle, one important influence of temperature is its enforcing of winter dormancy in the estuaries of the temperate latitudes (see Section 3.1). Water temperature in an estuary, however, is governed almost entirely by seasonal thermodynamics, so temperature is largely homogeneous. Thus, there is little differentiation across the estuary that might affect the spatial distribution of blue crabs.

The only stage of the blue-crab life cycle that requires a narrow range of salinity and temperature is the larval (Section 3.3 and 4.2), *viz*. high salinity above 20‰ and warm temperatures 25-30°C. (Postlarvae require temperatures above 15°C, optimally above 20°C, but survive over a wide range of salinity.) It is seeking these salinity conditions that impels the post-insemination migration of the female to the sea. Otherwise, the blue crab is a remarkably effective osmoregulator, which accounts for its abundance from Sabine Lake to the Laguna Madre (Table 8). This may also account for the general lack of a simple relationship between salinity and blue-crab density in the TPWD monitoring data for San Antonio Bay (Section 6.4). Acclimation is important in the tolerance of the blue crab to a range of salinity. On the lower Texas coast, and in San Antonio Bay in particular, the main threat that salinity presents is its sudden reduction to zero during a major flood hydrograph (Section 4.2.2). The negative correlation of blue-crab density in San Antonio Bay with 2-3-month lag after inflow (Table 12) may reflect an avoidance or mortality response to inflow events, while the positive correlation with 8-month lag may result

from beneficial effects of inflow. At the least, this indicates that more sophisticated time-series analysis will be necessary to expose a relation between inflow and blue crabs.

Estuary morphology is important to the migration of the blue crab because it dictates the primary forcings of currents and circulation within the estuary. While blue crabs are good swimmers (Section 2.3), they evidently prefer to ride currents to move about. In directed migration, it is clear from observations that blue crabs, as both megalops and adults, selectively enter the water column to ride favorable currents to their destination (Section 4.1.2). In foraging and deliberate movement over moderate distances crabs are likely to exploit currents in the same way, though observational data is lacking. Tidal currents are particularly important in this respect because they can carry directional information, i.e., chemical signals to which crabs are sensitive that indicate whether the current is directed into or out of the estuary, notably organic signatures from plants or animals (Section 5.4.3), and the time variation in salinity induced at any fixed point in the estuary by the current (Section 4.1.2).

Coastal plain (drowned river valley) estuaries have a cross section that converges with distance into the estuary, hence preserving, and sometimes amplifying, as in the case of the Delaware, the tidal current from the sea (see Ward and Montague, 1996, and citations therein). In these estuaries, the tidal excursion is sufficiently large and consistent that blue crabs can exploit it, using selective tidal stream transport (see Section 4.1.2). Megalops are known to employ selective flood transport to migrate up the estuary, mainly at night to avoid predators. Female blue crabs are known to use selective ebb transport in their spawning migration down the estuary.

In lagoonal estuaries, in contrast, tidal currents are concentrated within the locality of the inlets through the barrier islands, but in the interior of the lagoon the tidal excursion is small. In these systems, which include the Albemarle-Pamlico Sound, Chincoteague Bay, and all of the Texas bays, wind-driven currents are more important than tidal currents for large-scale transport through the estuary (Ward, 1997). While detailed observations have not been made of crab migration (in contradistinction to crab abundance) in San Antonio Bay, other than in the inlets, it seems likely that the same mechanism of current selection would be exploited. On the Texas

coast, some wind-driven currents, such as the seabreeze and the enhanced onshore flow in advance of a frontal passage (Ward, 1997, 2010b), will be directed inland from the sea, and the associated salinity change may serve as a cue for selective current transport analogous to STST. In general, however, a greater degree of randomness in the distribution of migratory stages of the crab would be expected in systems like this lacking a reliable current directed away from or toward the estuary mouth, such as a tidal current.

The megalop collections of Lochmann et al. (1995) in the Matagorda Entrance Channel are not only illustrative but of direct pertinence to San Antonio Bay, since the Pass Cavallo/Entrance Channel inlet complex is one of the two major megalop ingresses for the bay. The Entrance Channel is atypical of Texas inlets, being characterized by high tidal currents, large current-maintained depths and a U-shaped cross section (Ward, 1982). Depth at the sample station of Lochmann et al. ranged 15-18 m, compared to the channel *project depth* of 11.5 m. The inlet channel has never required maintenance because it is scoured by high currents. It is therefore unlikely that megalops descend to the bottom during an adverse current direction, as they would be scoured and entrained into the current. It is more probable that they are carried passively through the inlet. We note in passing that Pass Cavallo, the natural tidal inlet to Matagorda Bay, originally presented a range of depths and bottom types across its natural 2 n.m. width. While filling and reduction of the inlet have occurred in association with the tidal-prism capture of the Entrance Channel (Ward, 1982), even in its present diminished state, it is likely that Pass Cavallo is still more favorable for megalops to employ SFT than the Entrance Channel. It would be desirable for data collection like that of Lochmann et al. to be carried out in the pass.

The shallow vegetated regions of an estuary afford two attractions to crabs, a source of food and a shelter from predation (Hines, 2007 and citations therein). Both are particularly important to megalops and early juveniles during their initial grow-out. As noted earlier, juveniles and adults return to the shallows to molt, for which they require isolation and shelter (Section 3.1, Wolcott and Hines, 1990). Mating is a special molting event in which the usual requirement of refuge from predation is compounded by the male's need to avoid competitors (Section 3.2). Consequently, crabs also seek isolated protected shallows for mating. In most estuaries, these shallows are found in the upper reaches of the system, where also are usually located zones of

lower salinity. There does not seem to be a direct physiological requirement for low salinity *per se* for mating, however, since mating also takes place in homogeneous saline environments (e.g., Gelpi et al., 2009, Ramach et al., 2009). Ubiquity of blue crabs in these regions of San Antonio Bay and other Texas estuaries may be for reasons other than lower salinity, as suggested by recent studies on decapod habitat use in estuaries (e.g., Webb and Kneib, 2002), and as specifically noted by the GSA-BBEST (Section 4.2).

The domination of Chesapeake Bay in research on the blue crab life cycle (Sections 5.1 and 5.5) must be tempered with appreciation of the sheer size of this estuary, which affects the geographic delineation of the life-cycle stages of the crab. This is exemplified by the graphic of Figure 35. The Albemarle-Pamlico Sound system is nearly as imposing, being about half the size of the Chesapeake. Migrating crabs have been tracked moving several kilometres per day, which includes the use of STST. Mature females in Chesapeake Bay must migrate a distance on the order of 100 km to reach the spawning grounds in the lower segment.

Inseminated females have two options: (1) immediately migrate to the spawning grounds, (2) remain in the mating region, foraging for food and building energy stores (Medici et al., 2006). In a Texas bay, with the assumption that the best foraging is in the vegetated shallows in the inland sections of the bay, the inlet can still be reached in a matter of a few days to perhaps a couple of weeks. In the Chesapeake, several months may be needed. Therefore, there are trade-offs in the choice for the Chesapeake crab that are not faced by the Texas crab. After the pubertal molt and mating, the female is weak and undernourished, especially given her larger body size. To remain in the mating area where food is available improves the chances of eventually succeeding in spawning. But in the Chesapeake, the great distance to be negotiated means that the crab will arrive in the lower estuary too late to spawn, and will have to overwinter in the sediments, entailing additional risk. Immediately migrating to the spawning area requires foraging on the way, which itself is aleatory. The risk of finding inadequate food during migration, and spawning with limited energy stores, must be weighed against the dangers of overwintering to achieve a higher probability of hatching a first brood, typically the most

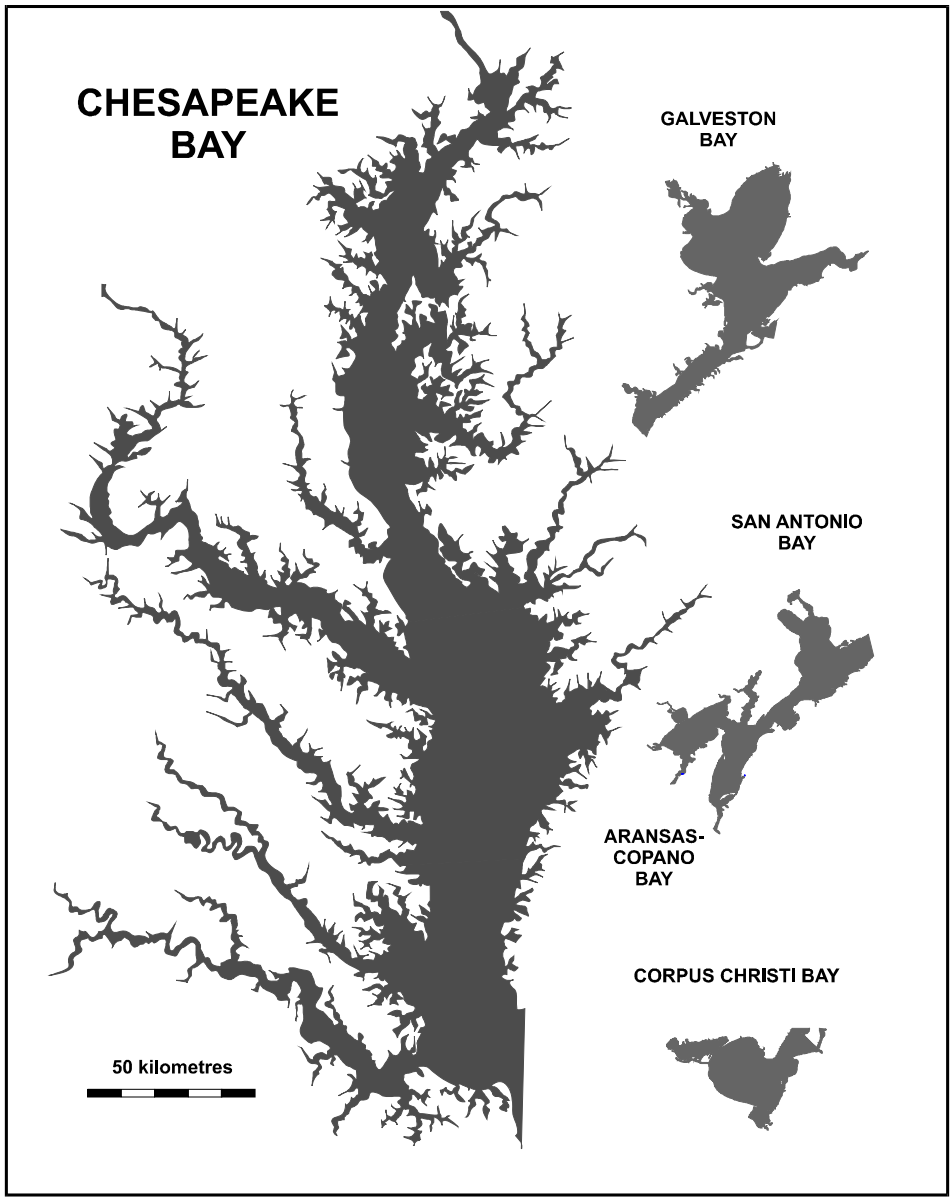


Figure 35 - Comparison of estuary scales, Chesapeake Bay versus Texas coast

successful, the following season. The second strategy is generally favored (e.g., Turner et al., 2003), the females beginning their migration in early fall and overwintering in the bay sediments.

In the mid-Atlantic, a clear break occurs between what are called Phase I and Phase II of the spawning migration (Section 5.1), consisting of the cold, winter period of crab inactivity. This

biphase migration is manifest in Delaware Bay, Chesapeake Bay, and Albemarle-Pamlico Sound, created by juxtaposition of the cold winter, requiring the overwinter hiatus, and the great migratory distance required by the size of the estuary. In the south Atlantic, in contrast, a winter hiatus is rare, and even rarer in the Gulf of Mexico. In Texas, the migration to the sea is determined by when mating occurs and the time devoted to foraging, and except for the occasional inclement winter generally takes place year-round.

Figure 36 displays the life cycle of a single crop (cohort) of blue crabs from its initial hatching period through development to maturity and the spawning of broods in the coastal ocean, for both Chesapeake Bay and San Antonio Bay (using elements of crab life cycle from Aransas-Copano through Galveston Bay to fill in the stages), based on data reviewed in previous sections and compiled in Appendix E. Water temperature data came from the Goodwin Islands NERR station in Chesapeake Bay and GBRA#1 in San Antonio Bay (disseminated by TAMU-CC TCOON). Daily temperatures were averaged over the 5-year period 2004-08 then cycled for the three years shown in Fig. 36. This figure presents the life cycle as a line-of-balance diagram, in which the horizontal bars indicate the calendar duration of the indicated activity and the rectangle the most intense period of that activity. Progression from one to the next, which corresponds to the development of the crab through various life stages, is indicated by the arrows. It should be emphasized that this does not diagram the life activity of a single crab, but of the population of (surviving) crabs that originated from a specific hatching season. Moreover, in a real estuary, there would be co-existing crab activities from earlier hatching periods, as well as later hatching periods, which are not indicated on the figure.

There are three major differences apparent between the two line-of-balance diagrams of Fig. 36. The first is the winter hiatus in the Chesapeake, noted above. The second is the shorter duration of the various life stage activities in the Chesapeake compared to San Antonio. For the Chesapeake, there is therefore a cleaner separation between these stage-related activies, and a more steplike progression through the life-cycle stages, while in San Antonio Bay all of the activities are underway nearly simultaneously. The third difference between the two is the

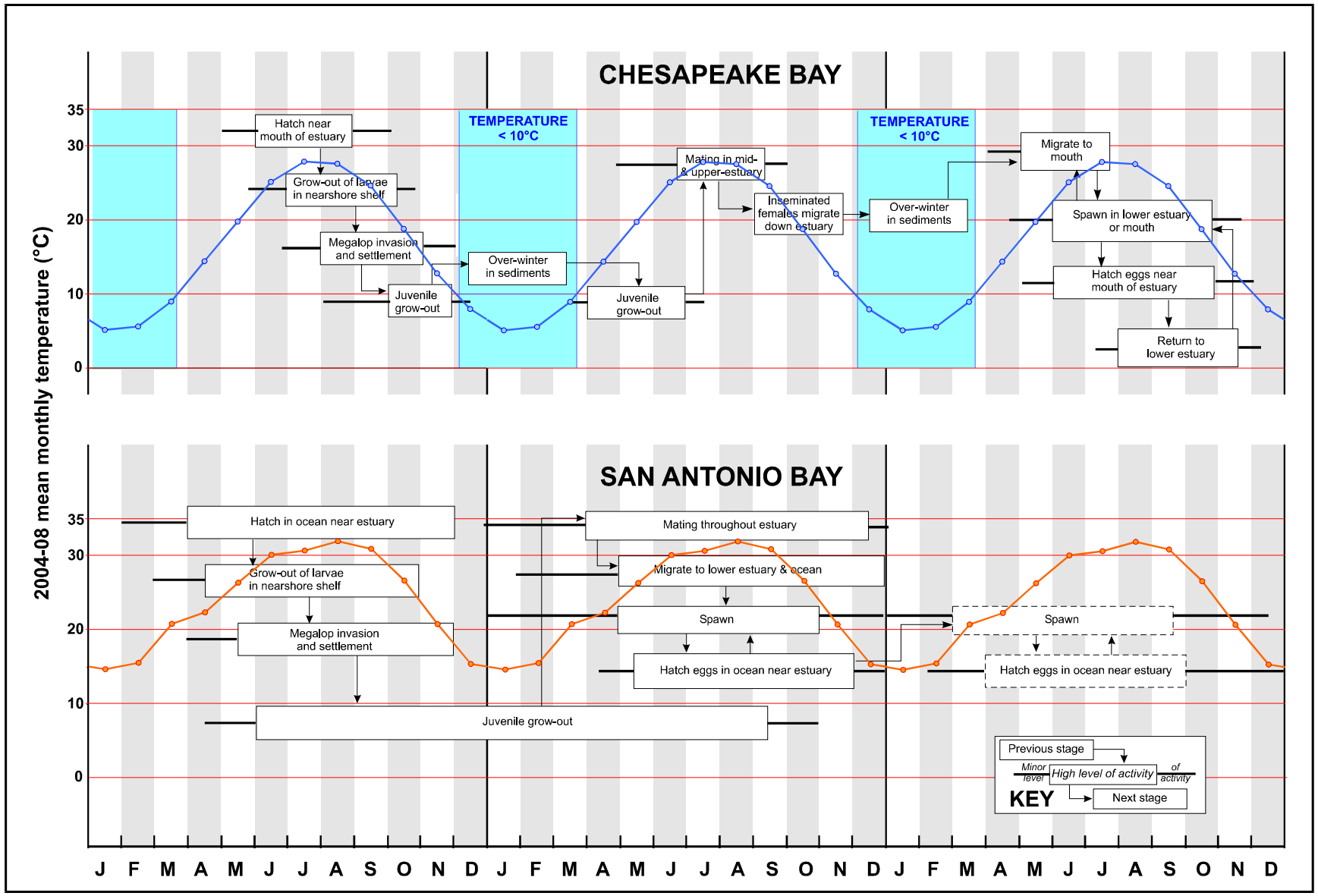


Figure 36 - Time line of life stages of a single year class of blue crab in representative estuaries of mid-Atlantic (above) and Texas coast (below))

shorter development to maturity in San Antonio Bay, completed about a year sooner than in the Chesapeake (cf. Fig. 6).

The least understood phase of the blue crab life cycle is the period of zoeal development, which takes place on the inner continental shelf. Patches of blue-crab larvae created by hatching events are carried along the coast by seasonal currents. Along both the mid-Atlantic and Texas coasts, the prevailing longshore current sets to the southwest following the bathymetric contours (Sections 5.3.1 and 5.3.2). This current is capable of carrying the larval patches many tens of kilometers down the coast. At the same time, cross-shelf transport associated with synoptic disturbances or local turbulence will mix the patches across the shelf potentially several tens of kilometers. During late summer, on both coasts, the longshore currents reverse and transport the larvae back up the coast. In the mid-Atlantic, where the reversal may take place farther offshore, creating a "banded" current pattern, this is regarded as a rentention mechanism, i.e., a circulation whose net result is to keep the larval patches confined to the same general area as their point of origin. Although there have apparently been no specific studies on the Gulf coast, it is reasonable to assume that the summer current reversal will play a similar rôle.

The discerning reader (if one has endured this far into this report) may have noted a latent symmetry in the conceptual model for mid-Atlantic estuaries that has gone unremarked in the literature. Just as early-stage zoeae hatched into the prevailing southward current may be returned in late summer by the reversed northward current, so may zoeae hatched into the late-summer northward current be returned to the south when the currents reverse back to southerly in fall. It was argued in Section 5.3.2 that the seasonal reversals of the Louisiana-Texas coastal current likewise would plausibly retain postlarvae from summer hatching on the Texas coast.

The plausibility of the mechanism of seasonally reversing currents for larval retention on the mid-Atlantic coast was supported by a recent modeling exercise. Tilburg et al. (2008b) coupled a model for hatching and grow-out of blue crab larvae with a coastal hydrodynamic model, a variant of the Princeton Ocean Model, described briefly in Section 5.4.4. The model was applied to Delaware Bay and adjacent continental shelf, and the modeled concentrations of larvae returning to the estuary as megalops were compared to the artificial-substrate time series

measured at the Broadkill, see, for example, Fig. 21. While the usual caveats apply to acceptance of the model predictions as representative of the real world (e.g., limited spatial resolution, influence of open boundary conditions, simplification of the boundary layers at surface and bottom, artificial quasi-random behavior, space-time simplification of driving inputs, etc.), the model appears to reproduce the measured results with a fair degree of success. It therefore presents a means for quantifying the complex interaction of a number of processes known or thought to be of importance to circulation, transport, and the resultant trajectories of advected tracers. It is a potentially better means of sorting out cause-and-effect than qualitative conceptual models such as equation (7). Analysis of the model simulation results yields the following conclusions:

(1) Only a small fraction (about 4% on average) of the larvae released at hatching eventually re-invade the estuary as megalops.
(2) The trajectories of these "successful" larvae fall into three categories: (i) the larvae remain in the general vicinity of the estuary mouth, (ii) the larvae are transported downcoast in the outflow plume, then offshore, and eventually back upcoast, (iii) the larvae are transported offshore from the mouth out of the outflow plume, then carried upcoast, eventually driven shoreward into the downcoast current to be returned to the estuary.
(3) The primary physical mechanisms in the model influencing the fate of larvae in the shelf are wind (and wind-driven currents) and freshwater inflow, the former being generally dominant.
(4) The maximum effect of a wind event occurs when the wind has both longshore and onshore components (directed about 20° across-shelf) so that both onshore wind stress and Ekman transport contribute. However, analysis of the model simulations of these onshore Ekman-transport wind events failed to expose a direct association with settlement events. Indeed, the majority of the simulated settlement events are not associated with particular downwelling events.*

* We note that the example trajectories displayed by Tilburg et al. are more confined to the nearshore (within about 10 km) than indicated by circulation studies on the shelf and the observed distribution of megalops.

By this point in the summer, the larvae will have become megalops. Seasonally varying winds are considered to concentrate the megalops in the nearshore along the beaches, though the precise mechanism and its relation to synoptic disturbances are a matter of debate (see Section 5.3). Some of these megalops will fall under the influence of estuary mouths or inlets, where they will be drawn into the estuary. In San Antonio Bay, entry will be through Paso Cavallo (and the Matagorda Entrance Channel) and Aransas Pass. Limited observations in these inlets and other inlets on the Texas coast confirm that the megalop influx occurs as large, sporadic pulses of high density superposed on a relatively constant, low density (Section 5.4.1). Artificial substrate collectors deployed on both the Atlantic and Gulf of Mexico coasts established that the megalop influx to the Gulf of Mexico estuaries is one-to-two orders of magnitude greater than the Atlantic. Yet, the densities of early juveniles in primary habitats on both coasts are about the same. This has led some researchers to propose that megalopal settlement on the Gulf coast is probably predation-limited, perhaps even self-regulated through cannibalism (Section 5.4.4). It should be noted, however, that the data is very limited upon which the judgment of equivalent juvenile densities is based (Sections 5.4.4 and 5.5.1). (For that matter, the megalopal influx in Texas was measured at only one inlet, *viz*. Bolivar Roads in the Galveston system.)

While a reasonable estimate can be made of spawning stock from TPWD observations of berried crabs, and a corresponding estimate of the initial hatching, there is little quantitative data on the development and fate of the larvae and postlarvae on the Texas inner shelf. Physical observations (currents and circulation) are spotty over time, as well. Routine monitoring of megalop influx to San Antonio Bay, were it to be implemented, would repair this deficiency to a large extent.

A basic question confronting the analysis of blue-crab data, such as that of TPWD, for dependencies on external variables (e.g., river flow) is: to what extent are the variations in blue crab density forced by variables other than those explicitly addressed? A statistical precept that governs our ability to extract quantitative relations from data is:

> Any external variable not explicity modeled represents a source of variance.

In this report, a number of such variables have been identified, including harvesting of crabs, mortality due to predation and disease, internal migration to seek or avoid habitat properties, climate effects on growth and metabolism, nutrient supply and planktonic food sources, and so on. A part of increasing sophistication in analysis is the quantification and inclusion of such variables.

One potentially important variable is the supply of megalops to the estuary. The status of Cedar Bayou is important in this respect, but it has received little attention in this report, because for most of the 1982-2008 period of this analysis it has been closed or only marginally open (see Section 6.5). Extension of analysis to the 1960-70's would require its explicit consideration, because during this period Cedar Bayou attained its largest recorded historical size (Ward, 2010b). As noted earlier (Sections 5.2 and 5.4.1), some megalop influx data were also collected during this period.

A common assumption (invoking the r-selected nature of blue crabs) is that the influx of megalops is so great that all habitats are populated, and the subsequent growth and organism densities are governed entirely by the bay environment, characterized by water chemistry, river flow, food availability, mortality, and related variables. This is the "saturation hypothesis" (e.g., Caley et al., 1996) and is a frequently-unstated premise of much of the environmental-forcing analyses of the literature. Its applicability to San Antonio Bay, and the other Texas bays, is strictly unknown. For now, megalop supply must be regarded as one more source of variance in the data. If, however, it were to prove limiting, then its explicit evaluation would be necessary. The possible coupling of the historical declining trend of blue crabs in the Coastal Bend estuaries with large-scale climate modes (the Atlantic multidecadal oscillation, specifically) noted in Section 6.5 might be an example.

Consonant with the limited resources for this review, the analytical methods have been limited to straightforward linear models and graphical comparisons. The data set of TPWD is rich, however, and capable of supporting much more sophisticated analyses. A second phase of this project is planned to concentrate more on the analysis of data than summary of literature, and will employ a more extensive data set synthesized from older observations as well as collections

performed by other researchers. While the effects of river flow will continue to be a central focus, it is recommended that additional variables be included. Other decapods, notably penaeid shrimp, have similar life histories, including larval grow-out on the inner shelf, and may provide insight into this phase of the blue crab life cycle. Multivariate methods, both linear and nonlinear should be applied. Because the blue crab data is essentially a record of observations taken quasi-regularly in time, as are the associated hydrographical and biological data sets, modern methods of discrete time-series analysis should be used, both in the frequency and time domains. Finally, almost nothing was said in this review about modern population modeling, since this topic clearly lay beyond the scope of the study. For future work, this may afford insight into the dynamics of blue-crab population, especially those aspects such as mortality that are presently not measured.

References

Adkins, G., 1972a: *A study of the blue crab fishery in Louisiana*. Tech. Bull. 3, Louisiana Wildlife and Fisheries Commission, Baton Rouge.

Adkins, G., 1972b: *Notes on the occurrence and distribution of the rhizocephalan parasite (Loxothylacus texanus Boschma) of blue crabs (Callinectes sapidus Rathbun) in Louisiana estuaries*. Tech. Bull. 2, Louisiana Wildlife and Fisheries Commission, Baton Rouge.

Adkins, G., 1982: The blue crab fishery of Louisiana. In: *Proceedings of the blue crab colloquium* (H. Perry and W. Van Engel, eds.), 15-16. Tech. Rep. 7, Gulf States Marine Fisheries Commission, Ocean Springs, MS.

Aguilar, R., A. Hines, T. Wolcott, D. Wolcott, M. Kramer and R. Lipcius, 2005: The timing and route of movement and migration of post-copulatory female blue crabs, *Callinectes sapidus* Rathbun, from the upper Chesapeake Bay. *J. Exp. Mar. Biol. Ecol. 319* , 117-128.

Aguilar, R., E. Johnson, A. Hines, M. Kramer, and M. Goodison, 2008: Importance of blue crab life history for stock enhancement and spatial management of the fishery in Chesapeake Bay. *Rev. Fish. Sci. 18* (1-3), 117-124.

Akin, S., K. Winemiller and F. Gelwick, 2003: Seasonal and spatial variations in fish and macrocrustacean assemblage structure in Mad Island Marsh estuary, Texas. *Est. Coast. Shelf Sci. 57*, 269-282.

Allen, T., H. Tolvanen, G. Oertel, and G. McLeod, 2007: Spatial characterization of environmental gradients in a coastal lagoon, Chincoteague Bay. *Estuaries & Coasts 30* (6), 959-977.

Alvarez, F., G. Alcaraz, and R. Robles, 2002: Osmoregulatory disturbances induced by the parasitic barnacle *Loxothylacus texanus* (Rhizocephala) in the crab *Callinectes rathbunae* (Portunidae). *J. Exp. Mar. Biol. Ecol. 278* , 135-140.

Archambault, J., E. Wenner and J. Whitaker, 1990: Life history and abundance of blue crab, *Callinectes sapidus* Rathbun, at Charleston Harbor, South Carolina. *Bull. Mar. Sci. 46*, 145-158.

Arudpragasam, K., and E. Naylor, 1964a: Gill ventilation and the role of reversed respiratory currents in *Carcinus maenas* (L.). *J. Exp. Biol. 41*, 299-307.

Arudpragasam, K., and E. Naylor, 1964b: Gill ventilation volumes, oxygen consumption and respiratory rhythms in *Carcinus maenas* (L.). *J. Exp. Biol. 41*, 309-321.

Atar, H., and S. Seçer, 2003: Width/Length-Weight relationships of the blue crab (*Callinectes sapidus* Rathbun 1896) population living in Beymelek Lagoon Lake. *Turk. J. Vet. Anim. Sci. 27*, 443-447.

Austin, J., and S. Lentz, 1999: The relationship between synoptic weather systems and meteorological forcing on the North Carolina inner shelf. *J. Geophys. Res. 104* (C8), 18,159-18,185.

Ballard, B., and W. Abbott, 1969: Osmotic accommodation in *Callinectes sapidus* Rathbun. *Comp. Biochem. Physiol. 29*, 671-687.

Batterton, C., and J. Cameron, 1978: Characteristics of resting ventilation and response to hypoxia, hypercapnia, and emersion in the blue crab *Callinectes sapidus* (Rathbun). *J. Exp. Zool. 203*, 403-418.

Beer, T., 1996: *Environmental oceanography, 2nd ed*. Boca Raton, FL: CRC Press.

Beron-Vera, F., and M. Olascoaga, 2009: An assessment of the importance of chaotic stirring and turbulent mixing on the West Florida shelf. *J. Phys. Oceanog. 39*, 1743-1755.

Bertics, V., and Z. Wiebke, 2009: Biodiversity of benthic micorbial communities in bioturbated coastal sediments is controlled by geochemical microniches. *The ISME Journal 3* , 1269-1285.

Bishop, J., E. Olmi,and G.Yianopoulos, 1984: Efficacy of peeler pots and experimental habitat pots for capture of premolt blue crabs. *Trans. Am. Fish. Soc. 113*, 642-654.

Bishop, R., H. Miller, R. Walker, D. Hurley, T. Menken and C. Tilburg, 2010: Blue crab (*Callinectes sapidus* Rathbun, 1896) settlement at three Georgia (USA) estuarine sites. *Estuaries & Coasts 33*, 688-698.

Blake, R.W., 1985: Crab carapace hydrodynamics. *J. Zool., London (A) 207*, 407-423.

Blackmon, D., and D. Eggleston, 2001: Factors influencing planktonic, post-settlement dispersal of early juvenile blue crabs (*Callinectes sapidus* Rathbun). *J. Exp. Mar. Biol. Ecol. 257*, 183-203.

Blanton, B., A. Aretxabaleta, F. Werner, and H. Seim, 2003: Monthly climatology of the continental shelf waters of the south Atlantic bight. *J. Geophys. Res. 108* (C8), doi:10.1029/ 2002JC001609.

Blanton, J., E. Wenner, F. Werner, and D. Knott, 1995: Effects of wind-generated coastal currents on the transport of blue crab megalopae on a shallow continental shelf. *Bull. Mar. Sci. 57* (3), 739-752.

Blanton, J., P. Verity, J. Amft, E. Wenner, C. Barans, D. Knott, B. Stender and S. Wilde, 1998: *Key factors influencing transport of white shrimp postlarvae in southeastern U.S. estuaries*. Georgia Sea Grant Program, University of Georgia, Athens.

Boicourt, W.C., 1982: Estuarine larval retention mechanisms on two scales. In: *Estuarine comparisons* (V. Kennedy, ed.), 445-458. New York: Academic Press.

Boicourt, W., W. Wiseman, A. Valle-Levinson, and L. Atkinson, 1998: Continental shelf of the southeastern United States and the Gulf of Mexico: In the shadow of the western boundary current. Chap. 6 in: *The sea 11: The global coastal ocean, regional studies and syntheses* (A. Robinson and K. Brink, eds.), 135-182. New York: John Wiley & Sons, Inc.

Boylan, J., and E. Wenner, 1993: Settlement of brachyuran megalopae in a South Carolina, USA, estuary. *Mar. Ecol. Prog. Ser. 97*, 237-246.

Breuer, J.P., 1962: An ecological survey of the Lower Laguna Madre of Texas, 1953-1959. *Publ. Inst. Mar. Sci. 8*, 153-183.

Brookins, K., and C. Epifanio, 1985: Abundance of brachyuran larvae in a small coastal inlet over six consecutive tidal cycles. *Estuaries 8* (1), 60-67.

Brumbaugh, R., and J. McConaugha, 1995: Time to metamorphosis of blue crab *Callinectes sapidus* megalopae: effects of benthic macroalgae. *Mar. Ecol. Prog. Ser. 129*, 113-118.

Brylawski, B., and T. Miller, 2006: Temperature-dependent growth of the blue crab (*Callinectes sapidus*): a molt process approach. *Can. J. Fish. Aquat. Sci. 63*, 1298-1308.

Bumpus, D. F., 1973: A description of the circulation on the continental shelf of the East Coast of the United States. *Prog. Oceanogr. 6*, 111-157.

Cadman, L., and M. Weinstein, 1985: Size-weight relationships of postecdysial juvenile blue crabs (*Callinectes sapidus* Rathbun) from the lower Chesapeake Bay. *J. Crust. Biol. 5*(2), 306-310.

Cadman, L., and M. Weinstein, 1988: Effects of temperature and salinity on the growth of laboratory-reared juvenile blue crabs *Callinectes sapidus* Rathbun. *J. Exp. Mar. Biol. Ecol. 121*, 193-207.

Cameron, J., and C. Batterton, 1978: Antennal gland function in the freshwater blue crab *Callinectes sapidus*: Water, electrolyte, acid base, and ammonia excretion. *J. Comp. Physiol. 123B*, 143-148.

Cargo, D. G., 1958: The migration of adult female blue crabs, *Callinectes sapidus* Rathbun, in the Chincoteague Bay and adjacent waters. *J. Mar. Res. 16* (3), 180-191.

Carpenter, J., and D. Cargo, 1957: *Oxygen requirement and mortality of the blue crab in the Chesapeake Bay*. Tech. Rep. 13, Chesapeake Bay Institute, Johns Hopkins.

Carr, S., R. Tankersley, J. Hench, R. Forward, and R. Luettich, 2004: Movement patterns and trajectories of ovigerous blue crabs *Callinectes sapidus* during the spawning migration. *Est., Coast. Shelf Sci. 60*, 567-579.

Carriker, M. R., 1951: Ecological observations on the distribution of oyster larvae in New Jersey estuaries. *Ecol. Monogr. 21* (1), 19-38.

Caley, M., M. Carr, M. Hixon, T. Hughes, G. Jones and B. Menge, 1996: Recruitment and the local dynamics of open marine populations. *Ann. Rev. Ecol. Sys. 27*, 477-500.

Cházaro-Olvera, S., and M. Peterson, 2004: Effects of salinity on growth and molting of sympatric *Callinectes* spp. from Camaronera Lagoon, Veracruz, Mexico. *Bull. Mar. Sci., 74* (1), 115-127.

Childress, R., E. Bradley, E. Hagen and S. Williamson, 1975: *The effects of freshwater inflows on hydrological and biological parameters in the San Antonio Bay system, Texas*. Coastal Fisheries Branch, Texas Parks & Wildlife Department, Austin, 190 pp.

Cho, K., R. Reid, and W. Nowlin, 1998: Objectively mapped stream function fields on the Texas-Louisiana shelf based on 32 months of moored current meter data. *J. Geophys. Res. 103* (C5), 10,377-10,390.

Choucair, P., K. Spiller and K. Meador, 2006: *Status and trends of selected marine fauna in the Coastal Bend Bays and Estuary Program study area, 1984-2004*. Report CBBEP-43, Project 0504, Coastal Bend Bays & Estuaries Program, Corpus Christi, Texas. Online URL: http://www.cbbep.org/publications/virtuallibrary/2008table/0504.pdf

Churchill, E.P., 1919: Life history of the blue crab. *Bull. Bur. Fish. 36*, 91-128.

Cochrane, J., and F. Kelly, 1986: Low-frequency circulation on the Texas-Louisiana continental shelf. *J. Geophs. Res. 91* (C9), 10,645-10,659.

Condrey, R., and C. Gelpi, 2010: *Blue crab (Callinectes sapidus) use of the Ship/Trinity/Tiger Shoal Complex as a nationally important spawning/hatching/foraging ground*. MMS 2009-043, LSU Coastal Marine Institute, Gulf of Mexico OCS Region, Minerals Management Service.

Copeland, B. J., 1965: Fauna of the Aransas Pass inlet, Texas. I. Emigration as shown by tide trap collections. *Publ. Inst. Mar. Sci. 10*, 9-21.

Copeland, D. and A. Fitzjarrell, 1968: The salt absorbing cells in the gills of the blue crab (*Callinectes sapidus* Rathbun) with notes on modified mitochondria. *Z. Zellforsch. Mikrosk. Anat. 92*, 1-22.

Costlow, J. D., 1965: Variability in larval stages of the blue crab, *Callinectes sapidus*. *Biol Bull. 128* (1), 58-66.

Costlow, J. D., 1967: The effect of salinity and temperature on survival and metamorphosis of megalops of the blue crab *Callinectes sapidus*. *Helgoländer Wissenschaftliche Meeresuntersuchungen 15* (1-4), 84-97.

Costlow, J., and C. Bookhout, 1959: The larval development of *Callinectes sapidus* Rathbun reared in the laboratory. *Biol. Bull. 116* (3), 373-396.

Costlow, J., and C. Bookhout, 1962: The effect of environmental factors on larval development of crabs. In: *Biological problems in water pollution, 3rd seminar* (C.M. Tarzwell, ed.), 77-86. Publ. 999-WP-25, U.S. Public Health Service, Cincinnati, Ohio.

Couch, J., and S. Martin, 1982: Protozoan symbionts and related diseases of the blue crab, *Callinectes sapidus* Rathbun, from the Atlantic and Gulf coasts of the United States. In: *Proceedings of the blue crab colloquium* (H. Perry and W. Van Engel, eds.), 71-80. Tech. Rep. 7, Gulf States Marine Fisheries Commission, Ocean Springs, MS.

Csanady, G. T., 2001: *Air-sea interaction: laws and mechanisms*. Cambridge, UK: Cambridge University Press.

Cushing, D. H., 1969: The regularity of the spawning season in some fishes. *J. Cons. Int. Explor. Mer. 33*, 81-92.

Dall, W., B. Hill, P. Rothlisberg, and D. Staples, 1990: The biology of the Penaeidae. *Adv. Mar. Biol. 27*, 1-489.

Darnell, R. M., 1959: Studies of the life history of the blue crab (Callinectes sapidus Rathbun) in Louisiana waters. *Trans. Am. Fish. Soc. 88* (4), 294-304.

Darnell, R., and J. McEachran, 1987: *Larval recruitment of estuarine related fishes and invertebrates of the Texas coast*. TWDB Contract Number 5571018, Departments of Oceanography and Wildlife and Fisheries Sciences, Texas A&M University, College Station.

Darnell, M.Z., D. Rittschof, K. Darnell, and R. McDowell, 2009: Lifetime reproductive potential of female blue crabs *Callinectes sapidus* in North Carolina, USA. *Mar. Ecol. Prog. Ser. 394*, 153-163.

Darnell, M.Z., D. Rittschof, and R. Forward, 2010: Endogenous swimming rhythms underlying the spawning migration of the blue crab, *Callinectes sapidus*: ontogeny and variation with ambient tidal regime. *Mar. Biol. 157*, 2415-2425.

Darnell, M. Z., T. Wolcott, and D. Rittschof, 2012: Environmental and endogenous control of selective tidal-stream transport behavior during blue crab *Callinectes sapidus* spawning migrations. *Mar. Biol. 159*, 621-631.

Das, T., and W. Stickle, 1993: Sensitivity of crabs *Callinectes sapidus* and *C. similis* and the gastropod *Stramonita haemastoma* to hypoxia and anoxia. *Mar. Ecol. Prog. Ser. 98*, 263-274.

Das, T., and W. Stickle, 1994: Detection and avoidance of hypoxic water by juvenile *Callinectes sapidus* and *C. similis*. *Mar. Biol. 120*, 593-600.

Daugherty, F. M., 1952: The blue crab investigation, 1949-50. *Texas J. Sci. 1* (1), 77-84.

Davis, C., 1965: A study of the hatching process in aquatic invertebrates: XX. The blue crab, *Callinectes sapidus*, Rathbun, XXI. The nemertean, *Carcinonemertes carcinophila* (Kolliker). *Chesap. Sci. 6* (4), 201-208.

Davis, J., and R. Sizemore, 1982: Incidence of *Vibrio* species associated with blue crabs (*Callinectes sapidus*) collected from Galveston Bay, Texas. *Appl. Environ. Microbiol. 43* (5), 1092-1097.

Defant, A., 1961: *Physical Oceanography, I*. New York: The Macmillan Company.

deFur, P., and A. Pease, 1988: Metabolic and respiratory compensation during long term hypoxia in blue crabs, Callinectes sapidus. In: *Understanding the estuary: advances in Chesapeake Bay Research* (M. Lynch and L. Crome, eds.), 608-616. Publ. 129, Chesapeake Research Consortium, Solomons MD.

deFur, P., A. Pease, A. Siebelink, and S. Elfers, 1988: Respiratory responses of blue crabs, *Callinectes sapidus*, to emersion. *Comp. Biochem. Physiol. 89A* (1), 97-101.

deFur, P., C. Mangum, and J. Reese, 1990: Respiratory responses of the blue crab *Callinectes sapidus* to long-term hypoxia. *Biol. Bull. 178* (1), 46-54.

DePaola, A., C. Kaysner, J. Bowers, and D. Cook, 2000: Environmental investigations of *Vibrio parahaemolyticus* in oysters after outbreaks in Washington, Texas, and New York (1997 and 1998). *Appl. Environ. Microbiol. 66* (11), 4649-4654.

DeVries, M., R. Tankersley, R. Forward, W. Kirby-Smith, and R. Leuttich, 1994: Abundance of estuarine crab larvae is associated with tidal hydrologic variables. *Mar Biol. 118*, 403-413.

Dickinson, G., D. Rittschof, and C. Latanich, 2006: Spawning biology of the blue crab, *Callinectes sapidus*, in North Carolina. *Bull. Mar. Sci. 79* (2), 273-285.

Dittel, A., and C. Epifanio, 1982: Seasonal abundance and vertical distribution of crab larvae in Delaware Bay. *Estuaries 5* (3), 197-202.

Dowse, H., and J. Ringo, 1989: The search for hidden periodicities in biological time series revisited. *J. Theor. Biol. 139*, 487-515.

Drach, P., 1939: Mue et cycle d'intermue chez les Crustacés Décapodes. *Ann. Inst. Océanog. (Paris) 19*, 103-391.

Dudley, D., and M. Judy, 1971: *Occurrence of larval, juvenile, and mature crabs in the vicinity of Beaufort Inlet, North Carolina*. Tech. Rep. SSRF-637, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle WA.

Dyke, P., 2007: *Modeling coastal and offshore processes*. London: Imperial College Press.

Dzwonkowski, B., J. Kohut, and X.-H. Yan, 2009: Seasonal differences in wind-driven across-shelf forcing and response relationships in the shelf surface layer of the central Mid-Atlantic bight. *J. Geophys. Res. 114*, C08018, doi: 10.1029/2008JC004888.

Eby, L., and L. Crowder, 2002: Hypoxia-based habitat compression in the Neuse River estuary: context-dependent shifts in behavioral avoidance thresholds. *Can. J. Fish. Aquat. Sci. 59*, 952-965.

Edwards, K., J. Hare, F. Werner, and B. Blanton, 2006: Lagrangian circulation on the southeast US continental shelf: Implications for larval dispersal and retention. *Cont. Shelf Res. 26*, 1375-1394.

Eggleston, D. B., 1990: Foraging behavior of the blue crab, *Callinectes sapidus*, on juvenile oysters, *Crassostrea virginica*: effects of prey density and size. *Bull. Mar. Sci. 46* (1), 62-82.

Eggleston, D., G. Bell, and A. Amavisca, 2005: Interactive effects of episodic hypoxia and cannibalism on juvenile blue crab mortality. *J. Exp. Mar. Biol. Ecol. 325*, 18-26.

Eggleston, D., N. Reyns, L. Etherington, G. Plaia and L. Xie, 2010: Tropical storm and environmental forcing on regional blue crab (*Callinectes sapidus*) settlement. *Fish. Oceanogr. 19* (2), 89-106.

Ekman, V. W., 1899: Ein Beitrag zur Erklärung und Berechnung des Stromverlaufes in Flußmündungen. *Ofers. Kgl. Vet. Akad. Handl. Stockholm* 5, 469.

Ekman, V. W., 1905: On the influence of the earth's rotation on ocean currents. *Arkiv. f. Math. Astron. o. Fysik. 2* (11), 1-53.

Ekman, V. W., 1928: A survey of some theoretical investigations on ocean currents. *J. Cons. Int. 3* (3).

Ekman, V. W., 1932: Studien zur Dynamik der Meeresströmungen. *Gerl. Beitr. z. Geophysik 36*, 385.

Epiranio, C. E., 1988: Transport of invertebrate larvae between estuaries and the continental shelf. *Am. Fish. Soc. Symp. 3*, 104-114.

Epifanio, C. E., 1995: Transport of blue crab (*Callinectes sapidus*) larvae in the waters off mid-Atlantic states. *Bull. Mar. Sci. 57* (3), 713-725.

Epifanio, C. E., 2003: Spawning behavior and larval ecology: a brief summary. *Bull. Mar. Sci. 72* (2), 325-330.

Epifanio. C. E., 2007: Biology of larvae. Chapter 12 in: *The blue crab, Callinectes sapidus* (Kennedy and Cronin, eds., 2007), 512-533.

Epifanio, C., and R. Garvine, 2001: Larval transport on the Atlantic continental shelf of North America: a review. *Est. Coast. Shelf Sci. 52*, 51-77.

Epifanio, C., and C. Tilburg, 2008: Transport of blue crab larvae in the Middle Atlantic Bight: a wet and windy journey. *J. Mar. Res. 66*, 723-749.

Epifanio, C.,C. Valenti, and A. Pembroke, 1984: Dispersal and recruitment of blue crab larvae in Delaware Bay, U.S.A. *Est. Coast. Shelf Sci. 18*, 1-12.

Epifanio, C., A. Masse, and R. Garvine, 1989: Transport of blue crab larvae by surface currents off Delaware Bay, USA. *Mar. Ecol. Prog. Ser. 54*, 35-41.

Etherington, L., and D. Eggleston, 2000: Large-scale blue crab recruitment: linking postlarval transport, post-settlement planktonic dispersal, and multiple nursery habitats. *Mar. Ecol. Prog. Ser. 204*, 179-198.

Etherington, L., and D. Eggleston, 2003: Spatial dynamics of large-scale, multistage crab (*Callinectes sapidus*) dispersal: determinants and consequences for recruitment. *Can. J. Fish. Aquat. Sci. 60*, 873-887.

Etherington, L., D. Eggleston and W. Stockhausen, 2003: Partitioning loss rates of early juvenile blue crabs from seagrass habitats into mortality and emigration. *Bull. Mar. Sci. 72* (2), 371-391.

Ettinger, W., and R. Blye, 1981: Occurrence of the blue crab *Callinectes sapidus* in the tidal freshwater reaches of the Delaware and Schuylkill Rivers in 1976. *J. Crust. Biol. 1* (2), 177-182.

Fingerman, M., 1955: Persistent daily and tidal rhythms of color change in *Callinectes sapidus*. *Biol. Bull. 109* (2), 255-264.

Fisher, M. R., 1999: Effect of temperature and salinity on size at maturity of female blue crabs. *Trans. Am. Fish. Soc. 128*, 499-506.

Florkin, M., and E. Schoffoniels, 1969: *Molecular approaches to ecology*. New York: Academic Press.

Fontaine, C. T., 1985. *A survey of potential disease-causing organisms in bait shrimp from west Galveston Bay, Texas*. NOAA Tech. Memo. NMFS-SEFC-169, National Marine Fisheries Service.

Forward, R., and D. Rittschof, 1994: Photoresponses of crab megalopae in offshore and estuarine waters: implications for transport. *J. Exp. Mar. Biol. Ecol. 182*, 183-192.

Forward, R., and J. Cohen, 2004: Factors affecting the circatidal rhythm in vertical swimming of ovigerous blue crabs, *Callinectes sapidus*, involved in the spawning migration. *J. Exp. Mar. Biol. Ecol. 299*, 255-266.

Forward, R., D. Frankel, and D. Rittschof, 1994: Molting of megalopae from the blue crab *Callinectes sapidus*: effects of offshore and estuarine cues. *Mar. Ecol. Prog. Ser. 113*, 55-59.

Forward, R., R. Tankersley, M. DeVries, and D. Rittschof, 1995: Sensory physiology and behavior of blue crab (*Callinectes sapidus*) postlarvae during horizontal transport. *Mar. Fresh. Behav. Physiol. 26*, 233-248.

Forward, R., M. DeVries, D. Rittschof, D. Frankel, J. Bischoff, C. Fisher and J. Welch, 1996: Effects of environmental cues on metamorphosis of the blue crab *Callinectes sapidus*. *Mar. Ecol. Prog. Ser. 131*, 165-177.

Forward, R., J. Swanson, R. Tankersley, and J. Welch, 1997: Endogenous swimming rhythms of blue crab, *Callinectes sapidus*, megalopae: effects of offshore and estuarine cues. *Mar. Biol. 127*, 621-628.

Forward, R., R. Tankersley, and D. Rittschof, 2001: Cues for metamorphosis of brachyuran crabs: an overview. *Amer. Zool. 41*, 1108-1122.

Forward, R., R. Tankersley and P. Pochelon, 2003a: Circatidal activity rhythms in ovigerous blue crabs, *Callinectes sapidus*: implications for ebb-tide transport during the spawning migration. *Mar. Biol. 142*, 67-76.

Forward, R., R. Tankersley and J. Welch, 2003b: Selective tidal-stream transport of the blue crab *Callinectes sapidus*: an overview. *Bull. Mar. Sci. 72* (2), 347-365.

Forward, R., R. Tankersley, K. Smith, and J. Welch, 2003c: Effects of chemical cues on orientation of blue crab, *Callinectes sapidus*, megalopae in flow: implications for location of nursery areas. *Mar. Biol. 142*, 747-756.

Forward, R., J. Cohen, R. Irvine, J. Lax, R. Mitchell, A. Schick, M. Smith, J. Thompson, and J. Venezia, 2004a: Settlement of blue crab *Callinectes sapidus* megalopae in a North Carolina estuary. *Mar. Ecol. Prog. Ser. 269*, 237-247.

Forward, R., N. Reyns, H. Diaz, J. Cohen and D. Eggleston, 2004b: Endogenous swimming rhythms of juvenile blue crabs, *Callinectes sapidus*, as related to horizontal transport. *J. Exp. Mar. Biol. Ecol. 299*, 63-76.

Forward, R., J. Cohen, M. Darnell and A. Saal, 2005a: The circatidal rhythm in vertical swimming of female blue crabs, *Callinectes sapidus*, during their spawning migration: a reconsideration. *J. Shellfish Res. 24* (2), 587-590.

Forward, R., N. Reyns, H. Diaz, J. Cohen, and D. Eggleston, 2005b: Endogenous swimming rhythms underlying secondary dispersal of early juvenile blue crabs, *Callinectes sapidus*. *J. Exp. Mar. Biol. Ecol. 316*, 91-100.

Freeman, J., G. Kilgus, D. Laurendeau and H. Perry, 1987: Postmolt and intermolt molt cycle stages of *Callinectes sapidus*. *Aquaculture 61*, 201-209.

Garland, E., C. Zimmer, and S. Lentz, 2002: Larval distributions in inner-shelf waters: the roles of wind-driven cross-shelf currents and diel vertical migrations. *Limnol. Oceanogr. 47* (3), 803-917.

Garvine, R. W., 2004: The vertical structure and subtidal dynamics of the inner shelf off New Jersey. *J. Mar. Res. 62*, 337-371.

Garvine, R., C. C. Epifanio, C. E. Epifanio, and K-C. Wong, 1997: Transport and recruitment of blue crab larvae: a model with advection and mortality. *Est. Coast. Shelf Sci. 45*, 99-111.

Gayon, J., 2000: History of the concept of allometry. *Amer. Zool. 40*, 748-758.

Gelpi, C., R. Condrey, J. Fleeger, and S. Dubois, 2009: Discovery, evaluation, and implications of blue crab, Callinectes sapidus, spawning, hatching, and foraging grounds in federal (US) waters offshore of Louisiana. *Bull. Mar. Sci. 85* (3), 203-222.

Gerard, J., and R. Gilles, 1972: The free amino-acid pool in *Callinectes sapidus* (Rathbun) tissues and its rôle in the osmotic intracellular regulation. *J. Exp. Mar. Biol. Ecol. 10*, 125-136.

Gifford, C. A., 1962: Some aspects of osmotic and ionic regulation in the blue crab, *Callinectes sapidus*, and the ghost crab, *Ocypode albicans*. *Publ. Inst. Mar. Sci. 8* , 97-125.

Gill, A. E., 1982: *Atmosphere-ocean dynamics*. International Geophysics Series 30. New York: Academic Press.

Gökçe, G., D. Ergüden, L. Sangün, M. Çekiç and S. Alagöz, 2006: Width/length-weight and relationships of the blue crab (*Callinectes sapidus* Rathbun, 1986) population living in Camlik Lagoon Lake (Yumurtalik). *Pakistan J. Biol. Sci. 9* (8), 1460-1464.

Goodrich, D., J. van Montfrans, and R. Orth, 1989: Blue crab megalopal influx to Chesapeake Bay: evidence for a wind-driven mechanism. *Est. Coast. Shelf Sci. 29*, 247-260.

Gould, S. J., 1971: Geometric similarity in allometric growth: a contribution to the problem of scaling in the evolution of size. *Amer. Nat. 105* (942), 113-136.

Govind, C. K., 2007: Muscles and neurons. Chapter 4 in: *The blue crab, Callinectes sapidus* (Kennedy and Cronin, eds., 2007), 133-171.

Govind, C., and J. Blundon, 1985: Form and function of the asymmetric chelae in blue crabs with normal and reversed handedness. *Biol. Bull. 168*, 321-331.

Graf, G., and R. Rosenberg, 1997: Bioresuspension and biodeposition: a review. *J. Mar. Sys. 11*, 269-278.

Gray, E., and C. Newcombe, 1938a: The relative growth of parts in the blue crab, *Callinectes sapidus* Rathbun. *Growth 2* (3), 235-246.

Gray, E., and C. Newcombe, 1938b: Studies of moulting in *Callinectes sapidus* Rathbun. *Growth 2* (4), 285-296.

Guadalupe, San Antonio, Mission, and Aransas Rivers and Mission, Copano, Aransas, and San Antonio Bays Basin and Bay Expert Science Team (GSA-BBEST), 2011: *Environmental Flows Recommendations Report*. Final submission to the Guadalupe, San Antonio, Mission, and Aransas Rivers and Mission, Copano, Aransas, and San Antonio Bays Basin and Bay Area Stakeholder Committee, Environmental Flows Advisory Group, and Texas Commission on Environmental Quality.

Guerin, J., and W. Stickle, 1992: Effects of salinity gradients on the tolerance and bioenergetics of juvenile blue crabs (*Callinectes sapidus*) from waters of different environmental salinities. *Mar. Biol. 114*, 391-396.

Guerin, J., and W. Stickle, 1997: A comparative study of two sympatric species within the genus *Callinectes*: osmoregulation, long-term acclimation to salinity and the effects of salinity on growth and moulting. *J. Exp. Mar Biol. Ecol. 218*, 165-186.

Guillory, V., and M. Elliot, 2001: A review of blue crab predators. In: *Proceedings: blue crab mortality symposium* (Guillory et al., eds), 69-83.

Guillory, V., H. Perry, and S. VanderKooy (Eds.), 2001a: *Proceedings: blue crab mortality symposium*. Report No. 90, Gulf States Marine Fisheries Commission, Ocean Springs, Mississippi.

Guillory, V., H. Perry, P. Steele, T. Wagner, W. Keithly, B. Pellegrin, J. Petterson, T. Floyd, B. Buckson, L. Harman, E. Holder, and C. Moss, 2001b: *The blue crab fishery of the Gulf of Mexico, United States: A regional management plan*. Report No. 96, Gulf States Marine Fisheries Commission, Ocean Springs, Mississippi.

Guinot, D., and J. Bouchard, 1998: Evolution of the abdominal holding systems of brachyuran crabs (Crustacea, Decapoda, Brachyura). *Zoosystema 20* (3), 612-694.

Gunter, G., 1950: Seasonal population changes and distributions as related to salinity, of certain invertebrates of the Texas coast, including the commercial shrimp. *Publ. Inst. Mar. Sci. 1* (2), 11-51.

Haefner, P., and C. Shuster, 1964: Length increments during terminal molt of the female blue crab, *Callinectes sapidus*, in different salinity environments. *Chesap. Sci. 5* (3), 114-118.

Hamilton, P, and T. Lee, 2005 : Eddies and jets over the slope of the northeast Gulf of Mexico. In: *Circulation in the Gulf of Mexico: Observations and models* (W. Sturges and A. Lugo-Fernandez, eds.), 123-142. Washington, D.C.: American Geophysical Union.

Hamlin, L., 2005: *The abundance and spatial distribution of blue crabs (Callinectes sapidus) in the Guadalupe estuary related to low freshwater inflow conditions*. M.S. Thesis, Texas State University, San Marcos.

Hammerschmidt, P., 1982: Life history of the blue crab, *Callinectes sapidus* Rathbun, along the Texas coast. In: *Proceedings of the blue crab colloquium* (H. Perry and W. Van Engel, eds.), 13-14. Tech. Rep. 7, Gulf States Marine Fisheries Commission, Ocean Springs, MS.

Hammerschmidt, P., T. Wagner and G. Lewis, 1998: Status and trends in the Texas blue crab (*Callinectes sapidus*) fishery. *J. Shellfish Res. 17* (2), 405-412.

Harris, R. E., 1982: Life history, ecology, and stock assessment of the blue crab *Callinectes sapidus* of the United States Atlantic Coast — a review. In: *Proceedings of the blue crab colloquium* (H. Perry and W. Van Engel, eds.), 59-63. Tech. Rep. 7, Gulf States Marine Fisheries Commission, Ocean Springs, MS.

Hasek, B., and N. Rabalais, 2001a: Settlement patterns of brachyuran megalopae in a Lousiana estuary. *Estuaries 24* (6A), 796-807.

Hasek, B., and N. Rabalais, 2001b: A comparison of molt states of blue crab meglopae, *Callinectes sapidus* (Rathbun), sampled with artificial collectors and plankton nets. *J. Exp. Mar. Biol. Ecol. 265*, 15-27.

Hay, W. P., 1905: *The life history of the blue crab (Callinectes sapidus)*. Appendix, Report of the Commissioner of Fisheries, 395-413. Washington, D.C.: Government Printing Office.

Hearn, C. J., 2008: *The dynamics of coastal models*. Cambridge, UK: Cambridge University Press.

Heck, K., and L. Coen, 1995: Predation and the abundance of juvenile blue crabs: a comparison of selected East and Gulf Coast (USA) studies. *Bull. Mar. Sci. 57* (3), 877-883.

Heck, K., and P. Spitzer, 2001: Post settlement mortality of juvenile blue crabs: patterns and processes. In: *Proceedings: blue crab mortality symposium* (Guillory et al., eds), 18-27.

Heck, K., L. Coen, and S. Morgan, 2001: Pre- and post-settlement factors as determinants of juvenile blue crab *Callinectes sapidus* abundance: results from the north-central Gulf of Mexico. *Mar. Ecol. Prog. Ser. 222*, 163-176.

Hedgpeth, J. W., 1950: Notes on the marine invertebrate fauna of salt flat areas in Aransas National Wildlife Refuge, Texas. *Publ. Inst. Mar. Sci. 1* (2), 103-119

Hench, J., R. Forward, S. Carr, D. Rittschof and R. Luettich, 2004: Testing a selective tidal-stream transport model: Observations of female blue crab (*Callinectes sapidus*) vertical migration during the spawning season. *Limnol. Oceanogr. 49* (5), 1857-1870.

Hiatt, R. W., 1948: The biology of the lined shore crab, *Pachygrapsus crassipes* Randall. *Pacific Sci. 2*, 135-213.

Hill, A. E., 1998: Buoyancy effects in coastal and shelf seas. Chap. 2 in: *The Sea 10: The global coastal ocean* (K. Brink and A. Robinson, eds.), 21-62. New York: John Wiley & Sons, Inc.

Hill, J., D. Fowler, and M. Van den Avyle, 1989: *Blue Crab. Species profiles: Life history and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic)*. Report EL-82-4, FWS-OBS-82/11.100, National Coastal Ecosystems Team, U.S. Fish & Wildlife Service, Washington, D.C.

Hines, A. H., 2007: Ecology of juvenile and adult blue crabs. Chapter 14 in: *The blue crab, Callinectes sapidus* (Kennedy and Cronin, eds., 2007), 565-654.

Hines, A., and G. Ruiz, 1995: Temporal variation in juvenile blue crab mortality: nearshore shallows and cannibalism in Chesapeake Bay. *Bull. Mar. Sci. 57* (3), 884-901.

Hines, A., R. Lipcius and A. Haddon, 1987: Population dynamics and habitat partitioning by size, sex, and molt stage of blue crabs *Callinectes sapidus* in a subestuary of central Chesapeake Bay. *Mar. Ecol. Prog. Ser. 36*, 287-310.

Hines , A., A. Haddon, and L. Wiechert, 1990: Guild structure and foraging impact of blue crabs and epibenthic fish in a subestuary of Chesapeake Bay. *Mar Ecol. Prog. Ser. 67*, 105-126.

Hines, A., Wolcott, E. González-Gurriarán, J. González-Escalante, and J. Freire, 1995: Movement patterns and migrations in crabs: telemetry of juvenile and adult behaviour in *Callinectes sapidus* and *Maja squinado*. *J. Mar. Biol. Assn. U.K. 75* , 27-42.

Hines, A., R. Aguilar, and E. Johnson, 2008: *Female blue crab migration in Chesapeake Bay*. Smithsonian Environmental Research Center, Edgewater, MD.

Hoese, H., and R. Jones, 1963: Seasonality of larger animals in a Texas turtle grass community. *Publ. Inst. Mar. Sci. 9*, 37-47.

Holland, J., D. Aldrich and K. Strawn, 1971: *Effects of temperature and salinity on growth, fodd conversion, survival and temperature resistance of juvenile blue crabs, Callinectes sapidus Rathbun*. Publ. TAMU-SG-71-222, Texas A&M University Sea Grant Program, College Station.

Hsueh, P.-W., J. McClintock and T. Hopkins, 1993: Population dynamics and life history characteristics of the blue crabs *Callinectes similis* and *C. sapidus* in bay environments of the northern Gulf of Mexico. *Mar. Ecol. 14* (3), 239-257.

Ichiye, T., H.-H. Kuo, and M. Carnes, 1973: *Assessment of currents and hydrography of the eastern Gulf of Mexico*. Dept. of Oceanography, Texas A&M University, College Station.

Iversen, E., D. Allen and J. Higman, 1993: *Shrimp capture and culture fisheries of the United States*. New York: Halsted Press.

Ives, A., K. Abbott, and N. Ziebarth, 2010: Analysis of ecological time series with ARMA(*p,q*) models. *Ecology 91* (3), 858-871.

Jarosz,E., and S. Murray, 2005 : Velocity and transport characteristics of the Lousiana-Texas Coastal Current. In: *Circulation in the Gulf of Mexico: Observations and models* (W. Sturges and A. Lugo-Fernandez, eds.), 143-156. Washington, D.C.: American Geophysical Union.

Jivoff, P., A. Hines, and L. Quackenbush, 2007: Reproduction biology and embryonic development. Chapter 7 in: *The blue crab, Callinectes sapidus* (Kennedy and Cronin, eds., 2007), 255-298.

Johnson, D. F., 1985: The distribution of brachyuran crustacean megalopae in the waters of the York River, lower Chesapeake Bay and adjacent shelf: implications for recruitment. *Est. Coast Shelf Sci. 20*, 693-705.

Johnson, D. R., 1985: Wind-forced dispersion of blue crab larvae in the Middle Atlantic Bight. *Cont. Shelf Res. 4* (6), 733-745.

Johnson, D., B. Hester and J. McConaugha, 1984: Studies of a wind mechanism influencing the recruitment of blue crabsin the Middle Atlantic Bight. *Cont. Shelf Res. 3* (4), 425-437.

Johnson, W., 2005 : Movies of drifters in the northern Gulf of Mexico. In: *Circulation in the Gulf of Mexico: Observations and models* (W. Sturges and A. Lugo-Fernandez, eds.), 157 and endpocket. Washington, D.C.: American Geophysical Union.

Jones, M., and C. Epifanio, 1995: Settlement of brachyuran megalopae in Delaware Bay: an analysis of time series data. *Mar. Ecol. Prog. Ser. 125*, 67-76.

Jouve-Duhamel, A., and J. Truchot, 1983: Ventilation in the shore crab *Carcinus maenas* (L.) as a function of ambient oxygen and carbon dioxide: Field and laboratory studies. *J. Exp. Mar. Biol. Ecol. 70* (3), 281-296.

Kalber, F. A., 1970: Osmoregulation in decapod larvae as a consideration in culture techniques. *Heloländer wiss. Meeresunters. 20*, 697-706.

Kennedy, V.S., 2007: External anatomy of blue crab larvae. Chapter 2 in: *The blue crab, Callinectes sapidus* (Kennedy and Cronin, eds., 2007), 23-54.

Kennedy, V., and E. Cronin, 2007a: Anatomy of the post-larval blue crab. Chapter 3 in: *The blue crab, Callinectes sapidus* (Kennedy and Cronin, eds., 2007), 55-101.

Kennedy, V., and E. Cronin (eds.), 2007b: *The blue crab, Callinectes sapidus*. College Park: Maryland Sea Grant.

King, B. D., 1971: *Study of migratory patterns of fish and shellfish through a natural pass*. Tech. Ser. 9, Texas Parks & Wildlife Department, Austin.

King, M., 1995: *Fisheries biology, assessment and management.* London: Blackwell Science, Ltd.

King, R., A. Hines, F. Craige, and S. Grap, 2005: Regional, watershed and local correlates of blue crab and bivalve abundances in subestuaries of Chesapeake Bay, USA. *J. Exp. Mar. Biol. Ecol. 319*, 101-116.

Kordos, L., and R. Burton, 1993: Genetic differentiation of Texas Gulf Coast populations of the blue crab Callinectes sapidus. *Mar. Biol. 117*, 227-233.

Laughlin, R. A., 1982: Feeding habits of the blue crab, *Callinectes sapidus* Rathbun, in the Apalachicola estuary, Florida. *Bull. Mar. Sci. 32* (4), 807-822.

Lee, R., and M. Frischer, 2004: The decline of the blue crab. *Amer. Sci. 92* , 548-553.

Leffler, C. W., 1972: Some effects of temperature on the growth and metabolic rate of juvenile blue crabs, *Callinectes sapidus*, in the laboratory. *Mar. Biol. 14*, 104-110.

Leffler, C. W., 1975: Ionic and osmotic regulation and metaboli response to salinity of juvenile Callinectes sapidus Rathbun. *Comp. Biochem. Physiol. 52A*, 545-549.

Lentz, S., and M. Fewings, 2012: The wind- and wave-driven inner-shelf circulation. *Ann. Rev. Mar. Sci. 4*, 317-343.

Lipcius, R., E. Olmi, and J. van Montfrans, 1990: Planktonic availability, molt stage and settlement of blue crab postlarvae. *Mar. Ecol. Prog. Ser. 58*, 235-242.

Lipcius, R., D. Eggleston, K. Heck, R. Seitz and J. van Montfrans, 2007: Ecology of postlarval and young juvenile blue crabs. Chapter 13 in: *The blue crab, Callinectes sapidus* (Kennedy and Cronin, eds., 2007), 535-564.

Little, K., and C. Epifanio, 1991: Mechanism for the re-invasion of an estuary by two species of brachyuran megalopae. *Mar Ecol. Prog. Ser. 68*, 235-242.

Lochmann, S., R. Darnell, and J. McEachran, 1995: Temporal and vertical distribution of crab larvae in a tidal pass. *Estuaries 18* (1B), 255-263.

Loesch, H., 1960: Sporadic mass shoreward migrations of demersal fish and crustaceans in Mobile Bay, Alabama. *Ecology 41*, 292-298.

Loder, J., B. Petrie, and G. Gawarkiewicz, 1998: The coastal ocean off northeastern North America: a large-scale view. Chap. 5 in: *The sea* (A. Robinson and K. Brink, eds.), 105-133. New York: John Wiley & Sons, Inc.

Lovett, D., T. Colella, A. Cannon, D. Lee, A. Evangelisto, E. Muller, and D. Towle, 2006: Effect of salinity on osmoregulatory patch epithelia in gills of the blue crab *Callinectes sapidus*. *Biol. Bull. 210*, 132-139.

Luckenbach, M., and R. Orth, 1992: Swimming velocities and behavior of blue crab (*Callinectes sapidus* Rathbun) megalopae in still and flowing water. *Estuaries 15* (2), 186-192.

Lumer, H., 1936: The relation between b and alpha in systems of relative growth functions of the form y equals b times x to the alpha. *Amer. Nat. 70*, 188-191.

Lykossov, V.N., 2001: Atmospheric and oceanic boundary layer physics. Chapter 3 in: *Wind stress over the ocean* (I. Jones and Y. Toba, eds.), 54-81. Cambridge, UK: Cambridge University Press.

Lynch, M., K. Webb, and W. Van Engel, 1973: Variations in serum constituents of the blue crab, *Callinectes sapidus*: chloride and osmotic concentration. *Comp. Biochem. Physiol. 44A*, 719-734.

Malmquist, D., 2004: Does giant blue crab set a new record? Online archive, Virginia Institute of Marine Science, William & Mary. http://www.vims.edu/newsandevents/topstories/archives/pre_2003/giant_crab.php

Mangum, C. P., 1985: Molting in the blue crab *Callinectes sapidus*: a collaborative study of intermediary metabolism, respiration and cardiovascular function, and ion transport. *J. Crust. Biol. 5* (2), 185-187.

Mangum, C., and L. Amende, 1972: Blood osmotic concentration of blue crabs (*Callinectes sapidus* Rathbun) found in fresh water. *Chesap. Sci. 13* (4), 318-320.

Mangum, C., and D. Towle, 1977: Physiological adaptation to unstable environments. *American Scientist 65*, 67-75.

Mantel, L., and L. Farmer, 1983: Osmotic and ionic regulation. Chapter 2 in: *The biology of crustacea, Vol. 5* (L. Mantel, ed.), 53-161. New York: Academic Press.

Marshall, S., and A. Orr, 1960: Feeding and nutrition. Chapter 6 in: *The physiology of crustacea, Vol. 1* (T. Waterman, ed.), 227-258. New York: Academic Press.

May, E., 1973: Extensive oxygen depletion in Mobile Bay, Alabama. *Limnol. Oceanogr. 18*, 353-366.

McClintock, J., K. Marion, J. Dindo, P.-W. Hsueh, and R. Angus, 2003: Population studies of blue crabs in soft-bottom, unvegetated habitats of a subestuary in the northern Gulf of Mexico. *J. Crust. Biol. 13* (3), 551-563.

McConaugha, J. R., 1988: Export and reinvasion of larvae as regulators of estuarine decapod populations. *Am. Fish. Soc. Symp. 3*, 90-103.

McConaugha, J., D.F. Johnson, A. Provenzano, and R. Maris, 1983: Seasonal distribution of larvae of *Callinectes sapidus* (Crustacea: Decapoda) in the waters adjacent to Chesapeake Bay. *J. Crust. Biol. 3* (4), 582-591.

McGaw, I. and C. Reiber, 2000: Integrated physiological responses to feeding in the blue crab *Callinectes sapidus*. *J. Exp. Biol. 203*, 359-368.

Medici, D., T. Wolcott, and D. Wolcott, 2006: Scale-dependent movements and protection of female blue crabs (*Callinectes sapidus*). *Can. J. Fish. Aquat. Sci. 63* , 858-871.

Mense, D., and E. Wenner, 1989: Distribution and abundance of early life history stages of the blue crab, *Callinectes sapidus*, in tidal marsh creeks near Charleston, South Carolina. *Estuaries 12* (3), 157-168.

Messick, G., and J. Shields, 2000: Epizootiology of the parsitic dinoflagellate *Hematodinium* sp. in the American blue crab *Callinectes sapidus*. *Dis. Aq. Org. 43*, 139-152.

Messick, G., and C. Sindermann, 1992: *Synopsis of principal diseases of the blue crab, Callinectes sapidus*. Tech. Memo. NEFS-F/NEC-88, National Marine Fisheries Service, National Oceanic and Atmospheric Administration.

Metcalf, K., and R. Lipcius, 1992: Relationship of habitat and spatial scale with physiological state and the settlement of blue crab postlarvae in Chesapeake Bay. *Mar. Ecol. Prog. Ser. 82*, 143-150.

Metcalf, K., J. van Montfrans, R. Lipcius, and R. Orth, 1995: Settlement indices for blue crab megalopae in the York River, Virginia: temporal relationships and statistical efficiency. *Bull. Mar. Sci. 57* (3), 781-792.

Miller, B., D. Gunderson, P. Dinnel, R. Donnelly, D. Armstrong, and S. Brown, 1990: *Recommended guidelines for sampling soft-bottom demersal fishes by beach seine and trawl in Puget Sound*. USEPA Region 10, Office of Puget Sound, Seattle, WA.

Miller, R., S. Sulkin and R. Lippson, 1975: Composition and seasonal abundance of the blue crab, *Callinectes sapidus* Rathbun, in the Chesapeake and Delaware Canal and adjacent waters. *Chesap. Sci. 16* (1), 27-31.

Miller, T. J., 2003: Incorporating space into models of the Chesapeake Bay blue crab population. *Bull. Mar. Sci. 72* (2), 567-588.

Millikin, M. and A. Williams, 1984: *Synopsis of biological data on the blue crab, Callinectes sapidus* Rathbun. NOAA Tech. Rep. NMFS 1, FAO Fisheries Synopsis No. 138, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Washington, D.C.

Minello, T., and L. Rozas, 2002: Nekton in Gulf coast wetlands: fine-scale distributions landscape patterns, and restoration implications. *Ecol. Appl. 12* (2), 441-455.

Minello, T., G. Matthews, P. Caldwell, and L. Rozas, 2008: Population and production estimates for decapod crustaceans in wetlands of Galveston Bay, Texas. *Trans. Am. Fish. Soc. 137*, 129-146.

Moksnes, P-O., R. Lipcius, L. Pihl, and J. van Montfrans, 2003: Cannibal-prey dynamics in young juveniles and postlarvae of the blue crab. *J. Exp. Mar. Biol. Ecol. 215*, 157-187.

Montagna, P., B. Vaughn, and G. Ward, 2011: The importance of freshwater inflows to Texas estuaries. Chap. 6 in: *Water policy in Texas: Responding to the rise of scarcity* (R. Griffin, ed.), 107-127. Washington, D.C.: RFF Press.

Morey, S., P. Martin, J. O'Brien, A. Allcraft, and J. Zavala-Hidalgo, 2003: Export pathways for river discharged fresh water in the northern Gulf of Mexico. *J. Geophys. Res. 108* (C10), 3303, doi: 10.1029/2002JC001674.

Morey, S., J. Zavala-Hidalgo and J. O'Brien, 2005 : The seasonal variability of continental shelf circulation in the northern and western Gulf of Mexico from a high-resolution numerical model. In: *Circulation in the Gulf of Mexico: Observations and models* (W. Sturges and A. Lugo-Fernandez, eds.), 203-218. Washington, D.C.: American Geophysical Union.

Morgan, S. G., 1990: Impact of planktivorous fishes on dispersal, hatching, and morphology of estuarine crab larvae. *Ecology 71* (5), 1639-1652.

Morgan, S. G., 1992: Predation by planktonic and benthic invertebrates on larvae of estuarine crabs. *J. Exp. Mar. Biol. Ecol. 163*, 91-110.

Morgan, S. G., 1996a: Influence of tidal variation on reproductive timing. *J. Exp. Mar. Biol. Ecol. 206*, 237-251.

Morgan, S. G., 1996b: Plasticity in reproductive timing by crabs in adjacent tidal regimes. *Mar. Ecol. Prog. Ser. 139*, 105-118.

Morgan, S., and J. Christy, 1995: Adaptive significance of the timing of larval release by crabs. *Amer. Nat. 145* (3), 457-479.

Morgan, S., and J. Anastasia, 2008: Behavior tradeoff in estuarine larvae favors seaward migration over minimizing visibility to predators. *Proc. Nat. Acad. Sci. 105* (1), 222-227.

Morgan, S., R.Zimmer-Faust, K. Heck, and L. Coen, 1996: Population regulation of blue crabs *Callinectes sapidus* in the northern Gulf of Mexico: postlarval supply. *Mar. Ecol. Prog. Ser. 133*, 73-88.

More, W. R., 1969: *A contribution to the biology of the blue crab (Callinectes sapidus Rathbun) in Texas, with a description of the fishery*. Tech. Ser. 1, Texas Parks and Wildlife Department, Austin.

Münchow, A., and R. Garvine, 1993: Buoyancy and wind forcing of a coastal current. *J. Mar. Res. 51*, 293-322.

Murchelano, R., and A. Rosenfield, 1980: *Diseases of North American marine fishes, crustaceans and mollusks*. National Marine Fisheries Service, NOAA.

Natunewicz, C. and C. Epifanio, 2001: Spatial and temporal scales of patches of crab larvae in coastal waters. *Mar. Ecol. Prog. Ser. 212*, 217-222.

Natunewicz, C., C. Epifanio, and R. Garvine, 2001: Transport of crab larval patches in the coastal ocean. *Mar. Ecol. Prog. Ser. 222*, 143-154.

Naylor, E., 1985: Tidally rhythmic behaviour of marine animals. *Symp. Soc. Exp. Biol. 39*, 63-93.

Naylor, E., 1988: Rhythmic behaviour of decapod crustaceans. *Symp. Zool. Soc. Lond. 59*, 177-199.

Naylor, E., 2005: Chronobiology. *Scientia Marina 69* (suppl 1), 157-167.

Nelson, J. 1917: An investigation of oyster propagation in Richmond Bay, P.E.I., during 1915. Sessional Paper 38A in: *Contributions to Canadian Biology, being studies from the biological stations of Canada 1915-1916*, 53-78. Supplement to the 6th Annual Report of the Department of Naval Service, Fisheries Branch. Ottawa: J. de L. Tache.

Neufeld, D., and J. Cameron, 1994: Mechanism of the net uptake of water in moulting blue crabs (*Callinectes sapidus*) acclimated to high and low salinities. *J. Exp. Biol. 188*, 11-23.

Newcombe, C., F. Campbell, and A. Eckstine, 1949a: A study of the form and growth of the blue crab *Callinectes sapidus* Rathbun. *Growth 13*, 71-96.

Newcombe, C., M. Sandoz, and R. Rogers-Talbert, 1949b: Differential growth and moulting characteristics of the blue crab, *Callinectes sapidus* Rathbun. *J. Exp. Zool. 110*, 113-152.

Nowlin, W., A. Jochens, R. Reid and S. DiMarco, 1998: *Texas-Louisiana shelf circulation and transport processes study: synthesis report, Vol. 1: Technical report*. Report MMS 98-0035, Gulf of Mexico OCS Region, Minerals Management Service, New Orleans.

Nowlin, W., A. Jochens, S. DiMarco, R. Reid, and M. Howard, 2005 : Low-frequency circulation over the Texas-Lousiana continental shelf. In: *Circulation in the Gulf of Mexico: Observations and models* (W. Sturges and A. Lugo-Fernandez, eds.), 219-240. Washington, D.C.: American Geophysical Union.

Oceana, 2002: *A description of bottom-trawl gear*. Oceana, Washington, D.C.

Odum, H. T., 1953: Factors controlling marine invation into Florida fresh waters. *Bull. Mar. Sci. Gulf. Carib. 3* (2), 134-156.

Oesterling, M. J., 1976: *Reproduction, growth, and migration of blue crabs along Florida's Gulf coast*. Report SUSF-SG-76-003, Marine Advisory Program, Florida Sea Grant, University of Florida, Gainesville.

Oesterling, M. J., 1995: *Manual for handling and shedding blue crabs (Callinectes sapidus)*. Special report in Applied Marine Science and Ocean Engineering No. 271, Virginia Institute of Marine Science, Gloucester Point, VA.

Oesterling, M., and G. Evink, 1977: Relationship between Florida's blue crab population and Apalachicola Bay. In: *Proceedings of the Conference on the Apalachicola Drainage System* (R. Livingston and E. Joyce, eds.), 101-121. Florida Marine Research Publ. 26, Florida Dept. Natural Resources, St. Petersburg.

Oesterling, M., and C. Adams, 1982: Migration of blue crabs along Florida's Gulf coast. In: *Proceedings of the blue crab colloquium* (H. Perry and W. Van Engel, eds.), 37-57. Tech. Rep. 7, Gulf States Marine Fisheries Commission, Ocean Springs, MS.

Ogburn, M., H. Diaz, and R. Forward, 2009: Mechanisms regulating estuarine ingress of blue crab *Callinectes sapidus* megalopae. *Mar. Ecol. Prog. Ser. 389*, 181-192.

Ogle, W. (Trans. & ed.), 1882: *Aristotle: On the parts of animals*. London: Kegan Paul, Trench & Co.

Ohlmann, J., P. Niiler, C. Fox and R. Leben, 2001: Eddy energy and shelf interactions in the Gulf of Mexico. *J. Geophys. Res. 106* (C2), 2605-2620.

Olascoaga, M. J., 2010: Isolation on the west Florida shelf with implications for red tides and pollutant dispersal in the Gulf of Mexico. *Nonlin. Proc. Geophys. 18*, 685-696.

Olmi, E. J., 1994: Vertical migration of blue crab *Callinectes sapidus* megalopae: implications for transport in estuaries. *Mar. Ecol. Prog. Ser. 113*, 39-54.

Olmi, E. J., 1995: Ingress of blue crab megalopae in the York River, Virginia, 1987-1989. *Bull. Mar. Sci. 57* (3), 753-780.

Olmi, E., and J. Bishop, 1983: Variations in total width-weight relationships of blue crabs, *Callinectes sapidus*, in relation to sex, maturity, molt stage, and carapace form. *J. Crust. Biol. 3* (4), 575-581.

Olmi, E., J. van Montfrans, R. Lipcius, R. Orth and P. Sadler, 1990: Variation in planktonic availability and settlement of blue crab megalopae in the York River, Virginia. *Bull. Mar. Sci. 46* (1), 230-243.

O'Mahoney, P., and R. Full, 1984: Respiration of crabs in air and water. *Comp. Biochem. Physiol. 79A* (2), 275-282.

Orth, R., and J. van Montfrans, 1987: Utilization of a seagrass meadow and tidal marsh creek by blue crabs *Callinectes sapidus*. I. Seasonal and annual variations in abundance with emphasis on post-settlement juveniles. *Mar. Ecol. Prog. Ser. 41*, 283-294.

Orth, R., and J. van Montfrans, 1990: Utilization of marsh and seagrass habitats by early stages of *Callinectes sapidus*: a latitudinal perspective. *Bull. Mar. Sci. 46* (1), 126-144.

Orth, R., J. van Montfrans, and J. Fishman, 1999: *A preliminary study of predation on blue crabs by three fish predators in a seagrass bed*. Report to Virginia Marine Resources Commission, Virginia Institute of Marine Science, Goucester Point, VA.

Ortner, P., T. Lee, P. Milne, R. Zika, M. Clarke, G. Podesta, P. Swart, P. Tester, L. Atkinson, and W. Johnson, 1995: Mississippi River flood waters that reached the Gulf Stream. *J. Geophys. Res. 100* (C7), 13,595-13,601.

Osborn, M., P. Chaie, J. Lin, A. Morgan, P. Rubec, S. Spanyers and A. Walton, 1992: Fisheries. Chap. 3 in: *Status and trends of selected living resources in the Galveston Bay system* (C. Loeffler and A. Walton, eds.), 12-264. Report GBNEP-19, Galveston Bay National Estuary Program, Webster, Texas.

Otwell, W., and J. Cato, 1982: Review of the soft-shell crab fishery in the United States. In: *Proceedings of the blue crab colloquium* (H. Perry and W. Van Engel, eds.), 129-136. Tech. Rep. 7, Gulf States Marine Fisheries Commission, Ocean Springs, MS.

Passano, L. M., 1960: Molting and its control. Chapter 15 in: *The physiology of crustacea, Vol. 1* (T. Waterman, ed.), 473-536. New York: Academic Press.

Patillo, M., T. Czapla, D. Melson and M. Monaco, 1997: *Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries. Vol. II: Species life history summaries.* ELMR Rep. No. 11, Strategic Environmental Assessments Division, National Ocean Service, National Oceanic and Atmospheric Administration, Silver Spring, MD.

Palmer, B. A., 1974: *Studies on the blue crab (Callinectes sapidus) in Georgia*. Contr. Ser. No. 29, Coastal Fisheries Office, Georgia Department of Natural Resources.

Pardieck, R., R. Orth, R. Diaz, and R. Lipcius, 1999: Ontogenetic changes in habitat use by postlarvae and young juveniles of the blue crab. *Mar. Ecol. Prog. Ser. 186*, 227-238.

Pedlosky, J., 1982: *Geophysical fluid dynamics*. New York: Springer-Verlag.

Peireira, M., J. Branco, M. Christoffersen, F. Junior, H. Fracasso, and T. Pinheiro, 2009: Population biology of *Callinectes danae* and *Callinectes sapidus* (Crustacea: Brachyura: Portunidae) in the south-western Atlantic. *J. Mar. Biol. Assn. U.K. 89* (7), 1341-1351.

Pelton, T., and B. Goldsborough, 2008: *Bad water and the decline of blue crabs in the Chesapeake Bay*. Maryland: Chesapeake Bay Foundation. Online URL: cbf.org/badwaters

Péqueux, A., 1995: Osmotic regulation in crustaceans. *J. Crust. Biol. 15* (1), 1-60.

Perret, W. S., 1967: Occurrence, abundance and size distribution of the blue crab, *Callinectes sapidus*, taken with otter trawl in Vermilion Bay, Louisiana, 1964-65. *Proc. Louis. Acad. Sci. 30*, 63-69.

Perry, H., and K. Stuck, 1982: The life history of the blue crab in Mississippi with notes on larval distribution. In: *Proceedings of the blue crab colloquium* (H. Perry and W. Van Engel, eds.), 17-22. Tech. Rep. 7, Gulf States Marine Fisheries Commission, Ocean Springs, MS.

Perry, H., C. Eleuterius, C. Trigg, and J. Warren, 1995: Settlement patterns of *Callinectes sapidus* megalopae in Mississippi Sound: 1991, 1992. *Bull. Mar. Sci. 57* (3), 821-833.

Peterson, G., and R. Turner, 1994: The value of salt marsh edge vs interior as a habitat for fish and decapod crustaceans in a Louisiana tidal marsh. *Estuaries 17* (1B), 235-262.

Pietrafesa, L., and G. Janowitz, 1988: Physical oceanographic processes affecting larval transport around and through North Carolina inlets. *Am. Fish. Soc. Symp. 3*, 34-50.

Pile, A., R. Lipcius, J. van Montfrans, and R. Orth, 1996: Density-dependent settler-recruit-juvenile relationships in blue crabs. *Ecol. Monogr. 55* (3), 277-300.

Provenzano, A., J. McConaugha, K. Philips, D. Johnson, and J. Clark, 1983: Vertical distribution of first stage larvae of the blue crab, *Callinectes sapidus*, at the mouth of Chesapeake Bay. *Est. Coast. Shelf Sci. 16*, 489-499.

Pullen, E., and W. Trent, 1970: Carapace width-total weight relation of blue crabs from Galveston Bay, Texas. *Trans. Am. Fish. Soc. 99* (4), 795-798.

Rabalais, N., F. Burditt, L. Coen, B. Cole, C. Eleuterius, K. Heck, T. McTigue, S. Morgan, H. Perry, F. Truesdale, R. Simmer-Foust, and R. Zimmerman, 1995: Settlement of *Callinectes sapidus* megalopae on artificial collectors in four Gulf of Mexico estuaries. *Bull. Mar. Sci. 57* (3), 855-876.

Ramach, S., M. Z. Darnell, N. Avissar and D. Rittschof, 2009: Habitat use and population dynamics of blue crabs, *Callinectes sapidus*, in a high-salinity environment. *J. Shellfish Res. 28* (3), 635-640.

Reyns, N., and D. Eggleston, 2004: Environmentally-controlled, density-dependent secondary dispersal in a local estuarine crab population. *Oecologia 140* (2), 280-288.

Reyns, N., D. Eggleston and R. Luettich, 2006: Secondary dispersal of early juvenile blue crabs within a wind-driven estuary. *Limnol. Oceanogr. 51* (5), 1982-1995.

Reyns, N., D. Eggleston and R. Luettich, 2007: Dispersal dynamics of post-larval blue crabs, *Callinectes sapidus*, within a wind-driven estuary. *Fish. Oceanogr. 16* (3), 257-272.

Rhodes, R., J. Thompson and A. Wallcraft, 1989: Buoy-calibrated winds over the Gulf of Mexico. *J. Atmos. Oceanic Tech. 6*, 608-623.

Robertson, R. L., 1938: *Observations on the growth stages in the common blue crab, Callinectes sapidus Rathbun, with special reference to post-larval development*. Thesis, University of Maryland.

Robinson, G. D., 1982: Water fluxes and urine production in blue crabs (*Callinectes sapidus*) as a function of environmental salinity. *Comp. Biochem. Physiol. 71A*, 407-412.

Robles, R., F. Alvarez, and G. Alcaraz, 2002: Oxygen consumption of the crab *Callinectes rathbunae* parasitized by the rhizocephala barnacle *Loxothylacus texanus* as a function of salinity. *Mar. Ecol. Prog. Ser. 235*, 189-194.

Romano, N., and C. Zeng, 2012: Osmoregulation in decapod crustaceans: implications to aquaculture productivity, methods for potential improvement and interactions with elevated ammonia exposure. *Aquaculture 334-337*, 12-23.

Rome, M., A. Young-Williams, G. Davis, and A. Hines, 2005: Linking temperature and salinity tolerance to winter mortality of Chesapeake Bay blue crabs (*Callinectes sapidus*). *J. Exp. Mar. Biol. Ecol. 319*, 129-145.

Rosenberg, R., and J. Costlow, 1976: Synergistic effects of cadmium and salinity combined with constant and cycling temperatures on the larval development of two estuarine crab species. *Mar. Biol. 38*, 291-303.

Roughgarden, J., S. Gaines and H. Possingham, 1988: Recruitment dynamics in complex life cycles. *Science 241* (4972), 1460-1466.

Rozas, L., and T. Minello, 1997: Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: a review of sampling design with focus on gear selection. *Estuaries 20* (1), 199-213.

Rozas, L., T. Minello and D. Dantin, 2012: Use of shallow lagoon habitats by nekton of the northeastern Gulf of Mexico. *Estuaries and Coasts 35*, 572-586.

Sánchez, A., and A. Raz-Guzman, 1997: Distribution patterns of tropical estuarine brachyuran crabs in the Gulf of Mexico. *J. Crust. Biol. 17* (4), 609-620.

Sanches-Rubio, G., H. Perry, P. Biesiot, D. Johnson, and R. Lipcius, 2011a: Climate-related hydrological regimes and their effects on abundance of juvenile blue crabs (*Callinectes sapidus*) in the northcentral Gulf of Mexico. *Fish. Bull. 109*, 139-146.

Sanches-Rubio, G., H. Perry, P. Biesiot, D. Johnson, and R. Lipcius, 2011b: Oceanic-atmospheric modes of variability and their influence on riverine input to coastal Louisiana and Mississippi. *J. Hydrol. 396*, 72-81.

Sandoz, M., and R. Rogers, 1944: The effect of environmental factors on hatching, moulting, and survival of zoea larvae of the blue crab *Callinectes sapidus* Rathbun. *Ecology 25* (2), 216-228.

Scharf, F., and K. Schlight, 2000: Feeding habits of red drum (*Sciaenops ocellatus*) in Galveston Bay, Texas: seasonal diet variation and predator-prey size relationships. *Estuaries 23* (1), 128-139.

Scheltema, R.S., 1974: Biological interactions determining larval settlement of marine invertebrates. *Thalassia Jugoslavica 10*, 263-296.

Schmidt, J., 1906: Contributions to the life-history of the eel (Anguilla vulgaris Flem.). *Rapports et Procs-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer 5*, 137-274.

Schmitz, W.S., 2003: *Notes on the circulation in and around the Gulf of Mexico, Vol I: A review of the deep water circulation.* On-line publication, Harte Research Institute, Texas A&M University–Corpus Christi: http://www.harteresearchinstitute.org/whats-news/books.

Scottish Executives Rural Affairs Department, 2001: *Fishing industry guide to offshore operators*. Freshwater Fisheries, Aquaculture and Marine Environment Division, Fisheries and Offshore Oil Consultative Group, Edinburgh.

Shaw, R., W. Wiseman, R. Turner, L. Rouse, R. Condrey, and F. Kelly, 1985: Transport of larval Gulf menhaden (*Brevoortia patronus*) in continental shelf waters of western Lousiana: a hypothesis. *Trans. Am. Fish. Soc. 114*, 452-460.

Shields, J., and R. Overstreet, 2007: Diseases, parasites, and other symbionts. Chapter 8 in: *The blue crab, Callinectes sapidus* (Kennedy and Cronin, eds., 2007), 299-417.

Simmons, E., and H. Hoese, 1959: Studies on the hydrography and fish migrations of Cedar Bayou, a natural tidal inlet on the centratl Texas coast. *Publ. Inst. Mar. Sci. 6* , 56-80.

Simpson, J. H., 1997: Physical processes in the ROFI regime. *J. Mar. Syst. 12*, 3-13.

Skinner, D. M., 1985: Molting and regeneration. In: *The Biology of Crustacea, Vol. 9* (D. Bliss and L. Mantel, eds.), 43-146. New York: Academic Press.

Smith, G., and E. Chang, 2007: Molting and growth. Chapter 6 in: *The blue crab, Callinectes sapidus* (Kennedy and Cronin, eds., 2007), 197-254.

N. P. Smith, 1978: Low-frequency reversals of nearshore currents in the northwestern Gulf of Mexico. *Contr. Mar. Sci. 21*, 103-116.

Smyth, P.O., 1980: *Callinectes* (Decapoda: Portunidae) larvae in the middle Atlantic bight, 1975-77. *Fish. Bull. 78* (2), 251-265.

Spirito, C. P., 1972: An analysis of swimming behavior in the portunid crab *Callinectes sapidus*. *Mar. Behav. Physiol. 1*, 261-276.

Spitzer, P., K. Heck, and J. Valentine, 2003: Then and now: a comparison of patterns in blue crab post-larval abundance and post-settlement mortality during the early and late 1990s in the Mobile Bay system. *Bull. Mar. Sci. 72* (2), 435-452.

Stagg, C., and M. Whilden, 1997: The history of Chesapeake Bay's blue crab (*Callinectes sapidus*): fisheries and management. *Invest. Mar. Valparaíso 25*, 93-104.

Steele, P., 1982: A synopsis of the biology of the blue crab *Callinectes sapidus* Rathbun in Florida. In: *Proceedings of the blue crab colloquium* (H. Perry and W. Van Engel, eds.), 29-35. Tech. Rep. 7, Gulf States Marine Fisheries Commission, Ocean Springs, MS.

Steele, P., 1991: Population dynamics and migration of the blue crab, *Callinectes sapidus* (Rathbun), in the eastern Gulf of Mexico. *Proc. 40th Gulf Carib. Fish Inst.*, 241-244.

Steele, P., T. Bert, K. Johnston, and S. Levett, 2002: Efficiency of bycatch reduction devices in small otter trawls used in the Florida shrimp fishery. *Fish. Bull. 100*, 338-350.

Stern, D., and D. Emlen, 1999: The developmental basis for allometry in insects. *Development 126*, 1091-1101.

Stuck, K., and H. Perry, 1981: Observations on the distribution and seasonality of portunid megalopae in Mississippi coastal waters. *Gulf Res. Rep. 7* (1), 93-95.

Sturges, W., 1993: The annual cycle of the western boundary current in the Gulf of Mexico. *J. Geophys. Res. 98* (C10), 18,053-18,068.

Sturges, W., and K. Kenyon, 2008: Mean flow in the Gulf of Mexico. *J. Phys. Oceanogr. 38*, 1501-1514.

Sturges, W., and A. Lugo-Fernandez (eds.), 2005: *Circulation in the Gulf of Mexico: Observations and models*. Geophys. Monogr. 161, American Geophysical Union, Washington, D.C.

Sturges, W., P. Niiler, and R. Weisberg, 2001: *Northeastern Gulf of Mexico inner shelf circulation study*. Final report, MMS Cooperative Agreement 14-35-0001-30787. OCS Report MMS2001-103, U.S. Minerals Management Service, Herndon, VA.

Sulkin, S. D., 1984: Behavioral basis of depth regulation in the larvae of brachyuran crabs. *Mar. Ecol. Prog. Ser. 15*, 181-205.

Sulkin, S., and C. Epifanio, 1986: A conceptual model for recruitment of the blue crab, *Callinects sapidus* Rathbun, to estuaries of the middle Atlantic bight. *Canad. Sp. Publ. Fish. Aquat. Sci. 92*: 117-123.

Sulkin, S., and W. Van Heukelem, 1986: Variability in the length of the megalopal stage and its consequence to dispersal and recruitment in the portunid crab *Callinectes sapidus* Rathbun. *Bull. Mar. Sci. 39* (2), 269-278.

Sulkin, S., I. Phillips and W. Van Heukelem, 1979: On the locomotory rhythm of brachyuran crab larvae and its significance in vertical migration. *Mar. Ecol. Prog. Ser. 1*, 331-335.

Sutton, G., and T. Wagner, 2007: *Stock assessment of blue crab (Callinectes sapidus) in Texas coastal waters*. Management Data Series No. 249, Texas Parks and Wildlife Department, Austin.

Tagatz, M. E., 1968a: Biology of the blue crab, *Callinectes sapidus* Rathbun, in the St. Johns River, Florida. *Fish. Bull. 67* (1), 17-33.

Tagatz, M. E., 1968b: Growth of juvenile blue crabs, *Callinectes sapidus* Rathbun, in the St. Johns River, Florida. *Fish. Bull. 67* (2), 281-288.

Tagatz, M. E., 1969: Some relations of temperature acclimation and salinity to thermal tolerance of the blue crab, *Callinectes sapidus*. *Trans. Am. Fish. Soc. 98* (4), 713-716.

Tagatz, M. E., 1971: Osmoregulatory ability of blue crabs in different temperature-salinity combinations. *Chesap. Sci. 12* (1), 14-17.

Tan, E.-C., and W. Van Engel, 1966: Osmoregulation in the adult blue crab, *Callinectes sapidus* Rathbun. *Chesap.Sci. 7* (1), 30-35.

Tankersley, R., and R. Forward, 1994: Endogenous swimming rhythms in estuarine crab megalopae: implications for flood-tide transport. *Mar. Biol. 118*, 415-423.

Tankersley, R., and R. Forward, 2007: Environmental physiology. Chapter 10 in: *The blue crab, Callinectes sapidus* (Kennedy and Cronin, eds., 2007), 451-483.

Tankersley, R., L. McKelvey, and R. Forward, 1995: Responses of estuarine crab megalopae to pressure, salinity and light: implications for flood-tide transport. *Mar. Biol. 122*, 391-400.

Tankersley, R., M. Wieber, M. Sigala, and K. Kachurak, 1998: Migratory behavior of ovigerous blue crabs *Callinectes sapidus*: Evidence for selective tidal-stream transport. *Biol. Bull. 195*, 168-173.

Tankersley, R., J. Welch and R. Forward, 2002: Settlement times of blue crab (*Callinectes sapidus*) meglopae during flood-tide transport. *Mar. Biol. 141*, 863-875.

Tatum, W. M., 1982: The blue crab fishery of Alabama. In: *Proceedings of the blue crab colloquium* (H. Perry and W. Van Engel, eds.), 23-28. Tech. Rep. 7, Gulf States Marine Fisheries Commission, Ocean Springs, MS.

Teissier, G., 1960: Relative growth. Chapter 16 in: *The physiology of crustacea, Vol. 1* (T. Waterman, ed.), 537-560. New York: Academic Press.

Texas Parks and Wildlife Department, 1999: *Marine Resource Monitoring Operations Manual*. TPWD, Austin.

Thomas, J., R. Zimmerman and T. Minello, 1990: Abundance patterns of juvenile blue crabs (*Callinectes sapidus*) in nursery habitats of two Texas bays. *Bull. Mar. Sci. 46* (1), 115-125.

Tilburg, C., A. Dittel, and C. Epifanio, 2007: Retention of crab larvae in a coastal null zone. *Est. Coast. Shelf Sci. 72*, 570-578.

Tilburg, C., C. Kernehan, A. Andon, and C. Epifanio, 2008a: Modeling estuarine ingress of blue crab megalopae: Effects of temporal patterns in larval release. *J. Mar. Res. 66*, 391-412.

Tilburg, C., J. Reager, and M. Whitney, 2008b: The physics of blue crab larval recruitment in Delaware Bay: a model study. *J. Mar. Res. 63*, 471-495.

Tilburg, C., A. Dittel, and C. Epifanio, 2009: High concentrations of blue crab (*Callinectes sapidus*) larvae along the offshore edge of a coastal current: effects of convergent circulation. *Fish. Oceanogr. 18* (3), 135-146.

Tindle, S., E. Boone, J. O'Brien, and A. Boettcher, 2004: Effects of salinity on larval stages of the rhizocephalan barnacle *Loxothylacus texanus*: survival and metomorphosis in response to the host, *Callinectes sapidus*. *J. Exp. Mar. Biol. Ecol. 302*, 165-176.

Towle, D. W., 1993: Ion transport systems in membrane vesicles isolated from crustacean tissues. *J. Exp. Zool. 265*, 387-396.

Towle, D., and D. Weihrauch, 2001: Osmoregulation by gills of euryhaline crabs: molecular analysis of transporters. *Amer. Zool. 41*, 770-780.

Towle, D., and L. Burnett, 2007: Osmoregulatory, digestive, and respiratory physiology. Chapter 9 in: *The blue crab, Callinectes sapidus* (Kennedy and Cronin, eds., 2007), 419-449.

Trent, L., E. Pullen, and R. Proctor, 1975: Abundance of macrocrustaceans in a natural marsh and a marsh altered by dredging, bulkheading, and filling. *Fish. Bull. 74* (1), 195-200.

Truitt, R. V., 1939: *Our water resources and their conservation*. Contr. 27, Chesapeake Biological Laboratory, University of Maryland.

Turner, H., D. Wolcott, T. Wolcott, and A. Hines, 2003: Post-mating behavior, intramolt growth, and onset of migration to Chesapeake Bay spawning grounds by adult female blue crabs, *Callinectes sapidus* Rathbun. *J. Exp. Mar. Biol. Ecol. 295*, 107-130.

Uphoff, J. H., 1998. Stability of the blue crab stock in Maryland's portion of Chesapeake Bay. *J. Shellfish Res. 17*, 519-528.

U.S. Weather Bureau and U.S. Navy Hydrographic Office, 1959: *Climatological and oceanographic atlas for mariners: 1 – North Atlantic Ocean*. Washington, D.C.: Government Printing Office.

Vallis, G.K., 2006: *Atmospheric and oceanic fluid dynamics: Fundamentals and large-scale circulation*. New York: Cambridge University Press.

Van den Avyle, M., and D. Fowler, 1984: *Blue Crab. Species profiles: Life history and environmental requirements of coastal fishes and invertebrates (South Atlantic)*. Report EL-82-4, FWS-OBS-82/11.19, National Coastal Ecosystems Team, U.S. Fish & Wildlife Service, Washington, D.C.

Van Engel, W. A., 1958: The blue crab and its fishery in Chesapeake Bay, Part 1 – Reproduction, early development, growth, and migration. *Comm. Fish. Rev. 20* (6), 6-17.

Van Engel, W. A., 1982: Blue crab mortalities associated with pesticides, herbicides, temperature, salinity, and dissolved oxygen. In: *Proceedings of the blue crab colloquium* (H. Perry and W. Van Engel, eds.), 89-92. Tech. Rep. 7, Gulf States Marine Fisheries Commission, Ocean Springs, MS.

Van Engel, W. A., 1990: Development of the reproductively functional form in the male blue crab, Callinectes sapidus. *Bull. Mar. Sci. 46* (1), 13-22.

Van Montfrans, J., C. Peery, and R. Orth, 1990: Daily, monthly and annual settlement patterns by *Callinectes sapidus* and *Neopanope sayi* megalopae on artificial collectors deployed in the York river, Virginia: 1985-1988. *Bull. Mar. Sci. 46* (1), 214-229.

Van Montfrans, J., C. Epifanio, D. Knott, R. Lipcius, D. Mense, K. Metcalf, E. Olmi, R. Orth, M. Posey, E. Wenner and T. West, 1995: Settlement of blue crab postlarvae in western north Atlantic estuaries. *Bull. Mar. Sci. 57* (3), 834-854.

Van Montfrans, J., R. Latour, and D. Combs, 2005: Natural mortality of juvenile blue crabs: quantifying predation impacts by finfish in lower Chesapeake Bay seagrass beds – a

preliminary analysis. In: *Chesapeake Bay Integrated Research Program Symposium Report* (D. Orner, ed.), 65-72. Chesapeake Bay Office, NOAA, Annapolis, MD.

Vogel, S., 1981: *Life in moving fluids: the physical biology of flow*. Princeton, NJ: Princeton University Press.

Walker, N. D., 1996: Satellite assessment of Mississippi River plume vaiability: Causes and predictability. *Remote Sens. Environ. 58*, 21-35.

Walker, N., G. Fargion, L. Rouse, and D. Biggs, 1994: Circulation of Mississippi River water discharged into the northern Gulf of Mexico by the Great Flood of summer 1993. *EOS, Trans. AGU 75* (36), 409,414-415.

Ward, G. H., 1982: Pass Cavallo, Texas: case study of tidal-prism capture. *J. Waterways, Port, Coastal & Ocean Div., Proc. Am. Soc. Civ. Engr. 108* (WW4), 513-525.

Ward, G. H., 1997: *Processes and trends of circulation within the Corpus Christi Bay National Estuary Program Study Area*. Report CCBNEP-21, Corpus Christi Bay National Estuary Program, Corpus Christi, Texas. (Distributed through Coastal Bend Bays Estuary Program.)

Ward, G. H., 2010a: *Inflows to San Antonio Bay*. Interagency contract 0900010973 report to Texas Water Development Board, Center for Research in Water Resources, University of Texas at Austin.

Ward, G. H., 2010b: *A time line of Cedar Bayou*. Interagency contract 0900010973 report to Texas Water Development Board, Center for Research in Water Resources, University of Texas at Austin.

Ward, G., and C. Montague, 1996: Estuaries. Chapter 12 in: *Water Resources Handbook* (L. Mays, ed.), 12.1 - 12.114. New York: McGraw-Hill Book Company.

Ward, G., and N. Armstrong, 1997: *Ambient water, sediment and tissue quality of Corpus Christi Bay study area, present status and historical trends: Technical report.* Publ. 23, Corpus Christi Bay National Estuary Program, Corpus Christi, Texas. (Distributed through Coastal Bend Bays Estuary Program.)

Wardle, W., and A. Tirpak, 1991: Occurrence and distribution of an outbreak of infection of *Loxothylacus texanus* (Rhizocephala) in blue crabs in Galveston Bay, Texas, with special reference to size and coloration of the parasite's external reproductive structures. *J. Crust. Biol. 11* (4), 553-560.

Warner, G. F., 1977: *The biology of crabs*. London: Van Nostrand Reinhold Company.

Webb, S., and R. Kneib, 2002: Abundance and distribution of juvenile white shrimp *Litopenaeus setiferus* within a tidal marsh landscape. *Mar. Ecol. Prog. Ser. 232*, 213-223.

Weinstein, M. P., 1988a: Epilogue. *Am. Fish Soc. Symp. 3*, 163-165.

Weinstein, M. P. (ed.), 1988b: *Larval fish and shellfish transport through inlets. Am. Fish. Soc. Symp. 3*.

Weisberg, R., R. He, Y. Liu and J. Virmani, 2005: West Florida shelf circulation on synoptic, seasonal, and interannual time scales. In: *Circulation in the Gulf of Mexico: Observations and models* (W. Sturges and A. Lugo-Fernandez, eds.), 325-247. Washington, D.C.: American Geophysical Union.

Weiss, R. F., 1970: The solubility of nitrogen, oxygen and argon in water and seawater. *Deep Sea Res. 17*, 721-735.

Weissburg, M., C. James, D. Smee and D. Webster, 2003: Fluid mechanics produces conflicting constraints during olfactory navigation of blue crabs, *Callinectes sapidus*. *J. Exp. Biol. 206* , 171-180.

Welch, J., D. Rittschof, T. Bullock, and R. Forward, 1997: Effects of chemical cues on settlement behavior of blue crab *Callinectes sapidus* postlarvae. *Mar. Ecol. Prog. Ser. 154*, 143-153.

Welch, J., R. Forward, and P. Howd, 1999: Behavioral responses of blue crab *Callinectes sapidus* postlarvae to turbulence: implications for selective tidal stream transport. *Mar. Eco. Prog. Ser. 179* , 135-143.

Welch, J., and R. Forward, 2001: Flood tide transport of blue crab, *Callinectes sapidus*, postlarvae: behavioral responses to salinity and turbulence. *Mar. Biol. 139*, 911-918.

Whitaker, J., L. Delancey, J. Jenkins, and M. Maddox, 1998: A review of the fishery and biology of the blue crab, *Callinectes sapidus*, in South Carolina. *J. Shellfish Res. 17* (2), 459-463.

White, J., and S. Gould, 1965: Interpretation of the coefficient in the allometric equation. *Amer. Nat. 99* (904), 5-18.

Whitney, J. O., 1974: The effect of external salinity upon lipid synthesis in the blue crab *Callinectes sapidus* Rathbun and in the spider crab *Libinia emarginata* Leech. *Comp. Biochem. Physiol. 49A*, 433-440.

Whitney, M., and R. Garvine, 2005: Wind influence on a coastal buoyant outflow. *J. Geophys. Res. 110* , C03014, doi:10.1029/2003JC002261.

Whitney, M., and R. Garvine, 2006: Simulating the Delaware Bay buoyant outflow: comparison with observations. *J. Phys. Oceanogr. 36*, 3-21.

Williams, A. B., 1971: A ten-year study of meroplankton in North Carolina estuaries: Annual occurrence of some brachyuran developmental stages. *Chesap. Sci. 12* (2), 53-61.

Williams, A. B., 1984: *Shrimps, lobsters and crabs of the Atlantic coast of the eastern U.S. Maine to Florida*. Washington, D.C.: Smithsonian Institution Press.

Williams, A. B., 2007: Systematics and evolution. Chapter 1 in: *The blue crab, Callinectes sapidus* (Kennedy and Cronin, eds., 2007), 1-21.

Williams, A. H., L. Coen and M. Stoelting, 1990: Seasonal abundance, distribution, and habitat selection of juvenile *Callinectes sapidus* (Rathbun) in the northern Gulf of Mexico. *J. Exp. Mar. Biol. Ecol. 137*, 165-183.

Wilson, K., K. Able and K. Heck, 1990: Predation rates on juvenile blue crabs in estuarine nursery habitats: evidence for the importance of macroalgae (*Ulva lactuca*). *Mar. Ecol. Prog. Ser. 58*, 243-251.

Wippelhauser, G., and J. McCleave, 1988: Rhythmic activity of migrating juvenile American eels *Anguilla rostrata*. *J. Mar. Biol. Assn. U.K. 68*, 81-91.

Wolcott, D., and M. De Vries, 1994: Offshore megalopae of *Callinectes sapidus*: depth of collection, molt stage and response to estuarine cues. *Mar. Ecol. Prog. Ser. 109*, 157-163.

Wolcott, T., and A. Hines, 1990: Ultrasonic telemetry of small-scale movements and microhabitat selection by molting blue crabs (*Callinectes sapidus*). *Bull. Mar. Sci. 46* (1), 83-94.

Wolcott, D., C. Hopkins, and T. Wolcott, 2005: Early events in seminal fluid and sperm storage in the female blue crab *Callinectes sapidus* Rathbun: Effects of male mating history, male size, and season. *J. Exp. Mar. Biol. Ecol. 319*, 43-55.

Wong, K.-C., and A. Münchow, 1995: Buoyancy forced interaction between estuary and inner shelf: observation. *Cont. Shelf Res. 15* (1), 59-88.

Wood, L., and J. Hargis, 1971: Transport of bivalve larvae in a tidal estuary. In: *Larval biology* (D. Crisp, ed.), 29-44. London: Cambridge University Press.

Wright, L., and J. Coleman, 1971: Effluent expansion and interfacial mixing in the presence of a salt wedge, Mississippi River delta. *J. Geophys. Res. 76* (36), 8649-8661.

Wrona, A., R. Wiegert and T. Bishop, 1995: Initial report of settlement patterns of brachyuran megalopae at Sapelo Island, Georgia, U.S.A. *Bull. Mar. Sci. 57* (3), 807-820.

Yang, H., R. Weisberg, P. Niiler, W. Sturges, and W. Johnson, 1999: Lagrangian circulation and forbidden zone on the West Florida shelf. *Cont. Shelf Res. 19*, 1221-1245.

Yudin, A., R. Diener, W. Clark and E. Chang, 1980: Mandibular gland of the blue crab, *Callinectes sapidus*. *Biol. Bull. 159*, 760-772.

Zeug, S., V. Shervette, D. Hoeinghaus, and S. Davis, 2007: Nekton assemblage structure in natural and created marsh-edge habitats of the Guadalupe estuary, Texas, USA. *Est., Coast. Shelf Sci. 71*, 457-466.

Zimmerman, R., and T. Minello, 1984: Densities of *Penaeus aztecus*, *Penaeus setiferus*, and other natant macrofauna in a Texas salt marsh. *Estuaries 7* (4A), 421-433.

Zohar, Y., A. Hines, O. Zmora, E. Johnson, R. Lipcius, R. Seitz, D. Eggleston, A. Place, E. Schott, J. Stubblefield, and J. Chung, 2008: The Chesapeake Bay blue crab (*Callinectes sapidus*): A multidisciplinary approach to responsible stock replenishment. *Rev. Fish. Sci. 16* (1-3), 24-34.

APPENDIX A
Notes on the allometric equation

Surveys of the history of the concept of allometry and its mathematical expression are included in Gould (1971), Stern and Emlen (1999), and Gayon (2000). As noted by Gould (1971) and Gayon (2000), the allometric equation

$$y = A\,x^{b} \tag{A-1}$$

appeared in the biological literature in the last years of the nineteenth century, at first in studies of the relative brain size of organisms. No doubt it arose from statistical fits of data in its logarithmic form

$$\log y = \log A + b \log x \tag{A-2}$$

This of course is the equation of a straight line $\log y = f(\log x)$ with slope b and y-intercept $\log A$, which could be fitted to a set of data by the conventional closed-form solution to the minimization of the sum of squared residuals, provided the original data is replaced by their logarithms. (Because of the general availability of base-10 logarithm tables, this is almost always the base used in the older literature. In this note, we assume napierian logarithms.) This was the only practical means of obtaining numerical results in those years. The resulting regression could then be exponentiated with the base of the logarithm (*viz.*, 10) to recover the form (A-1).

By differentiating (A-1) with respect to time, substituting (A-1) into the resulting derivative, and rearranging terms, one exposes the physical meaning of the exponential b:

$$b = \frac{\frac{1}{y}\frac{dy}{dt}}{\frac{1}{x}\frac{dx}{dt}} \tag{A-3}$$

As noted in Chapter 2 of the text, this affords the immediate interpretation that b is the ratio of the *specific* growth rate of y, i.e., the rate of growth per unit of y (or, in the case of crab mass, the variable of concern in the text, the rate of growth per unit mass), to the specific growth rate of x (in the text, carapace width).

The multiplier A is less straightforward. White and Gould (1965), as well as earlier workers cited in their review, observed that A has the undesirable quality of changing its value when the units of measurement of x change, unlike the "pure" (i.e., dimensionless) exponent b. They make the puzzling statement that since y and x are "usually recorded in equivalent units" then (A-1) is correct as it stands, but one must remember "that it is somewhat more complex." The fact that A is the value of y given by (A-1) when $x = 1$, Gould (1971) notes, led some scientists to dismiss it as having no general biological significance (since a change in units of x results in a change in magnitude of A).

This aspect of A is, in our view, easily resolved by the observation that A indeed has dimensions, namely

$$[A] = [y]\,[x]^{-b} \qquad \text{(A-4)}$$

and (A-1) is seen to be dimensionally homogeneous. For the application here, in which $[y]$ = mass (of the crab in grams) and $[x]$ = length (carapace width in millimeters), the units of A are g $(\text{mm})^{-b}$. Granted, these are rather peculiar units, but as derived units from an empirical relation, they are no more bizarre than, say, a Chézy coefficient in $\sqrt{m}$ /s, or Manning's n in $\text{s/m}^{1/3}$. As a corollary, if Y and X are measurements reported in units different from those native to (A-1), from which the corresponding exponential multiplier is $\mathscr{A}$, and if Q_y is the conversion of units of Y to units of y, i.e. in units of y per unit of Y, and Q_x is the conversion of units of X to units of x, i.e. in units of x per unit of X, then

$$Y = \mathscr{A} X^b$$

$$\Rightarrow \qquad Q_y\, Y = Q_y\, Q_x^{-b}\, \mathscr{A} (Q_x\, X)^b$$

$$\Rightarrow \qquad y = (Q_y\, Q_x^{-b}\, \mathscr{A})\, x^b$$

whence

$$A = Q_y\, Q_x^{-b}\, \mathscr{A} \qquad \text{(A-5)}$$

We note that if y and x are in exactly the same units then (A-5) is seen to be equation (2) of White and Gould (1965). The examples given by White and Gould (1965) all satisfy this condition of y and x having the same units, e.g., brain volume versus body volume. In general, however, we cannot expect this, since x and y frequently measure attributes with different dimensions, such as many of the examples considered in Gould (1971).

As an example, in the relation of crab mass to carapace width, the native units of equation (1) of the text are specified as g and mm. Table 1 of the text collects available data on the values of A and b for various literature reports on dimensions of blue crabs. Several of the sources in Table 1 measure width in cm. In this case, Q_x = 10 mm per cm (Q_y is unity because the mass is measured in g by all of the sources), so the A in Table 1 was computed from the reported $\mathscr{A}$ as:

$$A = 10^{-b}\, \mathscr{A}$$

in which b is the reported exponent.

It is often observed, at least in the older literature, that log$A$ and b are not independent but appear to be anticorrelated. This is addressed by White and Gould (1965), who seem to subscribe to the view of Lumer and associates (e.g., Lumer, 1936) that this is an artifact of the region of intersection of the various equations (A-2): when this region of intersection lies to the right of x = 1 ($\log x = 0$) then $\log A$ and b are "inversely related" (meaning anticorrelated), when this

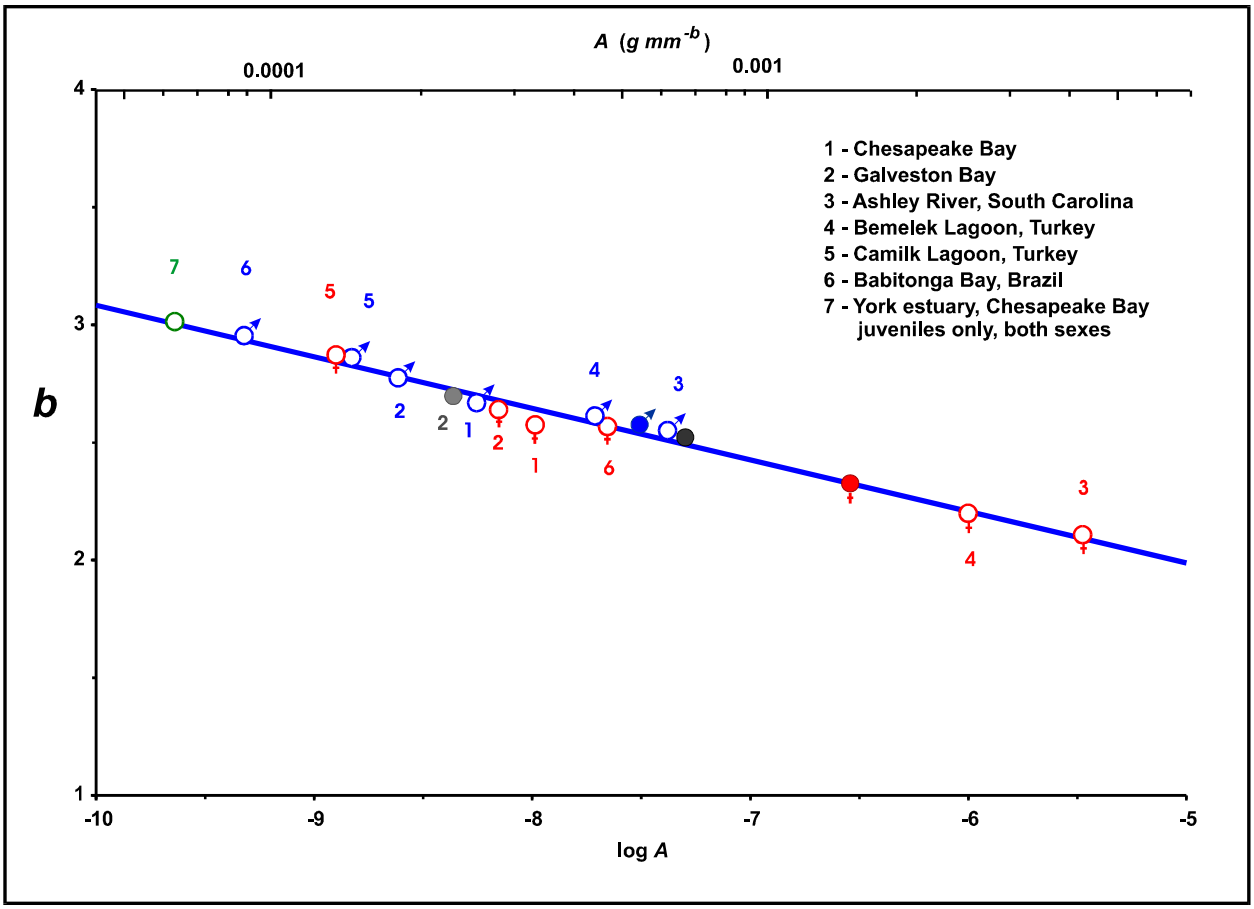


Figure A-1 - Regressed allometric equation parameters *b* (exponent) versus *A* (multiplier) from Table 1 as open circles, and least-squares regression line. Count-weighted pooled equations added for males, females and combined sexes (filled circles). Galveston Bay equation for combined sexes shown as grey-filled data point.

region is in the vicinity of $x = 1$ then log *A* and *b* are independent, and when this region lies to the left of $x = 1$ then log *A* and *b* are directly correlated. (The first case of the intersection lying to the right is restated by White and Gould that the measurements of *x* and *y* are large compared to their units.)

Figure A-1 displays the values of *b* from Table 1* plotted versus their corresponding values of log *A*. To say that they are anticorrelated is an understatement: the correlation is nearly perfect, with r = -0.991, an explained variance greater than 98%. To explore the reasons behind such a remarkable result is beyond the scope of this project. We can offer a hypothesis, however. Each of the allometric equations, log-transformed to the form (A-2), is fitted to a set of (log) measurement pairs of carapace width (*W*) and body mass (*M*). In Table 1, the number of such measurements runs from 75 to over 9,000. The regression line passes through the cloud of data,

* There is one more set of data, from Perry (unpublished) presented in Guillory et al. (2001) from Mississippi, probably the Mississippi Sound. This set is not included because there are unresolvable typographical errors in the given regression equations.

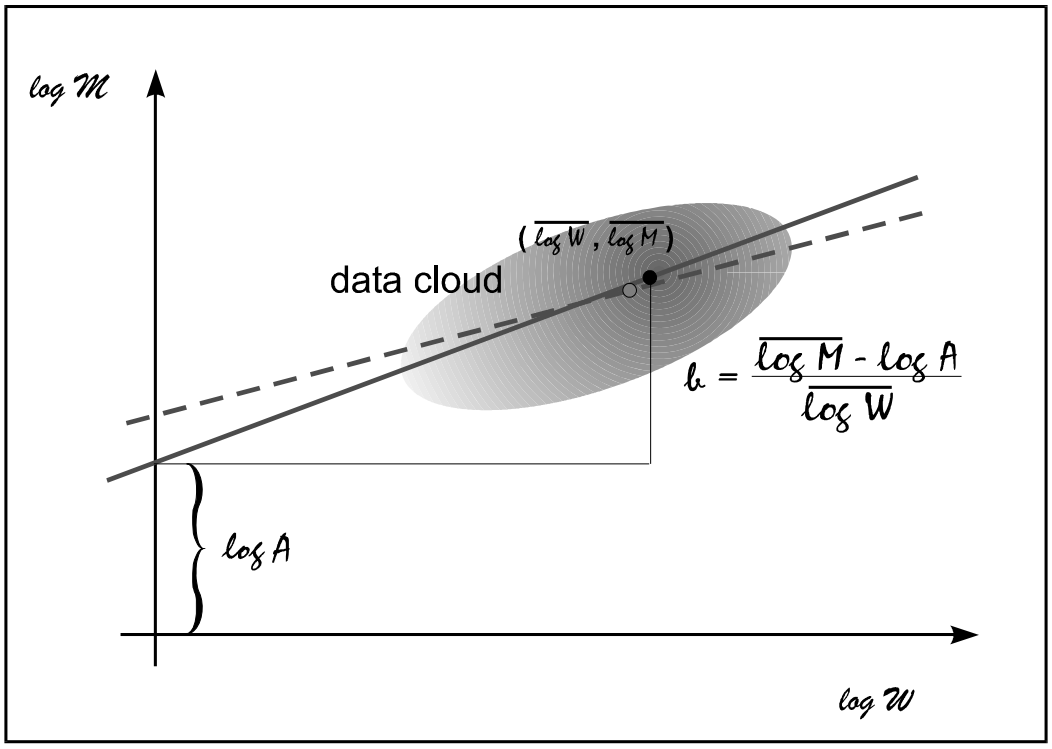


Figure A-2 - Sketch of regression line passing through cloud of log-transformed crab data.

and in particular through the mean of the data ($\overline{\log W}$, $\overline{\log M}$), as sketched in Figure A-2. Variation in the distribution of data in the cloud will alter the line. If the means are unchanged, then the slope only will be altered,

$$b = (\overline{\log M} - \log A) / \overline{\log W}$$

which demonstrates that *b* will exhibit exact anticorrelation with *log A*. If the means are different, but reasonably close to those of the first data cloud, the anticorrelated relation between *b* and *log A* will be approximately preserved, as suggested by the dashed line of Fig. A-2. The hypothesis is that crab dimensions exhibit sufficient consistency over the seven programs from which the allometric relations of Table 1 were compiled that the anticorrelated relation between *b* and *log A* is maintained. This is not saying that the anticorrelation of these parameters is an artifact of the statistics. Rather, despite the effect of variance in the data due to sampling errors, geographical separation, and gear that targets different size ranges, resulting in different means of the data, and different slopes and multipliers of the best-fit allometric power law, there is still exhibited a consistency between the slope and the multiplier over all of these data sets.

We would like to determine a pooled regression by combining all of the raw data from the various surveys listed in Table 1. In order to do this, we need either the raw data (which is obviously inaccessible) or the values of each of N, $\overline{x}$, $\overline{y}$, σ_x, σ_y, and *r*, from which we could construct the regression on the pooled data. While some of these values are provided by all of

the sources, the totality is provided by none. The best we can do is *estimate* the regression on the pooled data by a count-weighted mean of the regression parameters:

$$\bar{b} = \frac{\sum_i N_i b_i}{\sum_i N_i}, \quad \bar{A} = \frac{\sum_i N_i A_i}{\sum_i N_i} \tag{A-6}$$

where A_i, b_i are the regression parameters for the ith regression, and N_i is the count of data that regression is based on. This estimate is the source for the "pooled equations" data of Table 1 in the text. The count-weighted averages $\bar{A}, \bar{b}$ for males, females and both sexes combined are added to the regression plot of Fig. A-1 as filled data points (but not included in the determination of the regression line and associated correlation). We note that the South Carolina data set of Olmi and Bishop (1983) dominates these count-weighted pooled regressions, especially for the males, due to its great number of data, see Table 1 of the text. This is also why the combined-sexes pooled-equation data point (the black-filled circle) in Fig. A-1 lies closer to the pooled-equation data point for males than the data point for females.

The Pullen-Trent (1970) Galveston Bay equation for both sexes combined has also been added to Fig. A-1, because of the historical use of this relation by TPWD to estimate crab weight.

Of course, it must be recognized that all of the statistics performed on these data are carried out in logarithm space, and the reported explained variance, which is maximized when the residuals are minimized in the least-squares fit of a straight line, applies strictly to the *logarithms* of the measurements. **The best-fit straight line in logarithm space (A-2) does not correspond to the best-fit power law (A-1) in measurement space.** For example, the extreme measured values are given less weight when their logarithms are used as data, than would be accorded with non-transformed measurements. For most of the period of time represented in the data collections, a linear fit to the logarithms was the only means of computing a solution to the least-squares problem. With modern computing power, it is now possible to fit the non-transformed allometric equation (A-1) *directly* by minimizing the residuals of the power-law using numerical methods. The values of b and A so derived will differ, perhaps significantly, from those of Table (A-1). It is unfortunate that the raw data are not available in a digital format to carry out these calculations.

APPENDIX B
Juvenile stages: Chesapeake Bay data of Newcombe and associates

A seminal study of the growth and molting stages of juvenile blue crabs is reported by Newcombe et al. (1949). Data from two separate field studies are combined. The first addresses very young juvenile crabs that were cultured in the laboratory from wild-caught megalops from Chesapeake Bay, and their progression through the first seven or eight intermolt stages was monitored. The second, described in Gray and Newcombe (1938b), involved the acquisition of pre-molt crabs using standard biological gear or purchase from local crabbers. The crabs were maintained in floating compartments near the Chesapeake Biological Laboratory "under approximately natural conditions" until they molted, so that measurements of pre- and post-molt dimensions were performed. Although the main purpose of the study was to explore allometric-growth relations among various linear dimensions of the crab, the data on size ranges of the first seven or eight instars have proven useful in empirically assigning wild juveniles to an instar stage. There are discrepancies in the reported data, however.

The group designations (also the instar numbered from the first juvenile crab, i.e. after the molting of the megalop), corresponding size ranges, number of individuals and mean carapace width (CW, measured in mm) are repeated in Tables 1, 2, 5 and 6 of Newcombe et al. (1949). These data are collected in Table B-1. The ranges are irregular and overlapping, since these are the minima and maxima of measured CW's. The next groups in the respective tables are size categories in (non-overlapping) steps of 10 mm, and the data are measured pre-molt crabs from collections in Chesapeake Bay (so that the numbers of individuals vary from group to group). In two of the tables (Newcombe's 1 and 6), the oldest instars are seven (VII), Group VIII beginning the 10-mm size categories. In two of the tables (Newcombe's 2 and 5), there is an eighth instar (VIII) for which measurements are reported, Group IX beginning the 10-mm size categories. Moreover, the number column is clearly shifted up one row in Newcombe's Table 6. It is impossible to say whether these are data-entry errors originating in the data logs or the manuscript of the paper, or typographical errors originating in the type-setting. It is our judgment that the eighth instar represents real data and was omitted in Newcombe's Tables 1 and 6, and our "best-guess" array of these data is given as the final section of Table B-1. These data are the source for Figure 8 in the text.

It would be desirable to know how many individuals occur in the overlap regions of the early instar groups, as this would be a measure of the probability of error in using the size range as a means of determining how many molts a specific instar has experienced. Of course, the original data are not available, but the reported standard deviations from the means for each instar size interval can be used to estimate this, by assuming that these accurately parameterize the underlying (normal) distribution. The fraction of the underlying normally distributed population that lies below the lower limit b or above the upper limit a is given by the respective expressions:

$$\int_{-\infty}^{b} n(w;\mu,\sigma)dw \qquad\qquad 1 - \int_{-\infty}^{a} n(w;\mu,\sigma)dw \qquad\qquad \text{(B-1)}$$

where $n(w;\mu,\sigma)$ denotes the normal density function of random variable w with mean μ and standard deviation σ. These fractions for the limits of CW range for each instar given by

Table B-1
Data from Newcombe et al. (1949) on early juvenile instar carapace widths (CW, mm),
with best-guess at reconciliation, see text.

Table 1

Group	*CW interval (range)*		*number*	*mean CW*
I	2.2	3.0	50	2.47
II	3.0	4.2	50	3.68
III	4.1	6.0	50	5.10
IV	5.5	7.4	50	6.64
V	7.2	10.0	50	8.60
VI	8.7	12.4	50	10.19
VII	9.7	13.0	35	11.00

Tables 2 & 5

Group	*CW interval (range)*		*number*	*mean CW*
I	2.2	3.0	50	2.47
II	3.0	4.2	50	3.68
III	4.1	6.0	50	5.10
IV	5.5	7.4	50	6.64
V	7.2	10.0	50	8.60
VI	8.7	12.4	50	10.19
VII	9.7	13.0	35	11.00
VIII	13.5	16.5	6	14.50

Table 6

Group	*CW interval (range)*		*number*	*mean CW*
I	2.2	3.0	50	2.5
II	3.0	4.2	50	3.7
III	4.1	6.0	50	5.1
IV	5.5	7.4	50	6.6
V	7.2	10.0	50	8.6
VI	8.7	12.4	35	10.2
VII	9.7	13.0	6	11.0

Best guess corrected

Group	*CW interval (range)*		*number*	*mean CW*	*st dev CW*
I	2.2	3.0	50	2.47	0.14
II	3.0	4.2	50	3.68	0.25
III	4.1	6.0	50	5.10	0.42
IV	5.5	7.4	50	6.64	0.46
V	7.2	10.0	50	8.60	0.66
VI	8.7	12.4	50	10.19	0.85
VII	9.7	13.0	35	11.00	0.81
VIII	13.5	16.5	6	14.50	1.04

Table B-2
Fraction of underlying population distribution lying outside the bounds of the ranges of carapace width observed by Newcombe et al. (1949) or specified by Pile et al. (1996), cf. Fig. 8 of the text

	Newcombe et al. ranges				*Pile et al. categories*			
Instar	*lower*	*frac (%)*	*upper*	*frac (%)*	*lower*	*frac (%)*	*upper*	*frac(%)*
I	2.2	2.7	3.0	0.0	2.2	2.7	3.0	0.0
II	3.0	0.3	4.2	1.9	3.1	1.0	4.2	1.9
III	4.1	0.9	6.0	1.6	4.3	2.8	5.9	2.8
IV	5.5	0.7	7.4	4.9	6.0	8.2	7.4	4.9
V	7.2	1.7	10.0	1.7	7.5	4.8	9.1	22.4
VI	8.7	4.0	12.4	0.5	9.2	12.2	10.6	31.5
VII	9.7	5.4	13.0	0.7	10.7	35.6	12.6	2.4
VIII	13.5	16.8	16.5	2.7	12.7	4.2	14.1	65.0

Newcombe et al. (1949) are tabulated in Table B-2. We note that these fractions are equivalent to the probability that an instar will have a carapace width either less than or greater than the specified range. These distributions are displayed graphically in Fig. 8 of the text.

The complete data set Newcombe used in his evaluation of molt increments is not presented in the 1949 paper. Data from Table 6 of Newcombe (1949) and from Table II of Gray and Newcombe (1938b), combined with the reconciled data from Table B-1 have been compiled in Table B-3 to reconstitute this data set, including the correction of several minor typographical errors. While the upward shifting in Newcombe's Table 6 of the number of individuals for instars 6 & 7 noted above is erroneous, i.e. these should read 50 and 35, resp., it is likely that the omission of the laboratory instar VIII data is deliberate. Since the purpose of his Table 6 is to compile data on the size increment at molting, Newcombe apparently chose to use the wild-caught molting increment for Group VIII (from Gray and Newcombe, 1938b) rather than the Stage 8 instar data, probably because the latter had a smaller number of data but more-or-less corresponded to the same range as the former, and perhaps because the laboratory molting series were suspected of exhibiting lower growth rates than in the wild, whereupon the highest instars would exhibit the greatest error. This decision is retained in Table B-3, because there are no data reported in either paper on the pre-molt and post-molt CW's for laboratory instars VIII.

It is reasonable to express the increment in width associated with a molt as a fraction R of the pre-molt width, that is, as a Hiatt growth diagram (Hiatt, 1948). If this in fact holds, then the post-molt width y is given as a function of pre-molt width x by:

$$y = x + Rx = (1+R)\,x \qquad \text{(B-2)}$$

i.e., if y is regressed against x, the regression should pass through the origin and have slope $1+R$. The regression of the post-molt width versus the pre-molt width using the data of Table B-3

Table B-3
Data from Gray and Newcombe (1938b) and Newcombe et al. (1949) on carapace-width increment on molting

			Early juveniles, sexes combined				
Instar	*CW interval (range, mm)*		*number*	*initial (mm)*	*final*	*increment (mm)*	*(%)*
I	2.2	3.0	50	2.5	3.7	1.2	49.8
II	3.0	4.2	50	3.7	5.1	1.4	38.6
III	4.1	6.0	50	5.1	6.6	1.5	29.4
IV	5.5	7.4	50	6.6	8.6	2.0	29.5
V	7.2	10.0	50	8.6	10.2	1.6	18.6
VI	8.7	12.4	50	10.2	11.0	0.8	7.9
VII	9.7	13.0	35	11.0	14.5	3.5	31.8

			juveniles, female					***juveniles, male***				
Group	*CW interval (range, mm)*		*number*	*mean CW (mm) initial*	*final*	*increment (mm)*	*(%)*	*number*	*mean CW (mm) initial*	*final*	*increment (mm)*	*(%)*
VIII	10.0	19.9	8	16.8	18.8	2.0	11.9	5	17.6	20.1	2.5	14.1
IX	20.0	29.9	3	21.1	24.2	3.1	14.7	0				
X	30.0	39.9	4	33.9	41.1	7.2	21.2	7	36.2	44.6	8.4	23.2
XI	40.0	49.9	29	45.3	57.9	12.6	27.8	13	44.8	55.8	11.0	24.5
XII	50.0	59.9	52	55.4	71.9	16.5	29.8	25	54.4	69.4	15.0	27.5
XIII	60.0	69.9	66	65.0	87.5	22.5	34.6	31	64.9	84.0	19.1	29.3
XIV	70.0	79.9	40	74.4	101.6	27.2	36.6	24	74.1	98.1	24.1	32.5
XV	80.0	89.9	25	83.9	112.0	28.1	33.5	17	85.0	113.0	28.0	32.9
XVI	90.0	99.9	14	94.6	131.3	36.7	38.8	12	95.4	126.1	30.7	32.1
XVII	100.0	109.9	8	104.5	146.0	41.5	39.7	15	104.9	133.3	28.4	27.1
XVIII	110.0	119.9	5	116.3	157.8	41.5	35.7	19	115.2	144.3	29.1	25.3
XIX	120.0	129.9	3	122.0	165.1	43.1	35.3	13	123.7	153.5	29.8	24.1
XX	130.0	139.9	2	131.5	176.2	44.7	34.0	8	133.4	162.3	28.9	21.6
XXI	140.0	149.9						1	149.1	175.5	26.4	17.7
XXII	150.0	159.9						1	153.2	190.4	37.2	24.3

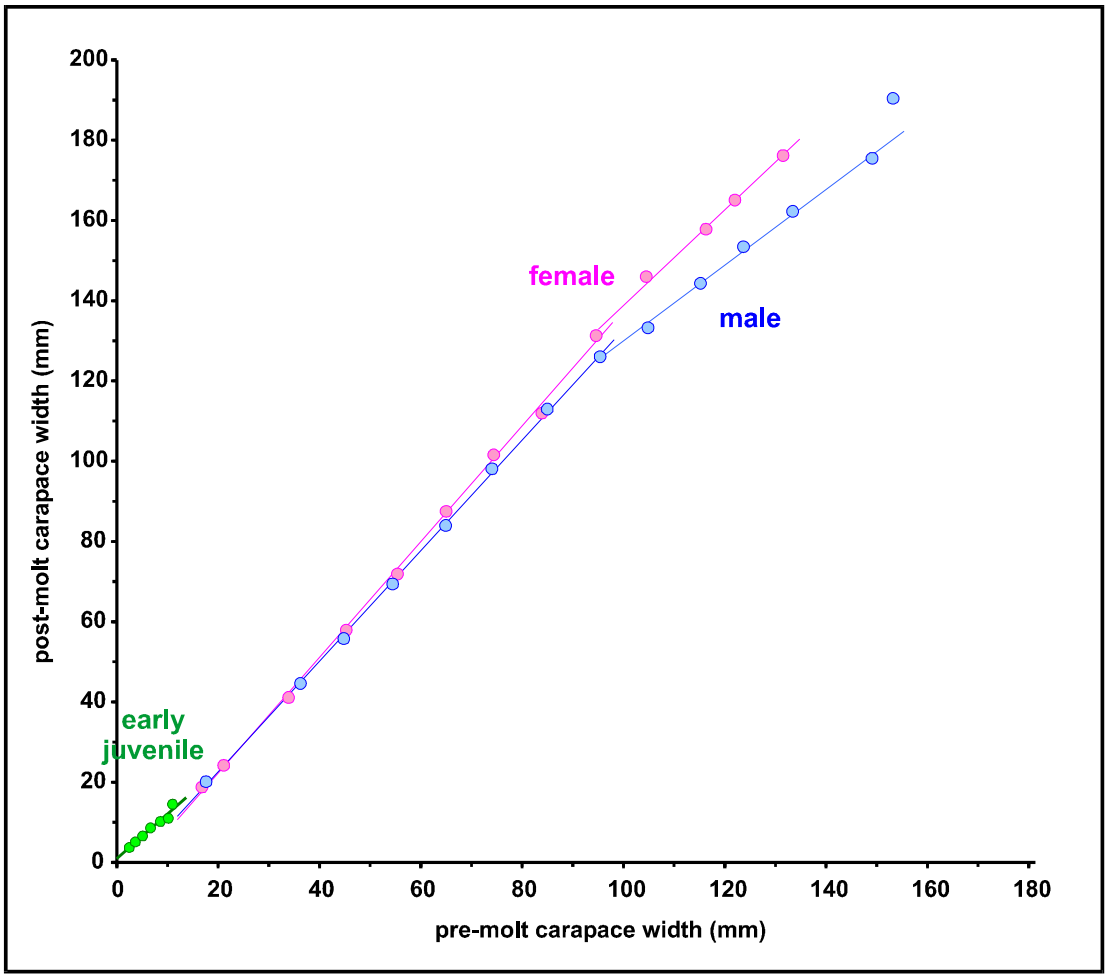


Figure B-1 - Post-molt carapace width regressed against pre-molt carapace width, data from Gray and Newcombe (1938b) and Newcombe et al. (1949)

yields a regression line y = 1.285 x + 0.36, which passes nearly through the origin and indicates an increment of 28.5% of the pre-molt width. The explained variance of this regression is over 99%.

If one isn't satisfied with this explained variance, then one might improve the model by performing separate regressions for males and females. The resulting regressions (in which the early juvenile data are included in both) have slopes 1.374 for females and 1.236 for males, and pass within 2 mm of the origin, with respective explained variances of 99.9% and 99.7%. This translates to an average post-molt increment of 37.4% for females and 23.6% for males.

If one still isn't satisfied with these explained variances, then one might further subdivide the range of the regressions according to the size of the crab, into "stanzas". Newcombe et al. (1949) pursued this, and obtained a set of regressions much like that shown in Figure B-1 above, which shows a different regression for the early juveniles and a break in slope at about 100 mm. This leads to an apparent variation in molt increment, as plotted in Fig. B-2. Much concern was indulged in by Newcombe et al. (1949) in explaining the variation in increment with carapace

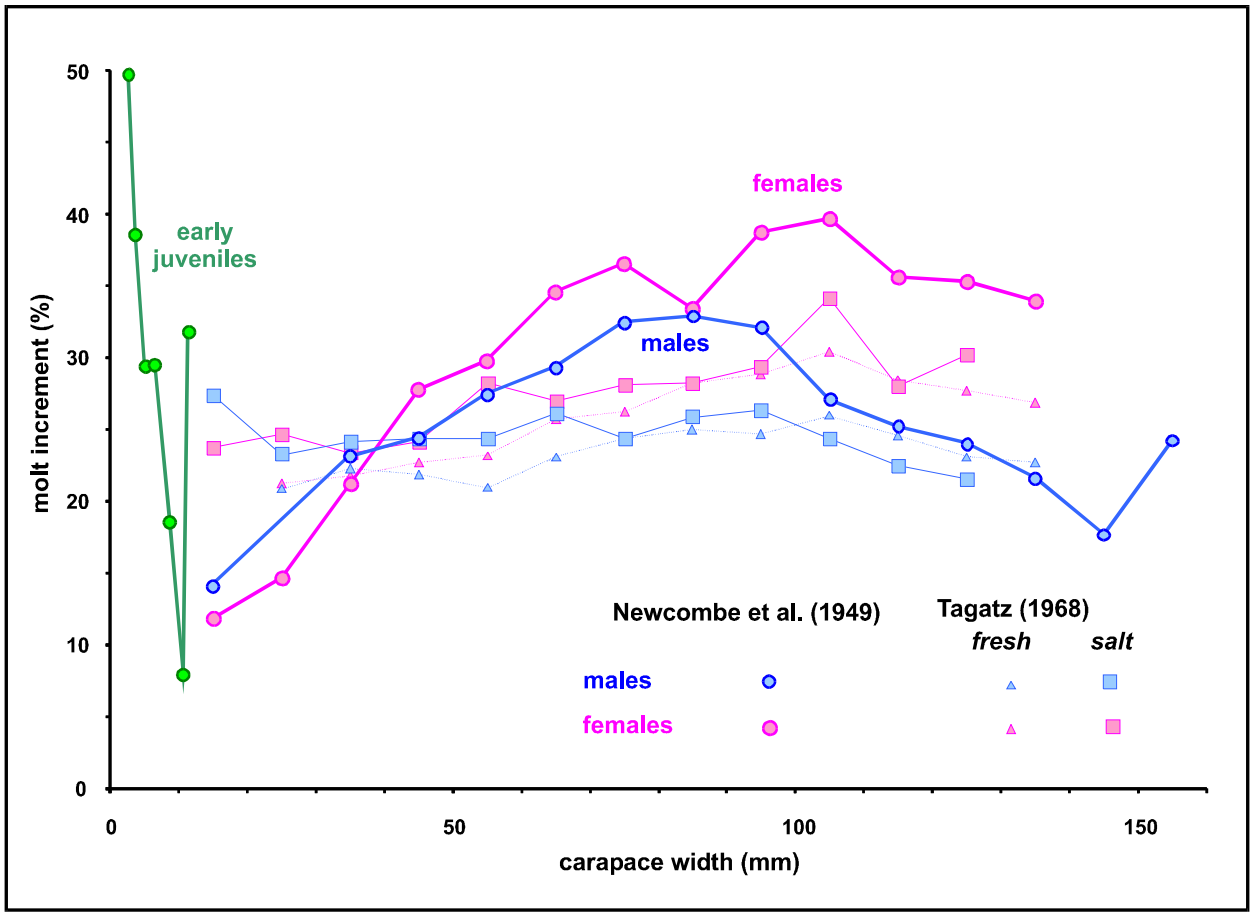


Figure B-2 - Apparent post-molt increment as fraction (%) of pre-molt carapace width as function of size of crab, data of Newcombe et al. (1949) and Tagatz (1968b)

width. This in fact arises from the nonzero y-intercept of the regression. The apparent increment as a fraction of the pre-molt width x then becomes

$$\Delta w = (mx+b-x) / x = m\text{-}1 + b / x \qquad \text{(B-3)}$$

which converges to equation (2) as x becomes large, but departs substantially for small x. Either one uses an affine regression relation or one accepts the increment as a fraction of the pre-molt size, but not both, because they are contradictory if $b \neq 0$. Tagatz (1968b) conducted a similar study on crabs in the St. Johns Estuary (Florida) and found generally comparable growth rates, but without the pronounced rise and decline below 100 mm, see Fig. B-2. Nonetheless, the reduction in growth rate as carapace width increases is significant because it quantifies a real reduction in post-molt carapace sizes of large crabs.

Pile et al. (1996) proposes a direct relation between carapace width and number of molts (i.e., instar number) for early juveniles that is roughly based on the ranges of Newcombe et al. (1949), with adjustments to eliminate the overlaps. Because the instar sizes do overlap, this categorization will lead to errors in instar identification. The probability that an instar will fall

Table B-4
Probabilities of instar carapace widths falling in Pile et al. (1996) size categories, based upon normal distribution with mean and standard deviation reported by Newcombe et al. (1949)

	Pile et al. (1996) category		*Probability (%) of instar (Column 1) occurring in Pile et al. instar categories:*							
Instar	*CW interval*		*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*
1	2.2	3.0	97.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
2	3.1	4.2	0.6	98.3	1.1	0.0	0.0	0.0	0.0	0.0
3	4.3	5.9	0.0	2.1	95.7	2.1	0.0	0.0	0.0	0.0
4	6.0	7.4	0.0	0.0	6.7	89.4	3.9	0.0	0.0	0.0
5	7.5	9.1	0.0	0.0	0.0	4.1	75.7	20.1	0.1	0.0
6	9.2	10.6	0.0	0.0	0.0	0.1	11.0	59.5	29.2	0.2
7	10.7	12.6	0.0	0.0	0.0	0.0	1.1	32.1	64.6	2.1
8	12.7	14.1	0.0	0.0	0.0	0.0	0.0	0.0	3.7	31.3
Fraction of occurrences of instar falling in Pile et al. category for that instar			97.3	98.3	95.7	89.4	75.7	59.5	64.6	31.3
Fraction of all instars falling in Pile et al. category that are correct			99.4	97.9	92.5	93.4	82.5	53.2	66.2	93.2
Fraction of all instars incorrectly falling in Pile et al. category			0.6	2.1	7.5	6.6	17.5	46.8	33.8	6.8

outside the correct bounds can be calculated with (1) in which *a* and *b* are now the upper (above) and lower (below) bounds specified by Pile et al. (1996). These are given in the right-hand section of Table B-2. This same basic method is used in Table B-4 to calculate various probabilities of the Pile et al. categories of correctly (or incorrectly) staging the instars. There are occurrences of each instar with CW's less than the lower limit for Instar 1 and more than the upper limit for Instar 8 that are not explicitly shown in Table B-4, which influence the probabilities.

We note that the bounds of the Pile et al. (1996) categories differ by 0.1 mm. This was done to facilitate placing a crab in the correct size category in the field, where the carapace is measured to the nearest 0.1 mm. For the calculations in Table B-4, this 0.1 gap between the categories corrupts the calculation of probabilities, and the total probabilities over each row of the table (including the occurrences below and above the Pile et al. limits) will not sum to unity. To repair this, the category CW bounds were actually specified as, e.g., 3.049 for Instar 1 and 3.050 for Instar 2, which round to 3.0 and 3.1, resp. This reduces the gap between categories to 0.001 mm without affecting the (rounded) bounds of the intervals.

APPENDIX C
Life stage terminology

General terminologies applied to stages of development of blue crab, with representative citations, are collected below.

Larva	(1) Zoeae, including prezoeae, Kennedy (2007) (2) All forms preceding the first crab instar, e.g., Robertson (1938), Truitt (1939, "two larval stages, zoea and megalops" (Van Engel, 1958), "zoea and megolopa larvae" (Kalber, 1970), "megalopal larval stage" (Tankersley et al., 1995), "megolopa larvae" (Epifanio, 2007), Dudley and Judy (1971), Adkins (1972), Smyth (1980), Perry and Stuck (1982)
Postlarva	(1) The megalop stage only, e.g. King (1971), Warner (1977), Welch et al. (1999), "postlarvae = megalopae" (Lipcius et al., 2007), Reyns et al. (2008) (2 Any stage after the zoeal, from megalop up to (but not including) mature, e.g., Tagatz (1968a), Jivoff et al. (2007).
Juvenile	(1) Any stage after the megalop not including mature, Jivoff et al. (2007). (2) Carapace width < 85 mm, King et al. (2005) (3) Carapace width < 50 mm, Adkins (1972), Perret (1967) (4) Carapace width 20-80 mm, McClintock et al. (1993) (5) Carapace width 50-70 mm, Osborn et al. (1992)
Subjuvenile	Carapace width less than 20 mm, McClintock et al. (1993)
Early juvenile	(1) Carapace width less than 10 mm, Perry and Stuck (1982), Mense and Wenner (1989) (2) Carapace width less than 30 mm, Smith and Chang (2007) (3) Young juvenile (1)
Benthic juvenile	The first 5-7 instars (< 20-30 mm), which remain in primary nursery habitat in Chesapeake Bay (Lipcius et al., 2007), the first 4-5 instars (< 6-9 mm), which remain in primary nursery habitat in Pamlico Sound (Etherington & Eggleston, 2003; Eggleston et al., 2010)
Young juvenile	(1) The first eight or nine instars (2) Small juvenile
Small juvenile	(1) Carapace width less than 60 mm, e.g., Cadman and Weinstein (1985), (2) Carapace width less 12-64, Wilson et al. (1990), (3) Carapace width less 20-65 mm, Rome et al. (2005) (4) Carapace width less than 70 mm, Hines et al. (1995)
Young of the year	Carapace width less than 45 mm (Osborn et al., 1992)

Large juvenile	Carapace width greater than 60 mm, Rome et al. (2005)
Late juvenile	(1) Carapace width greater than 30 mm, Smith and Chang (2007) (2) Carapace width greater than 40 mm, Perry and Stuck (1982) (3) Large juvenile
Young crab	Juvenile (1), Perry and Stuck (1982)
Subadult	(1) Immature male with carapace width greater than 100 mm, Smith and Chang (2007) (2) Large juvenile
Adult	(1) A male crab sufficiently large that it might be mature, e.g. >120 mm, Miller et al. (1975), Hines et al. (1995); 117-181, Tagatz (1971); >105, Guerin and Stickle (1997); >100, Eggleston et al. (2005); > 80 mm, McClintock et al. (1992); see also Breuer (1962), Tagatz (1968a) (2) Mature, Churchill (1919), Hines (2007) (3) Legal (harvestable) - Generally 127 mm (5.0 ins), but 114 mm (4.5 ins) in New York and New Jersey (4) Any stage above megalop (Smyth, 1980)
Mature	(1) Sexually functional (2) Legal (harvestable), see Adult (3), e.g., Palmer (1974)
First-time spawners	Mature female with carapace width 120-140 mm, Osborn et al. (1992)

APPENDIX D
Dissolved oxygen units

A bewildering variety of units is used in dissolved oxygen (DO) measurements. These include percent saturation, milligrams per liter (mg/L), parts per million (ppm), torrs, moles per liter, atmospheres, milliliters per liter (mL/L), liters per gram, and millibars (mb). These are derived from a variety of physical parameters, including mass concentration, mass per unit volume, volume concentration, and partial pressure. Interconversion requires not only information on units but also knowledge of the measurement procedure and the related physical processes. Some background for the units employed in this report is summarized here.

To a very good approximation, oxygen obeys the ideal gas equation

$$p\,V = n\,R\,T \qquad \text{(D-1)}$$

where
p = pressure of the gas
V = volume of gas
n = mass of the gas, expressed as number of moles
T = temperature of the gas
R = universal gas constant (82.06 cm^3 atm/mol K)

At standard temperature (273 K) and pressure (1 atm = 1013 mb = 101.3 kPa = 760 mm Hg),

$$RT/p \;=\; V/n \;=\; 22.42 \text{ L/mol} \qquad \text{(D-2)}$$

which is constant for oxygen, from which

$$1 \text{ mg } O_2\text{/L } H_2O \;(= 1 \text{ mg/L}) = 1.428 \text{ mL } O_2\text{/L } H_2O \;(= 1.428 \text{ mL/L}) \qquad \text{(D-3)}$$

The molar density is 1.428 g/L (or mg/mL).

Extensive work has been done in aquatic chemistry on determining the solubility of dissolved oxygen in water. One of the standard formulae is the regression of Weiss (1970):

$$log\{C_s\} = A_1 + A_2\, 100/T + A_3\, log\{T/100\} + A_4\, T/100 + S[B_1 + B_2\, T/100 + B_3\, (T/100)^2\,] \qquad \text{(D-4)}$$

at standard atmospheric pressure, for C_s in mL/L, S in ppt and T in K, where:

A_1 = -173.4292	A_3 = 143.3483
A_2 = 249.6339	A_4 = - 21.8492
B_1 = -0.033096	B_3 = -0.0017000
B_2 = 0.014259	

and $log\{\}$ denotes the Napierian logarithm. C_s is converted to mg/L using (D-3). Small fluctuations in atmospheric pressure about the sea-level value used above have a minimal effect on saturation.

Frequently, DO concentration c is restated as a fraction of saturation, i.e., c/C_s x 100 (in %) for c and C_s in the same units, e.g. mg/L. A related strategy is followed in stating DO as the partial pressure of O_2 in solution, pO_2. Since $pO_2/p = n/n_{atm}$, and the molar fraction of oxygen in the dry atmosphere is 20.946%, the partial pressure of oxygen at saturation pO_{2_s} is:

$$pO_{2_s} = (n/n_{atm})\, p = 0.2095\, p \qquad \text{(D-5)}$$

in units of pascals, millibars (1 mb = 100 Pa), atmospheres (=101.3 kPa), torrs (= 1 mm Hg = 1.333 mb = 1/760 atm), etc. At standard atmospheric pressure of 760 Torr †, the partial pressure of O_2 at saturation is 159 Torr. The actual DO partial pressure is then given by:

$$pO_2 = 0.2095\, p\, \frac{c}{C_s} \qquad \text{(D-6)}$$

The advantage of this measure is that it is a weak function of temperature, compared to c, which is a strong function of temperature. It is a favored measure in physiology (conventionally in units of torrs or atmospheres, though this is changing in favor of SI units). The disadvantage is that for aerobic organisms, it is the actual concentration of DO in the water that is important, not its fraction of saturation.

A correction is necessary if the actual atmosphere contains water vapor, as this will reduce the partial pressure exerted by the "dry" atmosphere (i.e., the sum of partial pressures of the components of the dry atmosphere). This requires replacing p in (D-5) and (D-6) with $p - e$, in which e is vapor pressure (the partial pressure of water vapor), given in turn by $r\, e_s$, in which r is relative humidity as a fraction (between 0 and 1), and e_s is the vapor pressure at saturation, computed from the Clasius-Clayperon equation:

$$e_s = 6.11\, exp\left\{ \frac{m_v L}{R^*} \left(\frac{1}{273.15} - \frac{1}{T} \right) \right\} \qquad \text{(D-7)}$$

for e_s in millibars, T in kelvin, m_v = 0.622 molecular weight ratio, R^* = 0.110 specific gas constant for water, and L = 597 - 0.566 T cal/g, the latent heat of evaporation.

† The unit of measurement is the torr. The symbol for the unit is Torr. The symbol requires more ink than the full name of the unit.

APPENDIX E

Literature synthesis of life cycle of blue crab

In the following tables is presented a compilation of timings of various life stages of the blue crab. This information is organized geographically, first by region (e.g., mid-Atlantic) then by specific estuarine system within the region. Major estuaries, such as Chesapeake Bay, are separated, but in other instances the information is organized by state (e.g., Georgia). In the latter case, more geographical specifics may be given under "Citation".

For some life stages, a "Duration" is given. This is the range of time durations reported for the specified stage in individual organisms. In contrast, the "Calendar" is the time period in the calendar year that the given life stage occurs in the wild, as represented by multiple organisms.

This compilation is not comprehensive, merely representative. Nor has an attempt been made to rank the citations by quality and/or rigor in their empirical basis. Much of the timing information reflects opinion (perhaps mythology) rather than observation, and some conflicts with rigorous mesocosm studies.

Table E-1
Literature synthesis of life cycle of blue crab: hatching through megalop

Stage	*Hatching*		*Development of zoeae*		*Megalop stage*		*Citation*
	Calendar	*Peak mos*	*Duration*	*Calendar*	*Duration*	*Calendar*	
Region:							
Mid-Atlantic			3-6 weeks		1-2 weeks		Natunewicz & Epifanio (2001)
			4-7 weeks		5-8 weeks		Costlow and Bookhout (1959)
					3-6 weeks		Sulkin & Van Heukelem (1986)
Delaware Bay	Aug-Sep		5 weeks			Sep-Oct	Epifanio et al. (1984)
	Jun-Sep	Jul-Aug	4-5 weeks				Epifanio and Tilburg (2008)
Chesapeake Bay		Jun-Jul			<1 month after hatching		Churchill (1919)
	July			Jul-Aug	1.5-2 mos after hatching	Jul-Sep	Truitt (1939)
						Jul-Sep	McConaugha et al. (1983)
	Jun-Aug	late Jul-Aug				Aug-Dec	Provenzano et al. (1983), Goodrich et al. (1989)
						Jul-Nov	van Montfrans et al. (1990), Olmi (1995)
North Carolina		Jun-Aug					Dudley & Judy (1971), offshore from Beaufort Inlet
	late Jul-Aug						Forward et al. (2004a), Newport River
South Atlantic							
South Carolina	late summer						Archambault et al. (1990)
	summer					early sprng & fall (main)	Mense and Wenner (1989)
Georgia	Mar-Sep	Apr-Jun					Palmer (1974)
Florida	Apr-Sep		2 months	May-Aug			Tagatz (1968a)
Gulf of Mexico							
Mississippi Sound	Mar-Nov					Mar-Nov peaks Jul-Sep	Perry and Stuck (1982)
						May-Nov	Stuck and Perry (1981) “abundant”
Louisiana				Feb-Nov		Feb-Nov	Adkins (1972)
Texas	Mar-Sep						Gunter (1950), Aransas-Copano
	May-Jun					Feb-Mar	Simmons & Hoese (1959), Cedar Bayou* (May-Jun, emigration to Gulf)
	Apr-Nov	Apr-May					Copeland (1965), Aransas Pass (emigration to Gulf)

* Simmons & Hoese comment on the peculiar absence of megalops entering Cedar Bayou during May – August, even though crabs were spawning in the Gulf.

Table E-2
Literature synthesis of life cycle of blue crab: settlement through early development

Stage	*Settlement*		*Development to 20 mm*		*Development to 60 mm*		*Citation*
	Calendar	*Peak*	*Duration*	*Calendar*	*Duration*	*Calendar*	
Region:							
Mid-Atlantic							
Delaware Bay							
Chesapeake Bay	Aug-Dec	Sep-Oct		Sep - Feb		Jun-Aug	Orth and van Montfrans (1987, 1990)
	Aug-Nov	Aug-Sep					van Montfrans et al. (1990)
North Carolina	Aug-Nov			Aug – Oct			Etherington & Eggleston (2000), APES
	Sep-Nov						Forward et al. (2004a), Newport River
South Atlantic							
South Carolina						Feb-Apr	Archambault et al. (1990)
	Aug-Oct						Boylan and Wenner (1993), intermittent
							Mense and Wenner (1989)
Georgia						Jan-Mar	Palmer (1974)
Florida	Sep-Dec			peak Aug-Dec			Tagatz (1968a)
Gulf of Mexico							
Mississippi Sound	Aug-Sep						Perry et al. (1995)
Louisiana					2-3 months	Nov-May	Adkins (1972), Vermilion
						Dec-Apr	Perret (1967), Vermilion
				May-Jun,Sep-Oct		summer	Darnell (1959), Pontchartrain
	year-round	Aug-Sep					Hasek & Rabalais (2001a)
Texas	year-round			year-round			More (1969), Galveston Bay
				peak Dec-Mar			
				peak late fall-early spring			More (1969), entire Texas coast
				year-round		year-round	Gunter (1950), Aransas-Copano
				Feb-Mar			Simmons & Hoese (1959), Mesquite Bay

Table E-3
Literature synthesis of life cycle of blue crab: grow-out through spawning

Stage	*Grow-out to maturity*		*Mating*		*Female migration down-estuary*		*Citation*
	Duration	*Calendar*	*Duration*	*Calendar*	*Duration*	*Calendar*	
Region:							
Mid-Atlantic							
Delaware Bay							
Chesapeake	14-24 mos	Jun-Jul		Jun-Sep peak Aug-Sep			Truitt (1939)
	6-20 mos						Van Engel (1958), Hines (2007)
			1-3 days	May-Oct	1 mo	Oct-Nov	Aguilar et al. (2008)
	14 mos			peak Jul-Sep			Williams (1984)
				Jun-Jul			Blackmon & Eggleston (2001)
					1-2 mos	Sep-Nov	Hines et al. (2008)
North Carolina						Oct-Dec	Medici et al. (2006)
				Feb-Nov			Wolcott et al. (2005)
South Atlantic							
South Carolina	11-12 mos	May-Aug		Apr-Jun,Sep-Oct			Archambault et al. (1990)
Georgia		Apr-Nov					Palmer (1974)
Florica	10-12 months			Mar-Jul,Oct-Dec		Sprng/Fall	Tagatz (1968a)
				for temp > 22°C			Steele (1982)
Gulf of Mexico							
Mississippi Sound	12 mos			Mar-Nov		Late fall	Perry and Stuck (1982)
Louisiana	10-12 mos	Sep-Oct					Adkins (1972)
				May, Sep		Jan-Mar	Darnell (1959), Pontchartrain
Texas						Mar-Jul	Daugherty (1952), Cedar Bayou
	12-15 mos	Mar-Oct					More (1969), Galveston Bay

Table E-4
Literature synthesis of life cycle of blue crab: spawning through egg development

Stage	*Spawning*		*Development of eggs*		*Next spawn-hatch*		*Citation*
	Calendar	*Peak months*	*Duration*	*Calendar*	*Duration*	*Calendar*	
Region:							
Mid-Atlantic			15 days				Churchill (1919), Williams (1984), Epifanio (2003)
	Jun-Oct	Jul-Aug					Tilburg et al. (2008)
	Jun-Sep	Jul-Aug	2 wks				Epifanio (1995, 2007), Epifanio and Tilburg (2008)
Delaware Bay	Apr-Oct	Jul-Aug					Dittel & Epifanio (1982), Epifanio et al. (1984)
Chesapeake Bay	Apr-Oct	Jun-Aug					Truitt (1939)
			7-10 days				Harris (1982)
North Carolina	Apr-Nov	Jun-Aug			1.5-3.5 weeks		Dickinson et al. (2006)
		Mar-Oct					Wolcott et al. (2005)
South Atlantic							
South Carolina	Apr-Aug						Archambault et al. (1990)
Georgia	Mar-Sep						Palmer (1974)
Florida	Mar-Sep			Jun-Oct			Tagatz (1968a)
	Water temps > 15						
Gulf of Mexico							
Mississippi Sound	Mar-Nov					Summer	Perry and Stuck (1982)
	Jun-Aug						Perry et al. (1995)
Louisiana	Mar-Jul			Mar-Jul			Adkins (1972)
	Mar, Aug-Sep						Darnell (1959), Pontchartrain
	Jun-Aug						Hasek & Rabalais (2001a),Terrebonne
Texas	Mar-Aug	Apr-Jun					Gunter(1950), Aransas & Copano Bays and adjacent Gulf of Mexico
	Dec-Oct	Jun-Aug					Daugherty (1952), Cedar Bayou
	Apr-Jul	May-Jun					Simmons & Hoese (1959), Cedar Bayou
	Apr-Nov	Apr-May					Copeland (1965), Aransas Pass
	Mar-Aug	Mar-Apr					More (1969), Galveston Bay
	Jul-Aug						More (1969), Gulf inshore

APPENDIX F
Estimating abundance as organism density
from standard active biological sampling gear

It is desirable to convert biological catch data, notably that of Texas Parks & Wildlife (TPWD), to a number representative of organism density in the bay. In order to do this, the volume used in the catch-per-unit-volume depiction, or mass-per-unit-volume for that matter, needs to correspond to the *volume* of *water* sampled by the gear. Thus there are two concepts involved: the geometry of the sampling gear as it is deployed and operated, to trace out some volume in space, and the movement of bay water through the sampling volume of the gear (or, depending upon one's viewpoint, *vice versa*). Both the otter trawl and the bag seine are *active* sampling gears, in the sense that they are moved through the water to entrap organisms, and both can be conceived as the movement of a vertical plane in space. A gill net, in contrast, is *passive*, because it is fixed in space and depends upon the movement of organisms into the sampling gear for entrapment. Passive gears are not considered here.

F-1. Otter trawls

The basic geometry of the otter trawl is sketched in Fig. F-1. The cross section presented by the mouth of the trawl as it is towed is approximated by a rectangular area **A**. Its estimation based on the rigging and dimensions of the TPWD otter trawl is described below. This area is towed at a speed **C** *relative to the water*, assumed constant. The volume sampled, shown in Figure F-2, is therefore dependent upon the trawling time **T** . The organism density per sampled volume is therefore:

$$n = R\,\mathbf{N} / (\mathbf{C}\,\mathbf{T}\,\mathbf{A}) \qquad \text{(F-1)}$$

where
n = organism density, count per unit volume
N = reported count of organisms
C = towing speed *relative to the water*

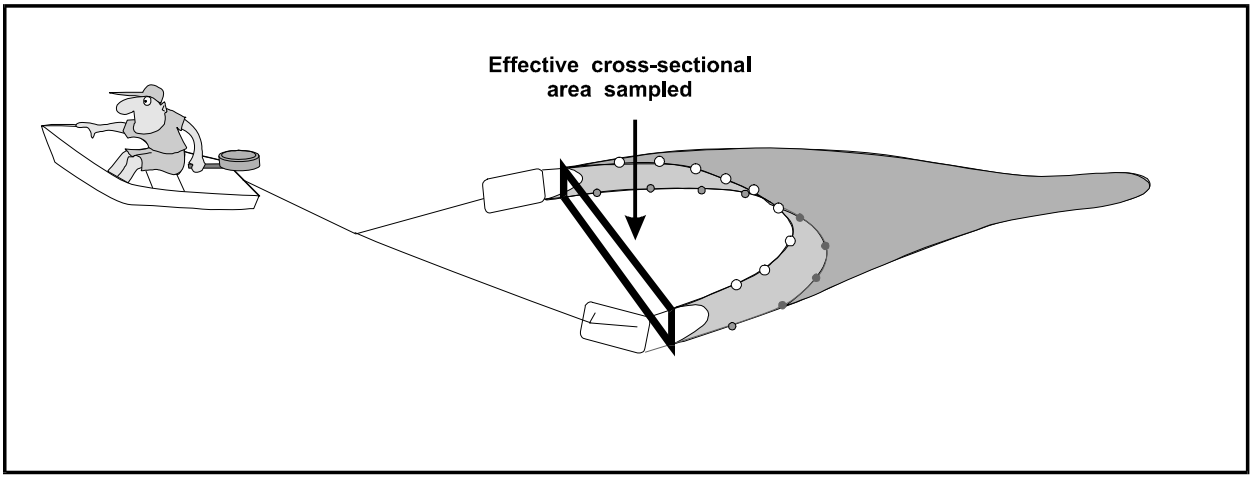


Figure F-1 - Geometry of otter trawl

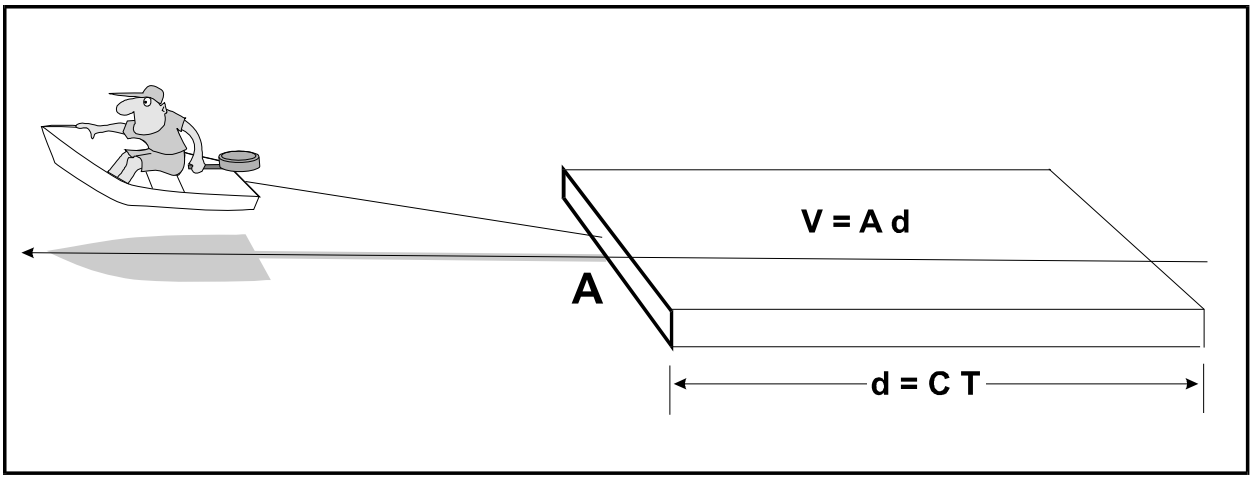


Figure F-2 - Sample volume intercepted by moving trawl

T = towing time duration
A = area of trawl opening
R = units conversion factor

WIth **A** in m^2, **T** in *hours*, **C** in *mph*, for the organism density in number/hectare-meter, R = 6.214, and in *number/ac-ft*, R = 0.7665 .

According to the TPWD manual (TPWD, 1999), the dimensions of the TPWD sampling trawl are:

headrope	-	5.7 m
footrope	-	7.0 m
cable	-	5.6 m
bridle	-	30.5 m
doors	-	1.2 m (length) x 0.5 m (height)
mesh	-	38-mm

The otter-trawl rigging nomenclature is not standard (cf., e.g., Iversen et al., 1993, King, 1995, Miller, 1990, Oceana, 2002, SERAD, 2001, Steele et al., 2002), and TPWD (1999) does not include the diagrams, so the rigging sketched in Figure F-3 is assumed to apply. We further assume that the headrope length L is controlling and under tow describes a semicircular arc, Fig. F-4. The resultant effective opening width w is therefore:

$$w = 2\ L/\pi$$

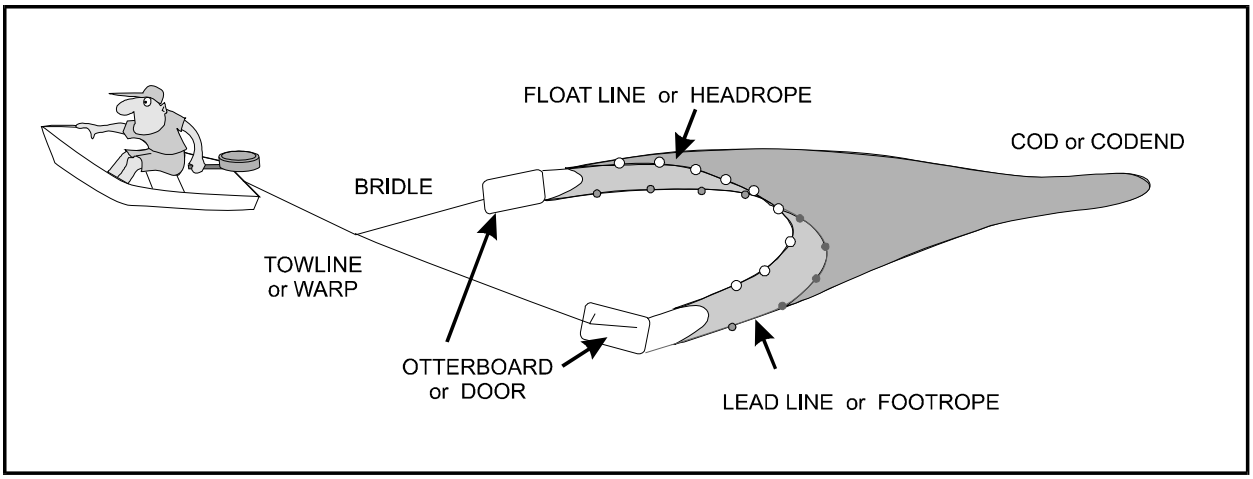


Figure F-3 - Trawl rigging nomenclature

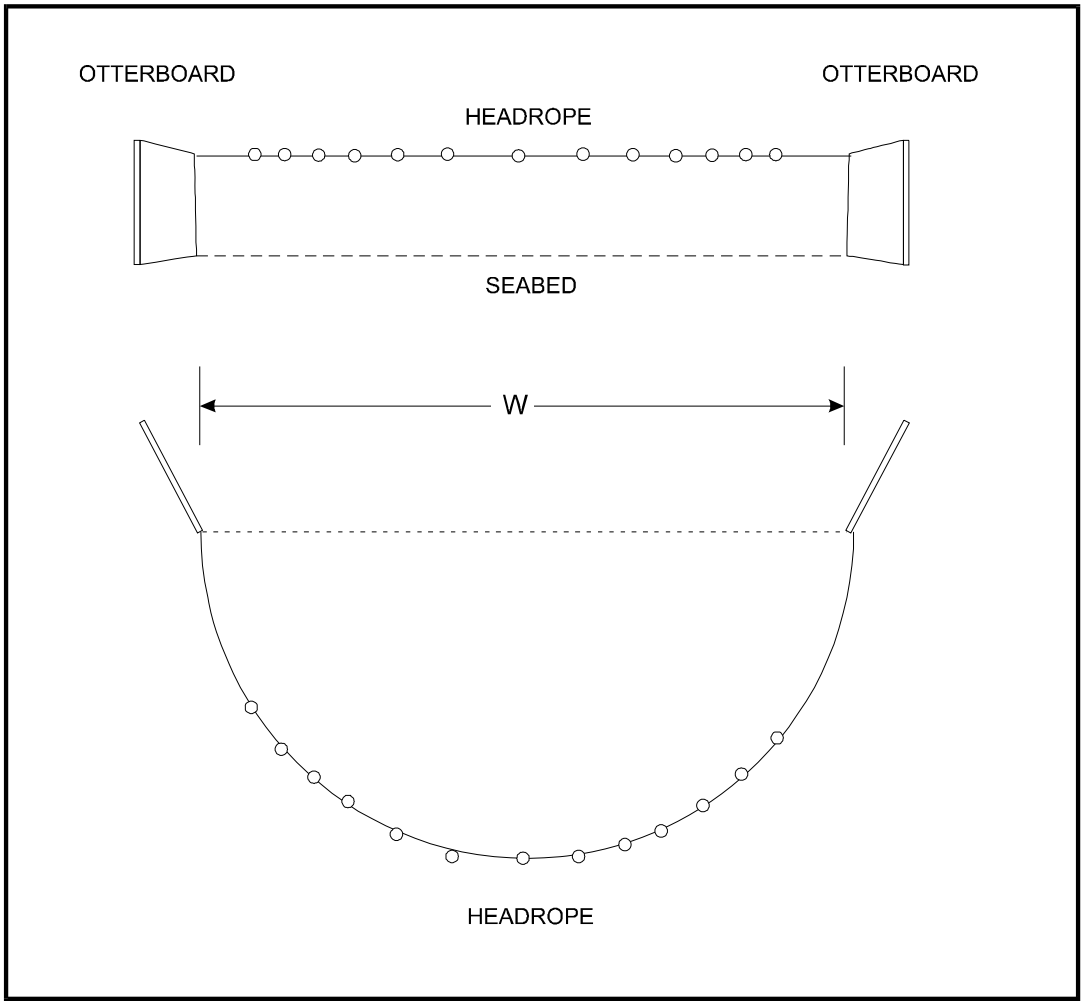


Figure F-4 - Trawl opening geometry in plane perpendicular to tow (above) and horizontal (below)

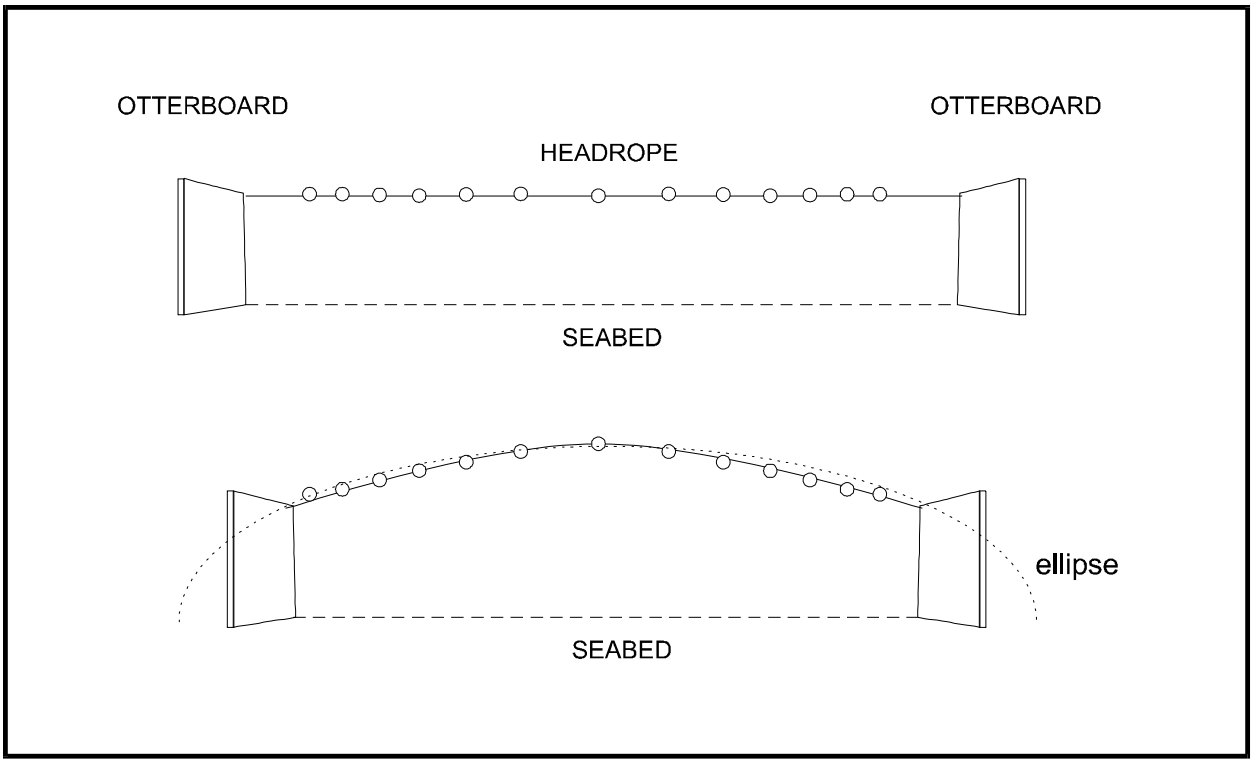


Figure F-5 - Hypothesized trawl opening geometry as in Fig. 2 (above) and with buoyancy of headrope (below)

The most suspicious assumption of this geometry is that the cross section of the trawl is rectangular with vertical height equal to that of the otterboards. In fact, the buoyancy of the floats on the headrope will increase the vertical extent of the opening. It is more likely, therefore, to be semi-elliptical. To estimate this will require much more effort, but, more importantly, any increase in vertical extent will be compensated by a decrease in the component arc length of the head rope in the horizontal plane, thus narrowing the width of the opening w, see Figure F-5. We judge that the increase in opening area due to buoyancy of the headrope will be approximately the same as the decrease in area due to the narrowing of the distance between the otterboards, so that the assumption of rectangular geometry will suffice.

For the TPWD trawl dimensions given above, w = 3.6 m. The effective height is that of the otterboard, 0.5 m, so the total area presented as the trawl is towed is 1.8 m^2. The towing speed **C** is stated by TPWD (1999) to be roughly 3 mph. The towing time is one of the variables included in the TPWD data base. (The standard TPWD tow time is 10 minutes, but in the data file there is a minority of sampling events with other values.)

It is important to observe that the boat speed is determined by a tachometer setting (TPWD, 1999, Mark Fisher, pers. comm. 2004). Indeed, in the open waters of the bay, without fixed references it is impossible to determine the speed of the boat in space. Therefore, operationally, the boat speed is referenced with respect to the water, not with respect to a fixed spatial coordinate. The resulting volume is that intercepted in the (perhaps moving) fluid by towing the

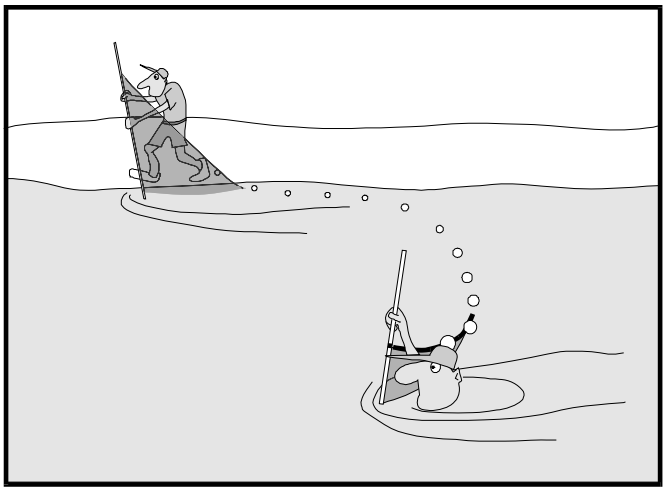


Figure F-6 - Bag seine execution

trawl through the fluid. The same volume will result whether the boat moves with the current or against the current. This is exactly the volume that is needed to estimate organism density, i.e. the volume of fluid actually swept by the towed trawl.

F-2. Bag seines

The bag seine is a net drawn parallel to the shore (Figure F-6) in such a way that the shoreline becomes one boundary of the sampled volume. The key dimensions are the distance **w** from the shore over which the net is extended, see Figure F-7, the length **S** along the shore, and the depths at the shoreline terminus of the seine $\mathbf{d_s}$ and at the offshore terminus **d**. In principle, $\mathbf{d_s}$ should be zero, but there may be instances, such as sampling along the front of a marsh or a

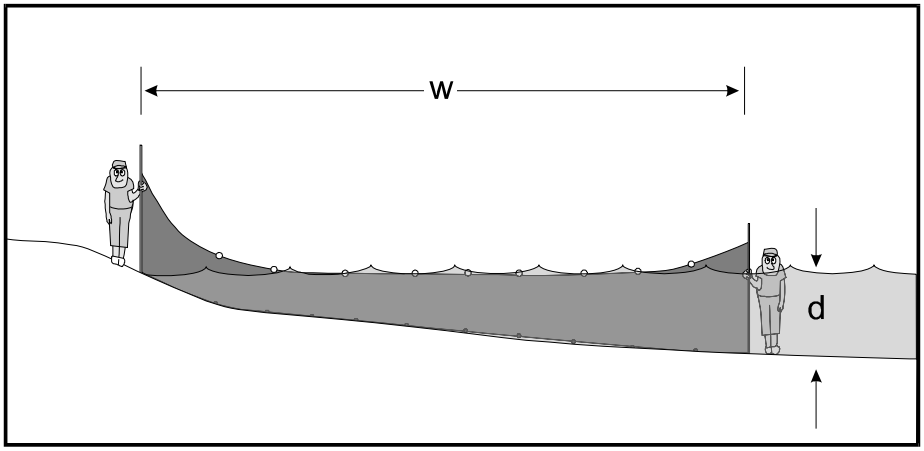


Figure F-7 - Bag seine position

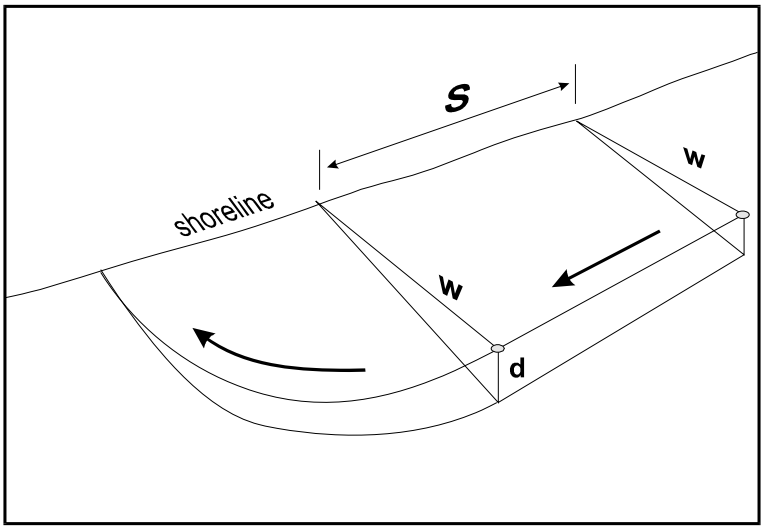


Figure F-8 - Volume sampled by bag seine

bulkhead, in which the shoreline is inaccessible. The execution of the bag seine haul is diagrammed in Figure F-8. The area sampled is a composite of a rectangle of area **w x S** and a quarter circle of radius **w** .

TPWD (1999) specifies that **S** = 15.2 m (50 ft) and **w** = 12.2 m (40 ft) (maintained by a pre-measured rope connecting the seine poles). The resulting area is 302 $m^2 \approx 0.030$ ha. TPWD (1999) specifies that the vertical dimension of the seine be 1.8 m (6 ft), which effectively limits the offshore location to waters less than this depth and is therefore the constraint on the distance from shore **w** . (In reality **w** is further constrained by the nostril height of the technician.) In a completely random site selection, therefore, **w** may be less than the specified 12.2 m. For this reason, apparently, the TPWD data base includes as a variable the area sampled by the bag seine. However, the field technicians of TPWD may modify the selection of shoreline section to ensure that the 12.2 section is capable of being sampled. (Presumably, this means wadeable out to 12.2 m depth.) Indeed, the vast majority of the entries in the TPWD data base have the value 0.03 ha.

Conversion of this area to an equivalent volume requires the average depth, approximated by the average of **d** and $\mathbf{d_S}$, whereupon

$$\text{Volume } (m^3) \approx 10^4\ \mathbf{AREA}(\text{ha})\ 0.5(\mathbf{d} + \mathbf{d_S}) \qquad \text{(F-2)}$$

where **AREA** is the entry in the TPWD data base (in ha). This will overestimate the actual area by about 10%. A more accurate estimate is:

$$\text{Volume } (m^3) = 10^4\ \mathbf{AREA}(\text{ha})\ 0.5(\mathbf{d} + \mathbf{d_S}) - 0.118\ (\mathbf{d} - \mathbf{d_S})\ \mathbf{w}^2$$

If **w** = 12.2 m,

$$\text{Volume } (m^3) = 10^4\ \mathbf{AREA}(\text{ha})\ 0.5(\mathbf{d} + \mathbf{d_S}) - 17.6\ (\mathbf{d} - \mathbf{d_S})\ . \qquad \text{(F-3)}$$

or $$\text{Volume (ha-m)} = \mathbf{AREA}(\text{ha})\ 0.5(\mathbf{d} + \mathbf{d_S}) - 17.6\ (\mathbf{d} - \mathbf{d_S})\ 10^{-4}\ .$$

A quick inspection of the TPWD data base suggests that if **AREA** departs from 0.030 ha, it is always larger, e.g. 0.06 ha, therefore even in the absence of information about **w**, equation (F-3) gives a better estimate of volume than equation (F-2).

In summary, the corresponding organism density is then:

$$n = \mathrm{R}\ \mathbf{N} \,/\, (\mathbf{A}\,\bar{d} + corr(\Delta d)) \qquad \text{(F-4)}$$

where

n = organism density, count per unit volume
N = reported count of organisms
A = reported area of seine sample
$\bar{d}$ = $0.5(\mathbf{d} + \mathbf{d_S})$
$\mathbf{d_S}$ = reported depth of water at shallow pole
d = reported depth of water at deep pole
$corr(\Delta d)$ = correction term, a function of Δd, in units of **A** x units of **d**
Δd = $(\mathbf{d} - \mathbf{d_S})$
R = units conversion factor

For the units employed in the TPWD data base, i.e., **A** in *ha* and **d** & $\mathbf{d_S}$ in *m*,

$$corr(\Delta d) \approx 0.00176\ \Delta d \qquad ha\text{-}m$$

For organism density n in *number/m*^{3}

$$\mathrm{R} = 10^{-4} \qquad ha\text{-}m/m^3$$

and for organism density n in *number/ac-ft*,

$$\mathrm{R} = 0.1233 \qquad ha\text{-}m/ac\text{-}ft$$

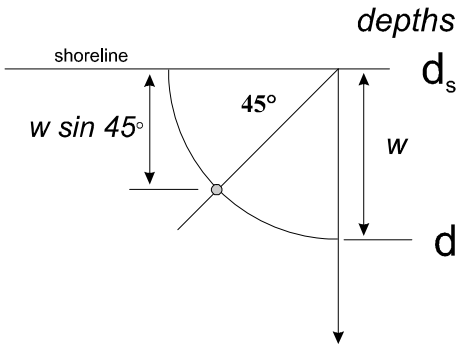
Unlike the otter trawl, the trajectory of the bag seine is referenced to coordinates fixed in space, *viz*. the shoreline and seabed. The volume of fluid intercepted by the seine as it passes from its starting position perpendicular to the shore to its ending position at the shoreface (Fig. F-8) depends upon the direction and magnitude of the longshore current. This is not reported by TPWD, nor is there any instruction in the monitoring manual (TPWD, 1999) as to whether the seine is to be carried into the current or with the current.

We can make a judicious estimate of the error due to a longshore current. If we assume 10 minutes to pull a seine through the longshore distance **S** (Fig. F-8), a shoreline depth $\mathbf{d_S}$ of 0 and an offshore depth **d** of 1.8 m (6 ft), and a longshore current speed of 0.5 knots, during this 10 minutes, an additional 50% of the intercepted volume (3040 ft^3 out of 6000 ft^3) will pass through the seine. Here "additional" means in the algebraic sense. The intercepted volume given by (F-4) will be an underestimate by this proportion if the seine is pulled against the current, and an overestimate by this proportion if the seine is pulled with the current. The error will increase with the time necessary to pull the seine and with the speed of the longshore current.

APPENDIX TO THE APPENDIX:
Average depth of seine sample area

With reference to Figure F-8, in the rectangle, $\bar{d} = \frac{1}{2}(d+d_s)$.

In the quarter circle:



depth $D(y) = d_s + [(d-d_s)/w]\, y$

$$D(w/\sqrt{2}) = d_s + [(d - d_s)/w]\, w/\sqrt{2}$$

average $\bar{D} \approx \frac{1}{2}[\, d_s + D(w/\sqrt{2})\,] = \frac{1}{2}[\, d_s + d_s + (d - d_s)/\sqrt{2}\,]$

$$= \frac{1}{2}[\, (d + d_s) - d + d_s + (d - d_s)/\sqrt{2}\,]$$

$$= \frac{1}{2}(d + d_s) - \frac{1}{2}[\, (1 - 1/\sqrt{2})(d - d_s)\,]$$

$$\approx \frac{1}{2}(d + d_s) - 0.15\,(d - d_s)$$